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RESEARCH ARTICLE

# Evaluating vegetation restoration following a transition from sheep to cattle grazing at a calcareous upland site

George Porton[1] | Robyn Wrigley[1] | Johanna Carr[2] | Dwayne Martindale[2] | Frank Morgan[3] | Steve Ryder[3] | Liz Coates[2] | Kay Shaw[3] | Christine Kelly[3] | Richard Birnie[2] | John Perry[3] | Eve Pegler[2] | Tim Thom[2] | Catherine E. Scott[1] | Dominick V. Spracklen[1]

[1]School of Earth and Environment, University of Leeds, Leeds, UK

[2]Yorkshire Wildlife Trust, York, UK

[3]Natural England, Ingleborough National Nature Reserve, Colt Park Barn, Chapel le Dale, UK

**Correspondence**
George Porton
Email: g.e.j.porton@leeds.ac.uk

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## Abstract

1. Much of the UK uplands are dominated by species-poor grasslands, largely a result of intensive sheep grazing. In some areas, efforts are underway to restore more natural habitats by reducing the number of sheep, with possible benefits to biodiversity, flood alleviation and carbon storage. Restoration aims to improve vegetation diversity, reduce the dominance of grasses and increase vegetation height and structural complexity.
2. This study evaluates whether changing grazing from light sheep grazing to light cattle grazing restored vegetation at an upland calcareous site in the Yorkshire Dales National Park in England. Vegetation surveys were conducted in 19 quadrats of 2 m × 2 m, surveyed every 4 years over a 12-year period. Generalised linear mixed models were used to understand how a number of key vegetation characteristics, relevant to restoration success, have changed with increasing years since sheep removal.
3. Changing from sheep to cattle grazing led to a change in vegetation species composition. Species richness, calcareous grassland indicators and proportion cover of bryophytes were found to increase with increasing years since sheep removal. In contrast, vegetation height and the proportion cover of grass decreased.
4. Our results show that switching from sheep to cattle grazing was highly successful in restoring diversity and habitat quality in calcareous landscapes. The less selective grazing of cattle led to a more open, less grass-dominated sward, allowing calcareous grassland wildflowers such as *Linum catharticum* and *Lotus corniculatus* to increase in frequency. However, the vegetation became shorter, another important objective for vegetation restoration in the uplands, suggesting a possible trade-off between diversity and vegetation height at a small scale.

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5. *Practical implication*. Changing from sheep grazing, even at a low intensity, to extensive cattle grazing restores calcareous habitat diversity and quality. Restoration of vegetation height and structure may require other grazing management such as livestock exclusion.

**KEYWORDS**
calcareous grassland, cattle, ecological restoration, livestock exclusion, sheep, upland grazing management, vegetation

## 1 | INTRODUCTION

Sheep grazing is the dominant land use across much of the UK uplands. This has resulted in large shifts in vegetation, with areas becoming dominated by grasslands whilst trees and shrubs are unable to regenerate (Fuller, 1996; Marrs, Lee, et al., 2020; Porton et al., 2024). Intensification of sheep grazing occurred over the 20th century, with an increase in sheep numbers from 19.7 to 41.2 million from 1950 to 1990 in Britain (Fuller & Gough, 1999). In northern England specifically, sheep numbers were 3–5 times higher in 2000 than they were in 1900 (Dallimer et al., 2009). The problem has gained mainstream attention (Monbiot, 2013), and in many areas, efforts are underway to try and restore vegetation through reduction or removal of sheep grazing. Vegetation restoration has the potential to benefit animal populations, mitigate downstream flood risk and increase carbon storage (Bond et al., 2020; Dennis et al., 2008; Edgar, 2019; Evans et al., 2015; Fletcher et al., 2021; Gao et al., 2017; Heathwaite et al., 1989; Marshall et al., 2014; Smith et al., 2014).

Restoration of vegetation, following sheep grazing, should seek to restore multiple vegetation characteristics. Firstly, the quality of the existing grassland habitats, by increasing diversity, heterogeneity of the vegetation and abundance of habitat indicator species (Lyons et al., 2018; Mitchley & Xofis, 2005). Secondly, reduce the dominance of grass, allowing the recovery of herbs, trees and shrubs. At a smaller scale this could mean a less grass-dominated sward, with greater forb coverage (Tóth et al., 2018; Watts et al., 2019). At a larger scale, a transition to other habitats such as woodland and heathland (Pollock et al., 2013; Porton et al., 2024). Lastly, increase the height and structure of vegetation and its structural heterogeneity (Fuller & Gough, 1999; Lyons et al., 2018; Pollock et al., 2013).

Despite the high grazing intensity of sheep across the UK uplands driving the homogenous vegetation in many areas (Pakeman & Fielding, 2021), simply reducing sheep grazing intensity may not fully restore vegetation. Typically, reducing grazing intensity to an intermediate level would be expected to be optimum for vegetation diversity (Wang & Tang, 2019). However, sheep are highly selective in how they graze, relative to other grazers such as cattle. Their small body and jaw size allow sheep to graze on the most nutritious species and parts of plants (Marrs, Lee, et al., 2020; Rook et al., 2004). Even at a low density, the selectivity of sheep would likely act to maintain low-diversity grasslands, with forbs and tree seedlings unable to regenerate (Lyons et al., 2018; Porton et al., 2024).

Livestock exclusion is the most common management used to restore vegetation at upland sites following sheep grazing and there is a wealth of research from other upland areas in the UK on the effects this may have (Evans et al., 2015; Lyons et al., 2017; Milligan et al., 2016). Generally, the results show increased vegetation height and structure and a transition from grassland towards woodland or moorland (Anderson & Radford, 1994; Grant, Bolton, & Torvell, 1985; Hope et al., 1996; Hulme et al., 2002; Pakeman & Nolan, 2009). However, species richness may be reduced as grazing tolerant species are replaced by more competitive species (Lyons et al., 2017).

The second option of using an alternative grazer, such as cattle or ponies, is less common and is mainly implemented in areas prioritising plant species diversity. Less evidence exists on the benefits of alternative grazers in the UK uplands and effects are often more complex to study, as grazing intensity, breed of livestock and seasonality of grazing can all be confounding factors (Hester et al., 1996; Lyons et al., 2018; Newborn, 2000; Tallowin et al., 2005). Switching to a less selective grazing animal would be expected to increase species richness of vegetation, whilst also allowing restoration of forbs and trees (Lyons et al., 2018; Porton et al., 2024). However, the increase in vegetation height, structure and biomass expected with grazing exclusion may not occur (Evans et al., 2015; Lyons et al., 2017; Lyons et al., 2018). Lower intensity grazing by grazers like cattle is often seen as a good trade-off, potentially combining the benefits of both approaches.

In this study we aim to understand and evaluate how transitioning from low intensity sheep grazing to low intensity cattle grazing has restored vegetation at an upland site dominated by calcareous grassland. The aims of this change in management were to improve the quality and diversity of the calcareous habitats and increase the structural diversity. To evaluate the success of these objectives we use data from long-term quadrat monitoring. Diversity was measured using species richness and evenness. Habitat quality was measured using the abundance of upland calcareous grassland indicators. Structural complexity was assessed using vegetation height data, with both average height and variation in height considered. A number of other key restoration measures were also evaluated including the proportion cover of

grasses, herbs and other plant groups and the abundance of individual plant species. This will allow a wider assessment of restoration success and allow greater understanding of how switching from sheep to cattle has changed the vegetation. This evidence will help inform future conservation strategies at similar sites across the UK uplands.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The study site was Ingleborough National Nature Reserve (NNR) in the Yorkshire Dales National Park, England (54.18°N, 2.36°E). This study focused on a 308-hectare area at the south of Ingleborough NNR, dominated by calcareous grassland, with smaller areas of limestone pavement, neutral grassland and dwarf shrub heath (Figure 1). The dominant species at the site were *Sesleria caerulea*, *Festuca ovina*, *Agrostis capillaris* and *Carex flacca*, with frequent herb species such as *Linum catharticum*, *Thymus polytrichus*, *Lotus corniculatus* and *Euphrasia* sp.

The dominant land use across the region is sheep grazing and historically the NNR was also grazed by sheep. However, over time, different land parcels on the NNR have had sheep replaced with red poll and short horn cattle, with some sites having a period of mixed grazing before switching exclusively to cattle. The first site removed sheep in 2004, with the last area seeing sheep removed in 2018 (Figure 1).

Cattle grazing intensity is approximately 0.2 livestock units (LU) $ha^{-1}year^{-1}$, when one adult individual is worth one livestock unit, with the cattle grazing throughout the year. The cattle grazing replaced sheep grazing of comparable intensity, with five to seven sheep being considered equal. Any changes in vegetation over time since sheep have been removed are therefore likely attributable to the change in livestock rather than a change in grazing intensity. Both previous sheep grazing and current cattle grazing were of a low intensity and much lower than the average stocking rate of 0.74 LU $ha^{-1}year^{-1}$ in upland areas of England (Harvey & Scott, 2016). Rotation of cattle between sites takes place and over time they have been able to roam an increasingly large area. The only other major vegetation management undertaken is thistle scything and ragwort pulling.

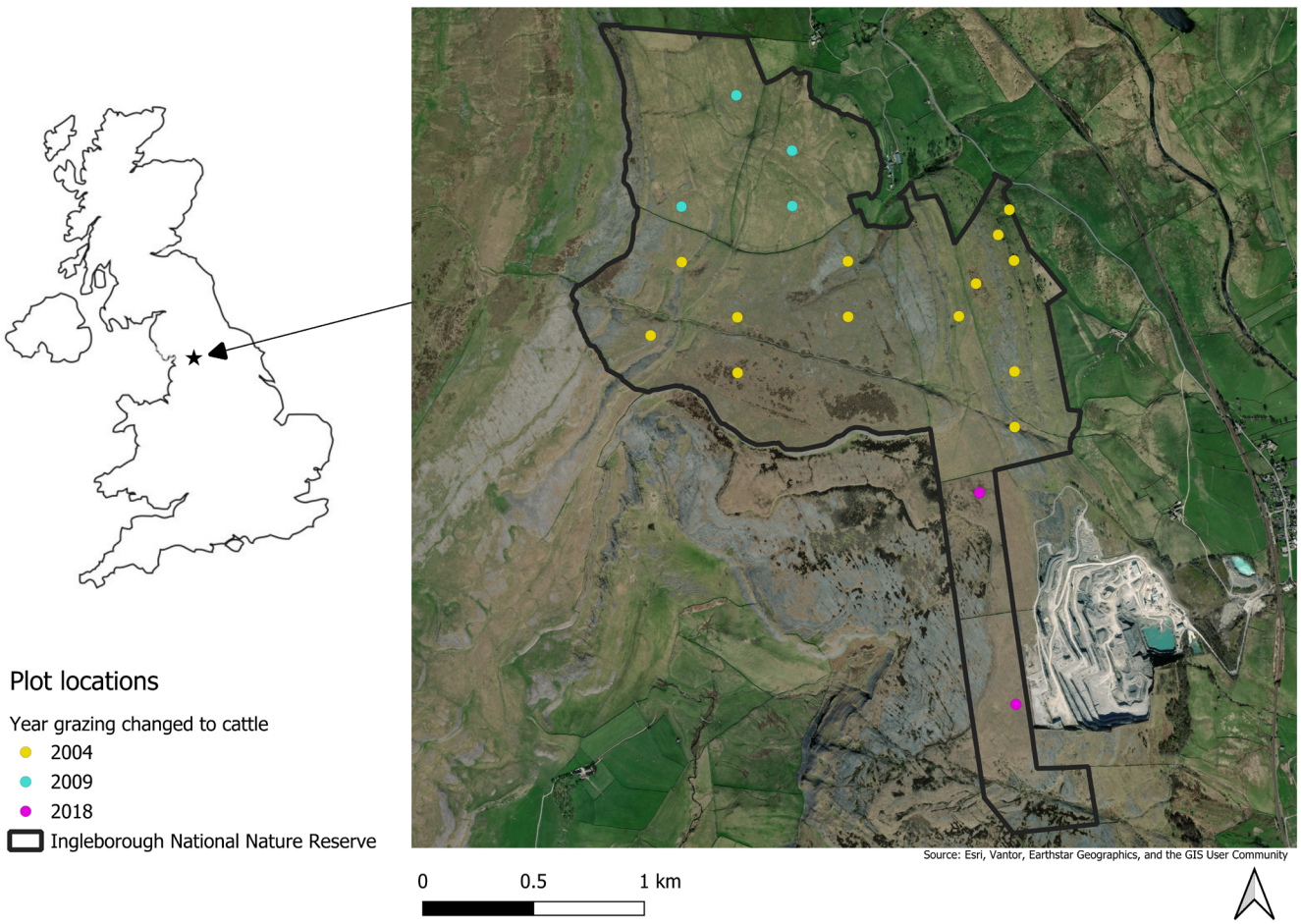



FIGURE 1 A map to show the locations of the 19 plots included in this study and the year grazing was changed from sheep to cattle. Ingleborough National Nature reserve boundary is shown in black.

## 2.2 | Data collection

Structured monitoring of vegetation started in 2010 on the NNR with Natural England's Long Term Monitoring Network (Nisbet et al., 2017). In this study we focussed on a subset of 19 of these plots (Figure 1) in the southern area of the NNR that have all undergone a change from sheep to cattle grazing. Plots not on limestone soil were also excluded (Soil Parent Material Model, 2018).

The methodology uses 2 m × 2 m quadrats, which have been monitored every 4 years in late July or August since 2010. The locations of these plots had been selected to ensure all habitats were covered across the entire NNR, with exact plot location being selected at random. Of the 19 plots in this study, 14 were calcareous grassland, with the remainder made up of: limestone pavement; acid grassland; purple moor grass and rush pasture; dwarf shrub heath and blanket bog. All plots are marked with a fenomarker in the southwest corner of the plot. The included plots (19) had a mean elevation of 350 m, with a range of 290–395 m.

The 2 m × 2 m plots are made up of 25 smaller cells, each measuring 40 cm × 40 cm. In each of these smaller cells, the presence of all vascular and non-vascular plants is recorded to species level where possible. This records both whether the species is present within the plot and also its frequency within the plot. The percentage of the whole plot that each species covers is also visually estimated.

Vegetation height is recorded in centimetres in each cell using a 200 g drop disc and metre ruler, with height being recorded at the centre of the disc. This method of measuring vegetation height also captures differences in biomass and structure. For example, a plot with thicker vegetation would have a greater height when recorded using the drop disc than another plot with more open vegetation, even if the maximum height in the plot is similar. The presence of bare rock, defined as rock with no soil overlaying it, is also recorded in each of the smaller cells, with a total frequency of bare rock then also calculated. The aspect and slope were also recorded in degrees, using a compass and clinometer.

## 2.3 | Vegetation characteristics

A number of vegetation characteristics were used for evaluating restoration success. These characteristics were: species composition; species richness; species evenness; proportion cover of herbs, grasses, sedges, rushes, bryophytes and trees and shrubs; vegetation height; variation in vegetation height; frequency of upland calcareous grassland indicators and lastly the frequency of individual plant species.

Species richness and evenness were used to represent diversity within plots. Species richness was simply the number of species recorded within each 2 m × 2 m quadrat. Species evenness was calculated using Shannon's evenness index, using the proportion cover of each species within a plot to represent the dominance of each species.

The frequency of upland calcareous grassland indicator species in a plot was used to assess habitat quality due to upland calcareous grassland being the dominant habitat. Upland calcareous grassland indicator species were taken from a Natural England (2012) report on assessing habitat restoration. Of these species, the following were present within the survey data: *Primula farinosa*, *Lotus corniculatus*, *Helianthemum nummularium*, *Euphrasia* sp., *Linum catharticum*, *Gentianella amarella*, *Campanula rotundifolia*, *Pilosella officinarum*, *Leontodon hispidus*, *Sanguisorba minor*, *Carex caryophyllea*, *Carex flacca*, *Carex panicea* and *Carex pulicaris*. The frequency of all these indicator species within a plot was summed to give a total upland calcareous grassland indicator frequency for each plot.

The next set of vegetation characteristics considered was the proportion of the total vegetation cover comprised of: herbs; bryophytes; trees and shrubs; grasses; rushes and sedges to understand if the change in management was reducing the dominance of grass. This was calculated by dividing the total summed percentage cover of all species within each vegetation type by the total percentage cover of all plants within the plot.

Vegetation height, measured using the drop disc, and the variation in vegetation height were also considered. Vegetation height for a plot was calculated as the mean height of the 25 measurements, with variation in vegetation height being the variance across those measurements. Values of zero were removed from both datasets.

Lastly, to provide further evidence of how habitats are changing, the proportion of cells within a plot that individual plant species occupied was considered. This was the number of cells the plant occurred in within the plot divided by 25 (the total number of cells). Species that were frequently only identified to genus level were grouped to the genus level.

## 2.4 | Data analysis

To investigate how the vegetation was changing over time since sheep were at the site, a variable (YEARS_SINCE_SHEEP) was created for the number of years since sheep had been removed and had been fully replaced with cattle. This would be the main variable of interest within this study and across surveys values ranged from 0 to 18 years since sheep.

Several other variables were used to account for environmental differences between the plots. Firstly, a continuous variable for the number of cells out of 25 containing bare rock (ROCK), ranging from 0 to 24. Secondly, a continuous variable for aspect was included to account for variation between north and south facing plots. The variable was the degrees from north of the aspect of the plot, such that east and west facing quadrats would both be 90°. Thirdly, slope was also included, with values ranging from 0° to 15°. Both slope (SLOPE) and aspect (ASPECT) were scaled using *z*-score normalisation. The ID of the plot (PLOT_ID) being surveyed and the year of survey (YEAR) were also considered important.

Analysis started by testing whether changing grazing from sheep to cattle had changed the plant community composition across all

19 plots across the 12 monitored years. A distance-based redundancy analysis (db-RDA) was used in the vegan package (Oksanen et al., 2007). The YEARS_SINCE_SHEEP variable was included, along with ROCK and an interaction term between SLOPE and ASPECT to account for environmental differences between plots. To control for repeated sampling of the same plots across multiple years, PLOT_ID and YEAR were included as conditioning terms. This allowed for the calculation of Bray–Curtis dissimilarities between plots, which accounted for the effects of each variable. The significance of each term was then evaluated using permutation-based ANOVA with 999 permutations, testing marginal effects sequentially.

To evaluate the effect that changing from sheep to cattle grazing had on the vegetation characteristics we used generalised linear mixed models, using the glmmTMB package (Brooks et al., 2017). This analysis included data from all 19 plots, each monitored every 4 years over a 12-year period. To aid interpretation, the following single model structure was applied throughout the modelling process and was chosen based on an a priori analysis:

$$\sim \text{YEARS_SINCE_SHEEP} + \text{ROCK} + \text{SLOPE} \times \text{ASPECT} + (1 \mid \text{PLOT_ID}) + (1 \mid \text{YEAR}).$$

Only the effect of YEARS_SINCE_SHEEP is reported, but full model outputs can be found in the Supporting Information. Multicollinearity between all variables included as fixed effects was ruled out using Pearson's correlation coefficient. Distance-based spatial autocorrelation was tested using Moran's *I* test using DHARMa::testSpatialAutocorrelation() (Hartig, 2024) with no issues found.

Species richness was modelled using a Poisson distribution, whilst species evenness was modelled using a Gaussian distribution after applying a logit transformation. The frequency of upland calcareous grassland indicators was modelled with a negative binomial distribution. Proportion cover for each vegetation type was modelled using a beta distribution, with values transformed following Smithson and Verkuilen (2006) to ensure they were bounded between 0 and 1. Vegetation height was modelled using a Gaussian distribution. Variation in vegetation height was modelled with a gamma distribution, following the removal of two outliers identified as having a *z*-score greater than 3.

The proportion of cells within a plot that a species occupied was modelled for a total of 44 different species and genus, with the other species occurring too infrequently to be included. Due to the large number of zeros in many species data, a zero-inflated beta model was chosen. This model uses a two-step approach, separately modelling the probability a species is absent from a plot and then the proportion of cells occupied in plots where it is present. Firstly, the probability of a species being absent from a plot is modelled using a binomial distribution, in the zero-inflated part of the model. Secondly, the proportion of cells a species occupied within a plot it was present is modelled with a beta distribution, in the conditional part of the model. The above-mentioned model structure was tested in both the conditional and zero-inflated part of the model. This was because the change in grazing management and the environmental variables could potentially explain why both a species was either present or absent from a plot and also its proportion cover when present. The exception to this structure was for Danthonia decumbens, Euphrasia sp., Fissidens sp., Helicotrichon pratense, Plantago lanceolata, Racomitrium lanuginosum, Luzula campestris, Veronica officinalis, Holcus lanatus and Potentilla erecta, which had the random effect of YEAR excluded due to the small sample size. Prior to modelling, species with a proportion of cells occupied of 1 were changed to 0.999 because zero-inflated beta models require non-zero proportions to be bounded between 0 and 1. Estimates from both components of the zero-inflated model were combined to calculate the predicted change in number of cells occupied for each modelled species 18 years after sheep grazing was replaced by cattle grazing. All analysis took place in R version 4.3.0 (R Core Team, 2023).

## 3 | RESULTS

Across all surveys (76 plots over 12 years) there was a total of 180 plant species recorded, with a mean of 29.54 (SD = 9.19) in each survey plot. Of these species, *Sesleria caerulea*, *Carex flacca* and *Festuca ovina* had the greatest percentage cover across all the plots (Table 1). *Rhytidiadelphus squarrosus*, *Festuca ovina* and *Pseudoscleropodium purum* were the species occupying the greatest proportion of plots. The most common herb species were *Potentilla erecta*, *Thymus polytrichus* and *Linum catharticum*.

The db-RDA showed that changing from sheep to cattle led to a significant change in the species composition ($F = 5.26$, $p < 0.001$). Both the frequency of bare rock ($F = 3.37$, $p < 0.003$) and the interaction between slope and aspect ($F = 7.74$, $p < 0.001$) had significant effects also. The latter, indicating that the effect of aspect on species composition was dependent on slope.

There was a significant increase in species richness following the transition from sheep to cattle grazing ($\beta = 0.02$, SE = 0.005, $z = 3.94$, $p < 0.001$). The model predicts that changing management from sheep to cattle grazing will increase the number of plant species per plot by 10, 95% CI [1, 20] after 18 years, equivalent to a 41%, 95% CI [3%, 93%] increase in species richness following sheep removal (Figure 2a). However, there was no change in species evenness following the cessation of sheep grazing ($\beta = -0.01$, SE = 0.02, $z = -0.73$, $p = 0.464$). The habitat quality of the upland calcareous grassland also improved, with indicator species showing a significant increase post sheep grazing ($\beta = 0.03$, SE = 0.01, $z = 3.96$, $p < 0.001$) (Figure 2b).

Across all plots and years, vegetation was dominated by grass, with a mean proportion cover of 0.49 (SD = 0.20). Herbs (mean = 0.17, SD = 0.13), sedges (mean = 0.17, SD = 0.13) and bryophytes (mean = 0.12, SD = 0.09) made up most of the rest of vegetation, with trees and shrubs (mean = 0.04, SD = 0.09) and rushes (mean = 0.01, SD = 0.05) covering the smallest area. However, grasses did become less dominant with increasing years since sheep,

| Top 10 species by mean percentage cover | | Top 10 species by percentage of plots occupied | |
|---|---|---|---|
| Species | Mean percentage cover (%) | Species | Percentage plots occupied (%) |
| *Sesleria caerulea* | 22.23 | *Rhytidiadelphus squarrosus* | 89.47 |
| *Carex flacca* | 11.82 | *Festuca ovina* | 86.84 |
| *Festuca ovina* | 11.26 | *Pseudoscleropodium purum* | 77.63 |
| *Agrostis capillaris* | 9.26 | *Potentilla erecta* | 76.32 |
| *Festuca rubra* | 7.80 | *Carex flacca* | 72.37 |
| *Rhytidiadelphus squarrosus* | 6.01 | *Sesleria caerulea* | 72.37 |
| *Trichophorum germanicum* | 5.39 | *Briza media* | 71.05 |
| *Calluna vulgaris* | 3.82 | *Thymus polytrichus* | 71.05 |
| *Anthoxanthum odoratum* | 3.39 | *Linum catharticum* | 69.74 |
| *Hypnum jutlandicum* | 3.09 | *Lotus corniculatus* | 65.79 |

**TABLE 1** Top 10 species by the mean percentage cover across all plots and the top 10 species by percentage of plots occupied.

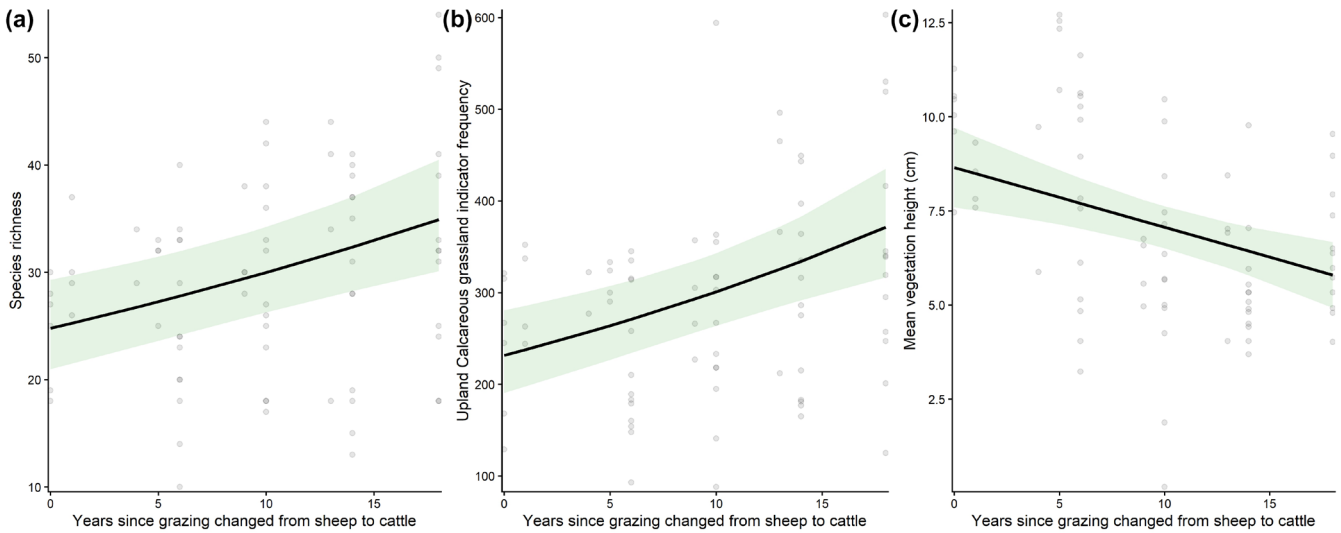



**FIGURE 2** Predicted change in species richness (a), frequency of calcareous grassland indicators (b) and mean vegetation height in centimetres (c) with increasing years since a change in management from sheep to cattle. All predictions are at the mean value for any other covariates within the model. 95% confidence intervals are shown with green shading and individual data points in grey.

with a decrease in proportion cover following cessation of sheep grazing ($\beta = -0.04$, SE = 0.01, $z = -2.98$, $p = 0.003$) (Figure 3a). The only vegetation type to increase following the change from sheep to cattle grazing was bryophytes ($\beta = 0.06$, SE = 0.02, $z = 2.75$, $p = 0.006$) (Figure 3b). There was no significant effect of switching to cattle grazing on the percentage cover of herbs ($\beta = 0.01$, SE = 0.02, $z = 0.63$, $p = 0.530$), sedges ($\beta = 0.03$, SE = 0.02, $z = 1.8$, $p = 0.073$), trees and shrubs ($\beta = 0.03$, SE = 0.08, $z = 0.40$, $p = 0.690$) or rushes ($\beta = -0.01$, SE = 0.02, $z = -0.23$, $p = 0.816$).

The mean vegetation height across all plots was 7.10 cm (SD = 2.64 cm). There was a significant decrease in vegetation height following the cessation of sheep grazing ($\beta = -0.16$, SE = 0.04, $z = -3.55$, $p < 0.001$). Vegetation height was predicted to be 8.65 cm, 95% CI [7.57 cm, 9.73 cm] at the point of sheep removal and then decrease to 5.80 cm, 95% CI [4.91 cm, 6.68 cm] after 18 years of cattle grazing (Figure 2c). There was no effect of the change from sheep to cattle grazing on the variation in vegetation height within a plot ($\beta = -0.02$, SE = 0.02, $z = -1.21$, $p = 0.227$).

The individual species models showed, from the tested 44 species, 20 species had a significant change following the removal of sheep (Figure 4). A total of 13 species significantly increased their frequency in plots in which they were present. Of these, four were herbs (*Linum catharticum*, *Achillea millefolium*, *Lotus corniculatus* and *Plantago lanceolata*) and three were upland calcareous grassland

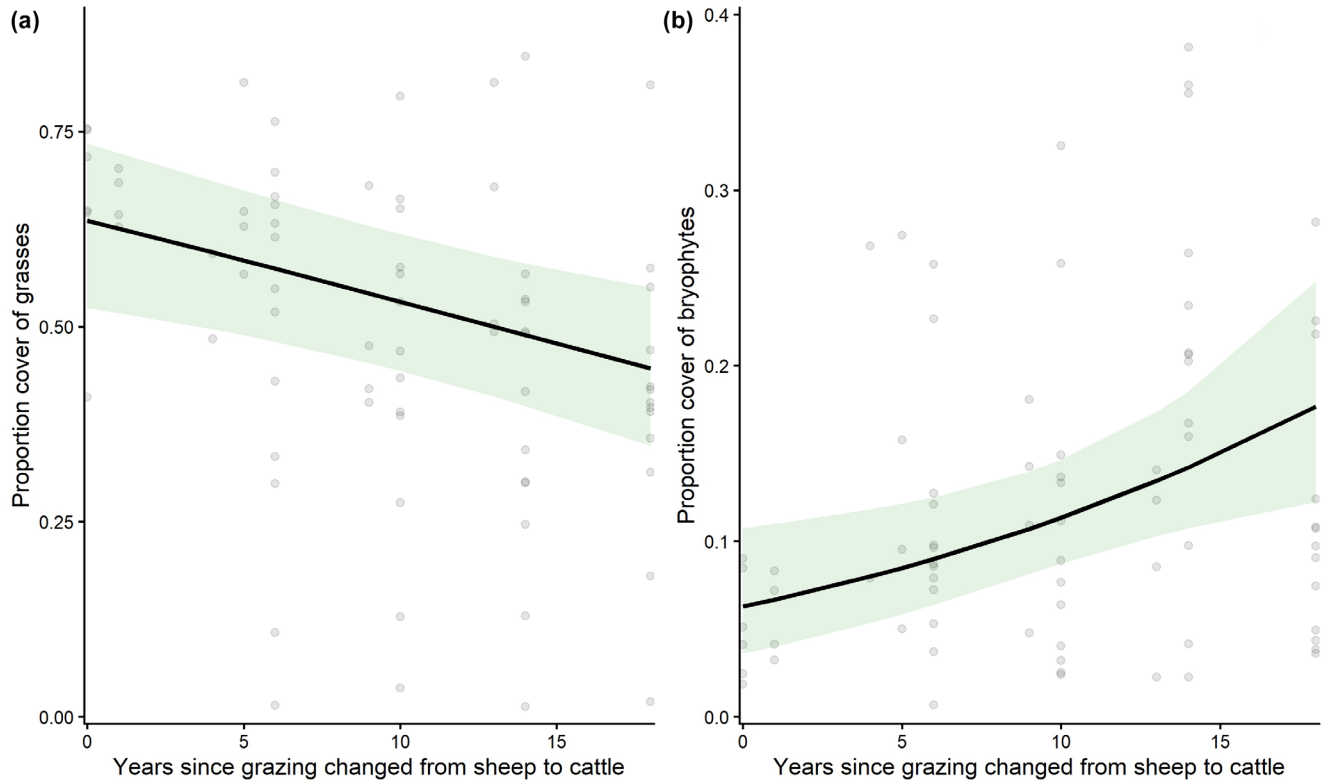



**FIGURE 3** Predicted change in the proportion cover of grass (a) and bryophytes (b) with increasing years since a change in management from sheep to cattle. All predictions are at the mean value for any other covariates within the model. 95% confidence intervals are shown with green shading and individual data points in grey.

indicator species (*Carex flacca*, *Lotus corniculatus* and *Linum catharticum*). However, the frequency of three species (*Carex pulicaris*, *Galium saxtile* and *Trifolium repens*) decreased in the plots they were present following the change to cattle grazing, with *Carex pulicaris* being an upland calcareous grassland indicator. The cessation of sheep grazing led to a significant increase in the probability of *Euphrasia* sp. and *Fissidens* sp. being present within a plot, with *Euphrasia* sp. being an upland calcareous grassland indicator species. Meanwhile, the probability of both *Helictotrichon pratense* and *Carex caryophyllea* being present decreased, with *Carex caryophyllea* being an upland calcareous grassland indicator.

## 4 | DISCUSSION

This study used 12 years of repeated vegetation monitoring to evaluate vegetation restoration after a transition from sheep to cattle grazing at a calcareous upland site. Replacing light sheep grazing with light cattle grazing changed the overall species composition of vegetation and increased vegetation species richness, frequency of upland calcareous grassland indicators and proportion cover of bryophytes. Vegetation height and proportion cover of grasses decreased following the transition.

Our results show that replacing sheep grazing with cattle grazing, at a similar low intensity (around 0.2 LU $ha^{-1}$ $year^{-1}$), led to increased species richness of plants at the calcareous upland site over 18 years. This supports previous research across similar habitats, where higher species richness was found on cattle grazed plots than sheep grazed plots with a low grazing intensity (Lyons et al., 2018). This outcome is likely due to differences in how sheep and cattle graze, with sheep being more selective in the species and parts of plants they target, as well as consuming more forbs (Cuchillo-Hilario et al., 2018; Grant, Suckling, et al., 1985; Putfarken et al., 2008; Rook et al., 2004). Sheep grazing has been shown to reduce the number of more nutritious, palatable and digestible species and so switching to a less selective grazing animal is likely to allow these plant species to recover (Marrs, Lee, et al., 2020). It is also likely that more plants will get a chance to set seed, due to fewer flowers being consumed. A second mechanism may be increased trampling and ground disturbance from cattle, creating more regeneration niches for species to colonise as it is unlikely the seed bed alone explains the increase in species richness (Grubb, 1977; Marrs, McAllister, et al., 2020). Seeds may also be spread by cattle being rotated between the sites and increasingly being able to roam a larger area (Baltzinger et al., 2019; Cosyns et al., 2005).

The switch from sheep to cattle grazing also reduced the proportion cover of grasses within the vegetation. Lower grass coverage on cattle grazed than sheep grazed sites has also been shown in other studies on calcareous grasslands (Lyons et al., 2017).

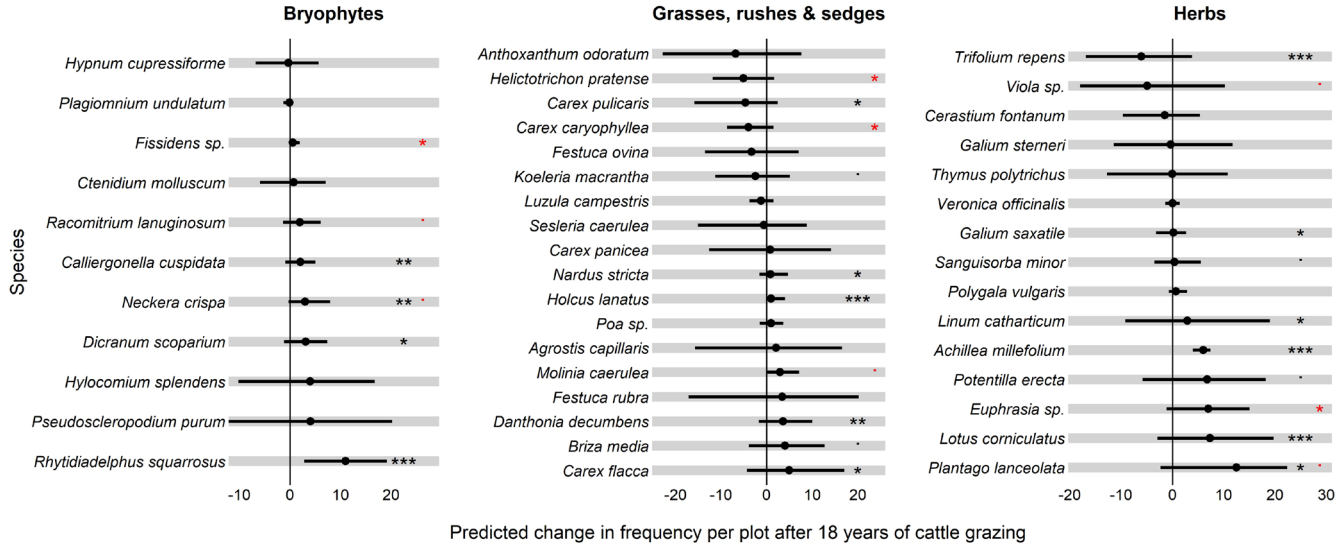



**FIGURE 4** Predicted change in frequency per plot for 44 plant species, with 95% confidence intervals, after 18 years of cattle grazing following sheep removal. Species are split into bryophytes; grasses, rushes and sedges and herbs and then sorted in ascending order. Predictions combine both conditional and zero-inflated estimates. Upland calcareous grassland indicator species are shown in bold. The significance level of each species for the conditional part of the model is indicated in black and the zero-inflated part in red (***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, •$p < 0.1$).

This change is also likely due to cattle being less selective when they graze, as they will consume more of the coarse grass species such as *Anthoxanthum odoratum*, previously not targeted by sheep (Cuchillo-Hilario et al., 2018; Grant, Suckling, et al., 1985; López et al., 2003; Rook et al., 2004). Bryophytes were the main plant type to replace the grass coverage, with species such *as Rhytidiadelphus squarrosus*, *Neckera crispa* and *Calliergonella cuspidata* increasing their frequency. This suggests the lower grass cover has resulted in a more open sward, allowing more light to reach bryophytes on the ground, allowing more space for these species to grow (Lyons et al., 2022; Van der Wal et al., 2005). The creation of microtopographical features through greater trampling by cattle may also provide new microhabitats for bryophytes to grow (Oldén & Halme, 2016).

There was no increase in proportion cover of herbs or trees and shrubs, which would have been expected given that sheep feed on a greater proportion of forbs in their diet (Grant, Suckling, et al., 1985). Despite this, the frequency of some key upland calcareous grassland herbs such as *Lotus corniculatus*, *Linum catharticum* and *Euphrasia* sp. increased, as well as other herb species such as *Achillea millefolium* and *Plantago lanceolata*. The small size of these species, particularly *Euphrasia* sp. and *Linum catharticum*, likely meant their increase in frequency was not enough to increase the proportion cover of herbs overall. The frequency of these herb species likely increased due to not being selected so heavily by cattle (Cuchillo-Hilario et al., 2018; Grant, Suckling, et al., 1985; Putfarken et al., 2008; Rook et al., 2004), with flowers also being able to set seed more frequently and spread. Rotation of cattle between sites may have also allowed greater seed dispersal, through both epizoochory and endozoochory (Baltzinger et al., 2019; Cosyns et al., 2005). The herb species will also face less competition with grasses due to reduced grass cover, and greater trampling by cattle is also likely to create more regeneration niches for their seeds to establish.

Vegetation height was found to decrease following the change from sheep to cattle grazing. This small reduction in vegetation height may be the result of a change in the vegetation composition rather than the direct removal of vegetation by grazing. The previous low intensity sheep grazing resulted in thick, grass dominated vegetation. The switch to cattle grazing reduced the grass coverage and is likely to have created a more open sward, leading to shorter vegetation height measurements. Previous studies on similar habitats, with similar low grazing intensity, also show a reduced height on cattle-grazed compared to sheep-grazed sites (Lyons et al., 2017).

Switching from sheep to cattle at this upland calcareous site proved to be highly successful for restoring the diversity and quality of upland calcareous grassland habitats, which was one of the key objectives for the change in management. Species richness was shown to increase by 41%, 95% CI [3%, 93%] following 18 years of cattle grazing. There was also a reduction of the dominance of grasses within the sward and although there was no increase in herb cover, several key herb species such as *Linum catharticum*, *Euphrasia* sp. and *Lotus corniculatus* did increase in frequency. Calcareous grassland restoration is important due to its high conservation value and importance to other biodiversity, particularly invertebrates (Van Swaay, 2002). Large areas have, however, been lost due to intensification, fertiliser application and land abandonment across Europe (Fischer & Stöcklin, 1997; Wallis de Vries et al., 2002). Cattle grazing at Ingleborough has indeed been shown to benefit butterfly populations, with five times the abundance on cattle grazed than sheep grazed sites (Wrigley et al., 2026). This increase is likely driven by the calcareous

grassland restoration, with greater species diversity leading to greater food plant and floral resource availability.

The evidence from this study, however, does not suggest that changing from sheep to cattle grazing restored the height and structural diversity of vegetation, another key objective for the change in management. However, the same plots studied here have shown increased tree colonisation following the change to cattle grazing (Porton et al., 2024). This suggests, at a larger scale, cattle grazing may have increased the structural heterogeneity of vegetation. Diversity of ground flora is often prioritised in restoration, particularly on calcareous habitats due to the high floral diversity and presence of rare species. However, often overlooked is the important role that structural heterogeneity plays in the restoration of biodiversity (Wallis de Vries et al., 2002). Increased vegetation height and structure from decreasing grazing intensity have been shown to lead to trophic cascades at other upland sites, with increased arthropod abundance leading to an increase in meadow pipit territories and increased field vole abundance in turn increasing fox activity (Evans et al., 2015; Villar et al., 2013). The diversity in vegetation height and structure is also important for creating a broad range of microhabitats, creating niches for a wider range of species and protection from climate extremes (Lyons et al., 2018; Scheffers et al., 2014).

There is, at the small scale of the plots studied here, a likely trade-off between species diversity and vegetation height and structure. Restoration of vegetation height and structure may require a reduction or cessation of grazing (Lyons et al., 2017; Lyons et al., 2018). This would, however, lead to competitive grass species dominating and the loss of grazing-tolerant species (Lyons et al., 2017). However, whilst simultaneous restoration of diversity and vegetation height may not be possible within the same plot, at a landscape scale both could be achieved. Different restoration managements at different sites, with different grazing animals, intensity and even total grazing cessation could be used to achieve multiple trajectories of restoration across a landscape. Habitat heterogeneity may also be achieved more naturally by herbivores being able to roam freely over even greater areas, simulating wild large herbivores (Trepel et al., 2024), however, more research is needed on how this can be used as a restoration tool. The diversity of habitats in a landscape, on top of the diversity of those habitats, is crucial for restoring biodiversity at a landscape scale (Hackett et al., 2024).

One of the key limitations of this study is the small (2 m × 2 m) plots of limited number ($n = 19$) surveyed over an area of 308 hectares. This means we could not assess restoration success of larger scale metrics of diversity, such as beta diversity and larger scale heterogeneity of vegetation height. Here, we assessed heterogeneity by using species evenness within a plot and with variation in height within a plot. Studying the variation in species composition and vegetation height between plots would likely provide better evidence to evaluate the success of objectives relating to vegetation heterogeneity. This would require an increase in the number of plots surveyed. Larger scale assessment of vegetation heterogeneity should therefore be a priority for future research at the site. The study does, however, highlight the importance of long-term monitoring like Natural England's Long Term Monitoring Network (Nisbet et al., 2017). Repeated vegetation surveys of the same plot every 4 years allow the tracking of long-term biodiversity change and helps understand the effect of a change in management.

## 5 | CONCLUSIONS

Changing management from low-intensity sheep grazing to low-intensity cattle grazing was shown to be highly successful at restoring vegetation species diversity, upland calcareous grassland habitat quality and helped create a more open, less grass-dominated sward. This evidence supports the ongoing management at Ingleborough NNR and highlights that sheep grazing, even when grazing intensity is reduced to much lower than is typical for the uplands, is not optimal for restoration of calcareous habitats. Agri-environment schemes aiming to increase vegetation diversity and the condition of upland calcareous grasslands should therefore be incentivising a transition to extensive cattle grazing instead.

The only key vegetation restoration metric that was not found to be restored by switching from sheep to cattle, within our small-scale plots, was vegetation height and structure. Restoration of this may require reducing grazing intensity or complete grazing exclusion. To ensure all restoration objectives are met at a landscape scale, different grazing management could be implemented at some sites, with some sites having a lower grazing intensity or being left ungrazed. A wider range of grazers and allowing them to roam greater areas may also help achieve this. Larger scale variation in vegetation diversity, height and structure should be a priority for future monitoring.

### AUTHOR CONTRIBUTIONS

George Porton, Dominick Spracklen and Robyn Wrigley conceived the ideas. George Porton analysed the data. George Porton led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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### CONFLICT OF INTEREST STATEMENT

There is no conflict of interest.

## PEER REVIEW

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## ORCID

*George Porton* https://orcid.org/0009-0006-8512-4222
*Robyn Wrigley* https://orcid.org/0009-0006-4944-0770
*Catherine E. Scott* https://orcid.org/0000-0002-0187-969X
*Dominick V. Spracklen* https://orcid.org/0000-0002-7551-4597

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Data S1:** Supporting information.

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