Science of the Total Environment xxx (xxxx) xxx

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Effects of long-term removal of sheep-grazing in a series of British upland plant communities: Insights from plant species composition and traits

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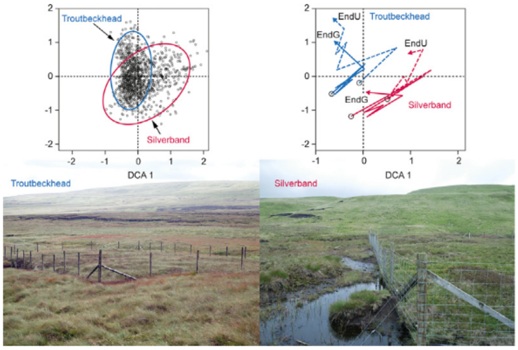
HIGHLIGHTS

- We assessed change in vegetation at Moor House NNR between 1953 and 2016.
- We measured change in twelve sites each with a grazed and ungrazed plot.
- Vegetation richness declined through time.
- Vegetation groups responded differently to removal of sheep-grazing.
- Liverworts and lichens were good indicators of grazing removal.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 24 August 2020
Received in revised form 14 October 2020
Accepted 26 October 2020
Available online xxxx

Editor: Manuel Esteban Lucas-Borja

Keywords:
Moorland
Blanket bog
Upland grassland
Ordination
Exclosures

ABSTRACT

Environmental and management pressures are considered a threat for preserving plant communities worldwide. Identification of long-term impacts of changing management practices on plant community composition must, therefore, be a major priority to ensure improvement in conservation value. Land abandonment/wilding is one topical area where there is little available information on long-term impacts. To address this, here, we describe plant species compositional change over relatively long-time scales in a range of four British upland communities (high-level grasslands, intermediate grasslands, blanket bogs and high-level bogs) and its relationships with a series of life-history and plant trait variables. Our aims were to determine whether the business-as-usual sheep grazing practice was maintaining these communities, and if grazing was to be removed as part of abandonment/wilding strategies, would there be a conservation benefit. We used a series of long-term experimental grazing-exclosure studies at twelve sites (>40 years) on the Moor House National Nature Reserve in northern England. Each site consisted of paired plots; i.e. sheep-grazed versus ungrazed. Our results showed that there was relatively little change in dominant plant species with most change occurring within sub-dominant species. Similarly, different temporal responses in plant species richness were detected between the experiments (richness was reduced in three experiments, only one increased). In any case, the vegetation temporal trajectories were moving in similar direction in grazed and ungrazed plots at most sites. Interestingly, blanket bog experiments showed a clear compositional convergence for both grazed and ungrazed plots, although, the between-site differences related to a combination of elevation and past burning testament. Finally, the bryophytes (especially liverworts) and lichens were the groups that contributed most to the reductions in species richness. Moreover, implementation of a no-stock grazing strategy under a land abandonment/wilding approach will not bring about much plant change in the short-term in the plant communities studied here.

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https://doi.org/10.1016/j.scitotenv.2020.143508
0048-9697/

Please cite this article as: J. Alday, J. O'Reilly, R.J. Rose, et al., Effects of long-term removal of sheep-grazing in a series of British upland plant communities: Insig..., Science of the Total Environment, https://doi.org/10.1016/j.scitotenv.2020.143508

1. Introduction

Land abandonment is a topical and contentious issue in northern Europe with a forecast that large areas of agricultural land will be affected in the next 20–30 years (Renwick et al., 2013). Most of this land is predicted to be in upland areas and in more northerly latitudes (Renwick et al., 2013; Kapfer and Popova, 2020). Much of the land likely to be affected is grazing land which plays an important role in global ecosystem functioning and human well-being (O'Mara, 2012; Steinfeld et al., 2006). However, many grassland and shrublands maintained by grazing are over-grazed, which is a key driver reducing productivity and sustainability (Conant, 2010; O'Mara, 2012) and altering plant communities, soil water and nutrient availability (Conant, 2010; McSherry and Ritchie, 2013). It is surprising, therefore, given this importance that a recent review suggested that few studies linked livestock pressures to biodiversity impacts (Kok et al., 2020). As most of the land is likely to be abandoned in northern Europe has a High Nature Value (Renwick et al., 2013), there must be scope to devise ecological restoration strategies to improve their conservation value (Xie et al., 2020).

One positive approach to land abandonment that is currently gaining momentum is re-wilding/wilding (henceforth referred to as wilding), which in its simplest form is the removal/reduction in livestock grazing with the intention that this will improve the conservation benefit of grassland and shrublands (Sandom et al., 2013; Marrs et al., 2018, 2020). This belief is inherent in the “wet-desert” description of the British uplands by Frank Fraser Darling (1955), who argued that sheep-grazing, in particular, was very detrimental to British upland plant communities, reducing the species diversity. Indeed, these uplands have recently been described as “sheep-wrecked” by Monbiot (2013). However, since Darling's time evidence from wide-scale surveys have shown that factors other than over-grazing can damage upland vegetation including acid deposition, nitrogen deposition and climate change (Mitchell et al., 2017). The situation is even more complex as recent evidence suggests that acid deposition has declined from the latter parts of the twentieth century and plant species richness has responded positively, even though there have also been an increase in dominant plant species (Mitchell et al., 2018), and biotic homogenization (Ross et al., 2012; Pakeman et al., 2019). Part of the difficulty in managing upland habitats is that the slow dynamics of these communities make it extremely difficult to predict the effects of management decisions taken. Clearly, if the reduction of grazing policy (i.e. wilding) is to be implemented wholesale, conservation managers need to know the likely outcomes of grazing removal on the long-term ecosystem dynamics.

In essence, before implementing new policies land managers need to know how ecosystems will respond to the changed management, given that these changes will interact with the other changing environmental drivers (Lindenmayer and Likens, 2018). It is also useful to understand the ecological requirements of the plant component species in order to describe the impacts of management through time (Alday et al., 2013a). Therefore, ideally, any conservation management should be validated using evidence derived from long-term manipulative experiments (Pullin and Knight, 2009; Stewart et al., 2005; Sutherland and Wordley, 2018). Unfortunately, to set such experiments up in advance of their need obviously requires considerable foresight.

One series of such long-term, experimental grazing exclosure studies were set up between 1953 and 1967 on a range of common plant community types of upland habitats at the Moor House National Nature Reserve in the North Pennines of England (Milligan et al., 2016, 2018). At each study area, two paired-plots were established, one fenced to exclude sheep grazing, the other where sheep grazing was allowed. These study areas collectively encompass a large proportion of British upland plant communities, including those dominated by dwarf-shrubs, grasses and sedges, and soil types ranging from deep blanket peat through to brown-earth soils (Rawes and Welch, 1969). Moreover, these different plant communities experience different grazing pressures (Rawes and Welch, 1969), and these pressures have themselves changed through time, reducing from ca. 4.4 to ca. 2 sheep ha^{-1} across the entire grazing unit in 1972, and a further reduction to ca. 1 sheep ha^{-1} in 2001. The studies, therefore, compare no sheep grazing to the “business–as-usual” grazing pressure across the North Pennines reserve over a considerable timescale (Milligan et al., 2016, 2018; Marrs et al., 2018). As these upland plant communities have been traditionally considered degraded by overgrazing (McGovern et al., 2011), conservation managers expected that grazing reductions would lead to an improvement in the conservation value of the vegetation, by increasing diversity including bryophytes and lichens, and by reducing the abundance of unpalatable species (Marrs et al., 2020).

From these long-term studies, some preliminary results have been published on species change in the individual study areas up to the early 2000s, covering experimental periods of between 24 and 45 years (Rawes, 1981, 1983; Milligan et al., 2016). However, as vegetation in upland areas tends to respond slowly because of adverse climatic conditions there is a need to obtain a much longer-term view of plant community change in response to grazing to inform conservation policies such as wilding. For example, Chen et al. (2020) have recently shown that information derived for short-term studies can be misleading when viewed in the light of longer-term data. Here, therefore, we report additional data (up to 2016) for vegetation change in eight of the nine experiments used by Milligan et al. (2016) plus data from four additional exclosures reported by Milligan et al. (2018) on the Moor House grazing unit, representing experimental periods of 48–63 years for twelve experiments composing four different plant community types (Milligan et al., 2016, 2018).

Our aims were first to describe the long-term changes in plant species composition in the four plant community types comparing grazed versus ungrazed plots and then to test two hypotheses: (a) grazing would maintain the plant community composition at a quasi-equilibrium state through time, and, (b) rewilding by grazing removal would improve the conservation value of the vegetation relative to the grazed situation. To test both hypothesis we analyzed the change in both (1) species composition to provide relative measures of the differential effects on sheep grazing versus no sheep grazing on the different types of upland communities across time, and (2) plant traits to provide additional information on potential indicator groups that would inform conservation managers about likely drivers of vegetation change (Pakeman, 2004; de Bello et al., 2010). Thus, we have assessed the long-term effectiveness of sheep grazing for preserving the original communities and the removal of livestock in rewilding schemes as part of an ecological restoration strategy. These results will help define practices that prevent future negative impacts on upland habitats. Based on these findings, we put forward recommendations for effective conservation and management of British uplands plant communities and other areas of northern Europe where stock removal may be implemented (Renwick et al., 2013).

2. Methods

2.1. Study sites

Moor House NNR is situated in northern England, straddling the Pennines (Appendix A: Fig. S1). The site was established in 1952 as an experimental reserve where long-term manipulative studies could be implemented. Between 1953 and 1967 a series of grazing exclosures were set up at 12 sites across the entire reserve. The sites covered a range of the most common vegetation types that occur in the North Pennines and across the UK; i.e. from relatively productive *Agrostis-Festuca* grassland on brown-earth soils at the near-neutral end of the soil spectrum through grasslands dominated by *Festuca ovina* or *Nardus stricta*, to *Juncus squarrosus*, *Eriophorum* spp. and dwarf shrub *Calluna vulgaris*, *Erica tetralix* or *Empetrum nigrum*-dominated vegetation on acidic blanket bog (least productive). A detailed description of Description of the twelve-paired monitored sheep-grazing and exclosure plots that are used in this work is included in Appendix A: Table S1.

2.2. Experimental design

Here, we used the complete dataset containing information from the 12 sites, each with paired plots; one being fenced to exclude sheep and the other left open to allow free-range, sheep-grazing (Rawes, 1981, 1983; Marrs et al., 1988). However, the 12 sites can be viewed as four long-term, structured-experiments based on the vegetation type that dominate each site (see Milligan et al., 2016 for further details). These are outlined in Appendix A: Table S1, summarized as: (1) High-level (*Agrostis/Festuca*) grasslands, on the more-base-rich soils with three replicate sites (Hard Hill, Little Dun Fell, Knock Fell), starting in 1955/6 (Rawes, 1981); (2) Intermediate (*Nardus stricta/Juncus squarrosus*) grasslands, with two replicate sites (Cottage Hill, River Tees), starting in 1967; (3) Blanket bog (*Calluna-Eriophorum)* with five replicate sites (4 Hard Hill Burning Blocks (HHA, HHB, HHC, HHD) and Bog Hill), starting between 1953 and 1955, and (4) High-level bog, *Eriophorum*-dominated, with two replicate sites (Silverband, Troutbeck Head) starting in 1966 (Rawes, 1983).

Throughout, point-quadrats have been used to measure vascular plant, bryophyte and lichen species abundance. To keep long-term recording structure, in all experiments the point-quadrat frame was positioned using a permanently-marked reference system within the plot with the sampling positions selected randomly at the outset. On many occasions, height-stratified pins (0–10 cm, 10–20 cm, 20–30 cm and >30 cm) were used to record vascular plants to provide information on canopy composition. However, the exact way in which the pin frame was used has varied between experiments and on different sampling occasions. For example, not all pins were sampled on every occasion, or only a selection of pins was sampled on a height-stratified basis. Full details of the pin frame technique are given in Marrs et al. (1986) and Milligan et al. (2016) and all data are available in Rose et al. (2018, 2020). As a consequence of these slight monitoring differences, a detailed pre-analysis data preparation was needed which is described in detail in Appendix A.

2.3. Data preparation and analyses

All data preparation and analyses were performed in the R Statistical Environment v.3.5.2 (R Core Team, 2019) using the 'vegan package' (Oksanen et al., 2019).

First, from the clean abundance-score database a series of variables were derived, including three diversity variables, species richness, Shannon-Wiener and Simpson's diversity indices and 41 variables based on taxonomy, life-form and traits (details in Appendix A: Table S2). For taxonomic and life-form variables, the total number of hits per class was calculated; for traits, abundance-weighted mean values were calculated (Milligan et al., 2016). The three diversity variables were calculated using the '*specnumber*' and '*diversity*' functions of the '*vegan*' package (Oksanen et al., 2019).

The species datasets for each of the four experiments were analyzed independently. Three datasets were Hellinger-transformed ('*decostand*' function) followed by Detrended Correspondence Analysis (DCA) using the 'decorana' function. No transformation was used for the high-level bog dataset because transformation produced conflicting eigenvalue ranks. Species that were present only once were removed before the analysis. The amount of variation explained by each axis was expressed as a percentage of the total variation explained in the data, estimated using Økland's (1999) method. The correlations between the DCA ordination axes and the three diversity measures were then calculated using the '*envfit*' function with 9999 permutations; as the three variables showed similar significant results ($P < 0.001$) and arrow directions only species richness data are discussed further. The distribution of sites within each experiment was visualized in ordination space as standard-deviational bivariate ellipses (SD-ellipses, 95% confidence limits) using the '*ordiellipse*' function; the trajectories of the grazed and ungrazed treatments were then plotted through time for each site. The area of each of the ellipse within the ordination space was considered as a measure of the size of the overall species pool.

The species abundance data was thereafter converted to a distance matrix using the '*vegdist*' function and the Bray and Curtis index, and the significance of each of the 41 trait variables were then assessed using the '*adonis*' function with 9999 permutations stratified by site and grazing treatment (i.e. restricting permutations to maintain special dependence). Those significant variables were then analyzed using redundancy analysis (function '*rda*') after standardization ('*decostand*' function) with the interaction of grazing treatment x time as the constraining variables (EtG = grazing through elapsed time; EtU = ungrazed treatments through time). Summary statistics from all DCA and RDA analyses are presented in Appendix A: Table S3.

3. Results

3.1. Plant community response to removal of sheep grazing

3.1.1. High-level grasslands

The three high-level grasslands sites were separated along DCA axis 1 (40% of variance), with Little Dun Fell and Hard Hill towards the negative end and Knock Fell at the positive end with Hard Hill being more or less subsumed within the Little Dun Fell community space (Fig. 1b). Hard Hill had the smallest species pool, Little Dun Fell was intermediate and Knock Fell had the largest with the deviational ellipses being 1.58, 4.62, 6.96 units respectively. However, most of the within-site variation is described across axis 2 (major ellipse axes for all sites; 25% of variance). The site separation was linked with a species gradation along DCA axis 1 from an *Avenella flexuosa*, *Carex bigelowii*, and *Nardus stricta* community at the negative end (Fig. 1a) to *Agrostis canina*, *A. capillaris*, *Anthoxanthum odoratum*, *Carex caryophyllea*, *Deschampsia cespitosa*, *Festuca rubra*, *Luzula campestris/multiflorum*, *Achillea millefolium*, *Rumex acetosa* and *Thymus polytrichus* at the positive end. The bryophytes showed a similar gradation (Fig. 1a) with *Dicranum fuscescens*, *Polytrichum strictum* and the lichens *Cladonia uncialis* and *C. portentosa* at the negative end through to *Hylocomium splendens*, *Lophocolea bidentata* and *Thuidium tamariscinum* at the positive end. In contrast, Axis 2 (25% of the variance) reflected a bryophyte/lichen rich community at the negative end with vascular plants at the positive end (Fig. 1a), these effects were more marked in Little Dun Fell and Knock Fell. Interestingly, species richness was correlated positively with axis 1 and negatively with axis 2 indicating that Knock Fell quadrats with vascular, lichen and bryophytes were the more diverse ones (Fig. 1a).

The three high-level grassland sites also showed marked differences in successional trajectories between grazed and ungrazed plots (Fig. 1c–e). Both grazed and ungrazed plots at Hard Hill were compositionally stable, fluctuating slightly around the same ordination area with temporal vectors of similar magnitude (Fig. 1d). In contrast, both the Little Dun Fell and the Knock Fell sites showed different compositional trajectories between the grazed and ungrazed plots. At Little Dun Fell the successional trajectory of the ungrazed plots moved in the positive direction of axis 2 towards increased vascular plants and reduced bryophytes/lichens; whilst the grazed plots showed a more erratic trajectory ending also on positive side of axis 2, although some distance from the ungrazed plots (Fig. 1c). At Knock Fell the compositional trajectories of ungrazed plots moved towards the positive end of axis 2 with increased graminoid cover and reduced bryophytes/lichens, while the grazed plots were moving in a positive direction on axis 1 with increasing graminoids (Fig. 1e). At all sites the trajectories were moving in the opposite direction to species richness.

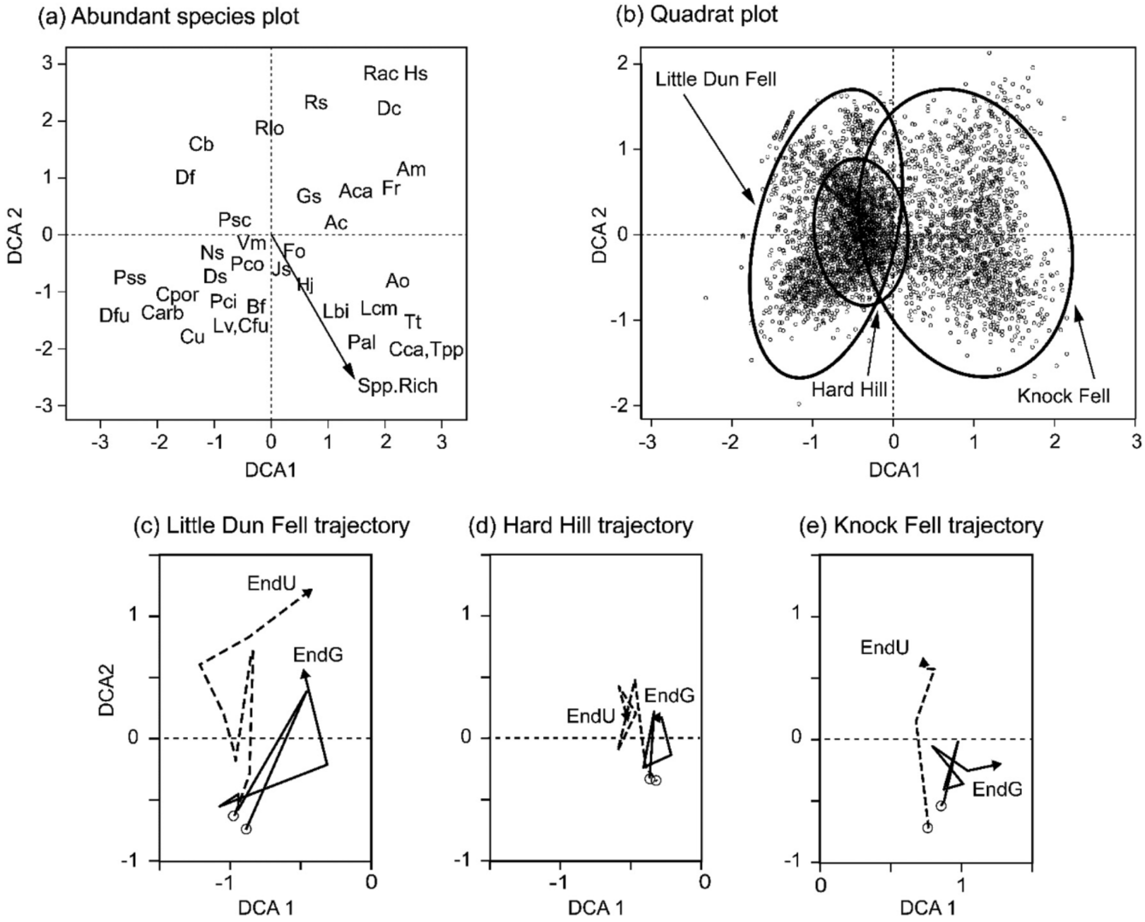


Fig. 1. Decorana plots from the grazed and ungrazed treatments from three high-level grassland sites (Hard Hill, Knock Fell and Little Dun Fell) at Moor House NNR: (a) the most abundant species, (b) quadrat plot with sites displayed by standard deviational ellipses (95%CL) and (c–e) temporal trajectories through time. Species Key: Ac = *Agrostis canina* sl; Aca = *Agrostis capillaris*; Af = *Avenella flexuosa*; Am = *Achillea millefolium*; Ao = *Anthoxanthum odoratum*; Bf = *Barbilophozia floerkei*; Carb = *Cladonia arbuscula*; Cb = *Carex bigelowii*; Cca = *Carex caryophyllea*; Cfu = *Cladonia furcata*; Cpor = *Cladonia portentosa*; Cu = *Cladonia uncialis*; Dc = *Deschampsia cespitosa*; Dfu = *Dicranum fuscescens*; Ds = *Dicranum scoparium*; Fo = *Festuca ovina*; Fr = *Festuca rubra*; Gs = *Galium saxatile*; Hj = *Hypnum jutlandicum*; Hs = *Hylocomium splendens*; Js = *Juncus squarrosus*; Lbi = *Lophocolea bidentata*; Lcm = *Luzula campestris/multiflora*; Lv = *Lophozia ventricosa*; Ns = *Nardus stricta*; Pal = *Polytrichastrum alpinum*; Pci = *Ptilidium ciliare*; Pco = *Polytrichum commune*; Psc = *Pleurozium schreberi*; Pss = *Polytrichum strictum*; Rac = *Rumex acetosa*; Rlo = *Rhytidiadelphus loreus*; Rs = *Rhytidiadelphus squarrosus*; Tpp = *Thymus polytrichus*; Tt = *Thuidium tamariscinum*; Vm = *Vaccinium myrtillus*. Start and end points of trajectories are illustrated with and open circles and diamonds respectively; dotted lines = ungrazed; solid = grazed.

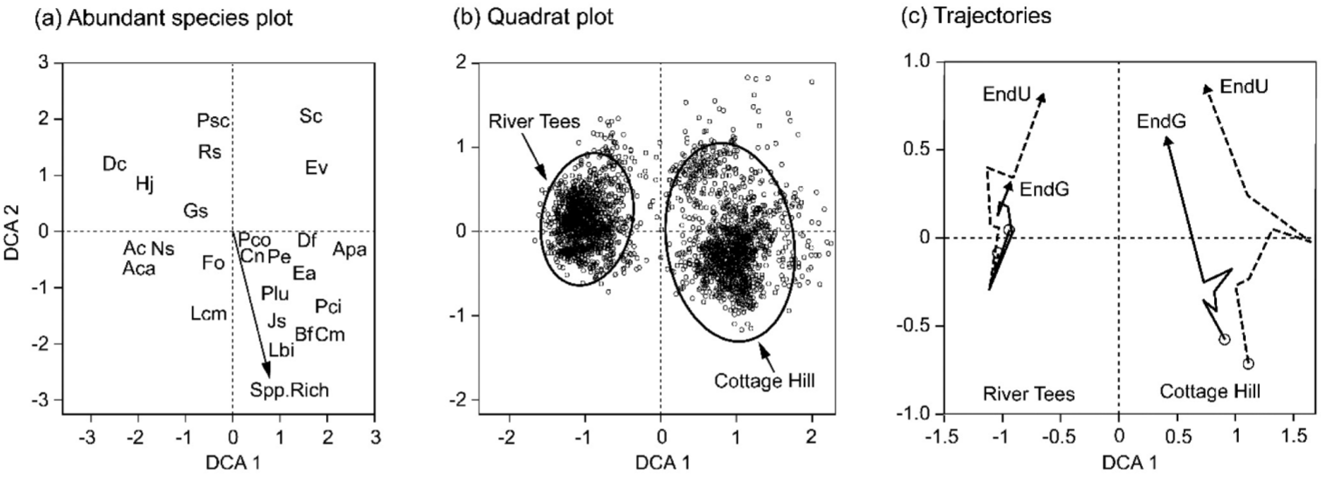


Fig. 2. Decorana plots from the grazed and ungrazed treatments from two Intermediate grassland sites (Cottage Hill and River Tees) at Moor House NNR: (a) the most abundant species, (b) quadrat plot with sites displayed by standard deviational ellipses (95%CL) and (c) temporal trajectories through time. Species Key: Ac = *Agrostis canina* sl; Aca = *Agrostis capillaris*; Af = *Avenella flexuosa*; Apa = *Aulacomnium palustre*; Bf = *Barbilophozia floerkei*; Cm = *Calypogeia muelleriana*; Cn = *Carex nigra*; Dc = *Deschampsia cespitosa*; Ea = *Eriophorum angustifolium*; Ev = *Eriophorum vaginatum*; Fo = *Festuca ovina*; Gs = *Galium saxatile*; Hj = *Hypnum jutlandicum*; Js = *Juncus squarrosus*; Lbi = *Lophocolea bidentata*; Lcm = *Luzula campestris/multiflora*; Ns = *Nardus stricta*; Pci = *Ptilidium ciliare*; Pco = *Polytrichum commune*; Pe = *Potentilla erecta*; Plu = *Plagiothecium undulatum*; Psc = *Pleurozium schreberi*; Rs = *Rhytidiadelphus squarrosus*; Sc = *Sphagnum capillifolium*. Start and end points of trajectories are illustrated with and open circles and diamonds respectively; dotted lines = ungrazed; solid = grazed.

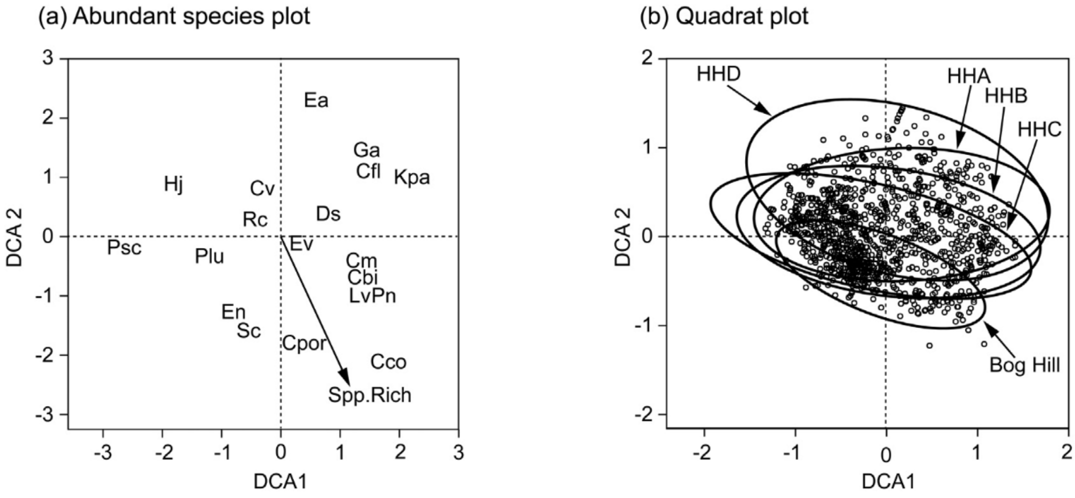
3.1.2. Intermediate grasslands

The two intermediate grassland sites were significantly separated along DCA axis 1 ($p < 0.05$; 55% of variance); River Tees site was located at the negative side and Cottage Hill on the positive side of DCA axis 1 with compositional differences between both (Fig. 2b). The Cottage Hill site deviational ellipse covered almost double the ordination space of the River Tees site, 3.13 and 1.49 units respectively, indicating a greater species pool (species heterogeneity), although the main within-sites variation was represented along DCA axis 2 (major ellipses axes; 20% of variance). The site compositional differences were also translated into species gradients (Fig. 2a) from *Agrostis canina*, *A. capillaris*, *Deschampsia cespitosa*, *Nardus stricta* and *Hypnum jutlandicum* at the negative end of DCA axis 1 (correlated with the river River Tees site) through to *Avenella flexuosa*, *Eriophorum angustifolium* and *E. vaginatum* at the positive end (correlated with river Cottage Hill site), Bryophytes moved from *Hypnum jutlandicum* through to *Aulacomnium palustre*, *Barbilophozia floerkei*, *Calypogeia muelleriana*, *Ptilidium ciliare* and *Sphagnum capillifolium* (Fig. 2a). DCA Axis 2 showed a gradation from a *Juncus squarrosus*-*Luzula campestris*/*multiflora* and bryophyte-dominated community with *Barbilophozia floerkei*, *Calypogeia muelleriana*, *Lophocolea bidentata*, *Ptilidium ciliare*, *Plagiothecium undulatum* at the negative end and *Deschampsia cespitosa*, *Eriophorum vaginatum*, *Pleurozium schreberi*, *Rhytidiadelphus squarrosus*, *Sphagnum capillifolium* at the positive end. Species richness was mainly correlated negatively with axis 2 (Fig. 1a).

Both sites showed similar successional trajectories for both grazed and ungrazed plots converging towards the upper central ordination space where *Pleurozium schreberi*, *Rhytidiadelphus squarrosus*, *Sphagnum capillifolium* was located. At the River Tees site, both plots moved in a positive direction on DCA axis 2, with the grazed plots moving less far than the ungrazed plot (Fig. 2c). At Cottage Hill, both plots also moved in a positive direction on DCA axis 2, but the ungrazed plot trajectory was displaced further to the right in a positive direction (Fig. 2c). At both sites the trajectories were moving in the opposite direction to species richness.

3.1.3. Blanket bogs

The five blanket bogs sites were superimposed around the center of the ordination with the deviational ellipses located along the entire gradient of DCA axis 1 (major ellipse axes, 39% of variance). This indicates that although there is a lack of compositional differences between sites (main species are shared at the ordination center, Fig. 3a), the DCA axis 1 showed similar within-site differences for all experiments in response to changes in bryophytes/lichens (i.e. main successional trends). In contrast, there was a slight separation of experiments up DCA axis 2 (24% of variance; in order from lowest to highest Bog Hill through Plots HHC > HHB > HHA to HHD; Fig. 3b) essentially reflecting a reduction in species richness, at least partly linked to increasing elevation. The analysis of deviational ellipses areas showed that the Bog Hill ellipse was at least half that of the Hard Hill sites at 1.64 units compared to 3.76, 3.72, 3.33 and 5.01 units for HHA, HHB, HHC and HHD respectively, which may reflect differences in sampling intensity. Interestingly, the trajectories of all sites moved in a reverse direction along DCA axis 1,



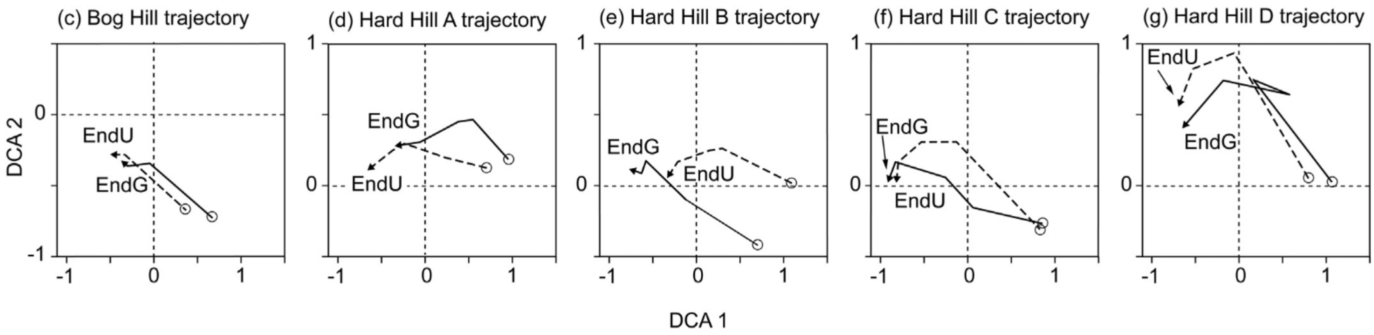


Fig. 3. Decorana plots from the grazed and ungrazed treatments from five blanket bog sites (Bog Hill and Hard Hill with Blocks denoted A, B, C, D) at Moor House NNR: (a) the most abundant species, (b) quadrat plot with sites displayed by standard deviational ellipses (95%CL) and (c–g) temporal trajectories through time. Species Key: Cbi = *Cephalozia bicuspidata*; Cco = *Cephalozia connivens*; Cfl = *Campylopus flexuosus*; Cm = *Calypogeia muelleriana*; Cpor = *Cladonia portentosa*; Cv = *Calluna vulgaris*; Ds = *Dicranum scoparium*; Ea = *Eriophorum angustifolium*; En = *Empetrum nigrum*; Ev = *Eriophorum vaginatum*; Ga = Green alga terrestrial; Hj = *Hypnum jutlandicum*; Kpa = *Kurzia pauciflora*; Lv = *Lophozia ventricosa*; Plu = *Plagiothecium undulatum*; Pn = *Pohlia nutans*; Psc = *Pleurozium schreberi*; Rc = *Rubus chamaemorus*; Sc = *Sphagnum capillifolium*. Start and end points of trajectories are illustrated with and open circles and diamonds respectively; dotted lines = ungrazed; solid = grazed.

which similar movements and direction for grazed and ungrazed plots towards communities with more bryophytes (Fig. 3c–g).

The main species in these blanked bog sites, such as *Calluna vulgaris*, *Dicranum scoparium*, *Eriophorum vaginatum*, *Rubus chamaemorus*, were centered around the origin and the main first gradient reflected to a large extent successional changes in distribution of bryophytes and lichens (Fig. 3a). The bryophytes at the negative end of DCA axis 1 were *Hypnum jutlandicum*, *Plagiothecium undulatum*, *Pleurozium schreberi* through to *Campylopus flexuosus*, *Calypogeia muelleriana*, *Cephalozia bicuspidata*, *Lophozia ventricosa* and *Pohlia nutans* at the positive end. DCA axis 2 reflected a gradient from *Cephalozia connivens*, *Cladonia portentosa*, *Empetrum nigrum* and *Sphagnum capillifolium* at the negative end to Green algae, *Calluna vulgaris*, *Campylopus flexuosus*, *Eriophorum angustifolium* and *Kurzia pauciflora* at the positive end (Fig. 3a). Species richness was mainly correlated negatively with axis 2 (Fig. 3a).

3.1.4. High-level bogs

The two high-level bogs occupied relatively similar positions in the DCA ordination center with considerable overlap, although DCA axis 1 (28% of variance) showed that compositional differences between plots of both sites were caused by species richness (negatively correlated, Fig. 4a). The sd-deviational ellipse for Silverband occupied more than double the ordination space of Troutbeckhead, 4.46 compared to 1.61 units (Fig. 4b), with the major ellipse axes diagonal to both axes. The DCA axis 1 gradient shows *Avenella flexuosa*, *Calluna vulgaris*, *Empetrum nigrum* and *Vaccinium myrtillus* among the vascular plants at the negative end and *Carex nigra*, *Narthecium ossifragum*, *Rubus chamaemorus* and *Trichophorum cespitosum* at the positive end (Fig. 4a). The bryophytes were mainly placed at the negative end of axis 1, and placed in the same general direction as increasing species richness (Fig. 4a). DCA Axis 2 (27% of the variance) showed a gradient from a community dominated by *Festuca ovina*, *Carex nigra*, *Vaccinium myrtillus* and *Rubus chamaemorus* through to one dominated by *Avenella flexuosa*, *Calluna vulgaris*, *Empetrum nigrum*.

The successional trajectories of grazed and ungrazed plots for both sites started in similar areas of the ordination. At Troutbeckhead both treatments moved in a negative manner on axis 1 and a positive one on axis 2, moving towards *Avenella flexuosa*, *Calluna vulgaris* and in the same direction as increasing species richness (Fig. 4c); the ungrazed plot moved slightly further than the grazed one. (Fig. 4c). At, Silverband, the successional trajectories grazed trajectory moved positively on axis 1 and was fairly close to the grazed Troutbeck Head plot at the end of the study period. The ungrazed plot moved marginally in a positive direction on axis 2 (same as the other sites) but also moved marginally positively on axis 1, and in an opposite direction to species richness (Fig. 4c).

3.2. Trait and life-history responses to removal of sheep grazing

In many respects the RDA analyses showed similarities between the four experimental groups in that the general effect of elapsed time in species composition was in a positive direction on axis 1 (Fig. 5a). For three experiments this was in the opposite direction to species richness, the exception was the high-level bogs where species richness was correlated with successional trajectories of grazed and ungrazed plots (Fig. 5a). These results agree with the previous DCA results reported above. All three climatic variables were associated with the vegetation temporal trajectories to some extent; on both grasslands and high-level bog they were associated with the ungrazed plot whereas on the blanket bog they were linked to the grazed plot. The Ellenberg values were also correlated with the vegetation temporal trajectories, however, in both grasslands and the high-level bog Ellenberg values were correlated with ungrazed trajectory, while, in the blanket bogs they were with the grazed one (Fig. 5b). The grazing index showed mixed effects being placed towards the negative end of the vegetation temporal trajectories in the intermediate grassland and the blanket bog, but with the grazed treatment in the high-level grasslands and high-level bog (Fig. 5b).

The taxonomic groups showed that liverworts and lichens were at the negative end of the four successional trajectories and vascular plants and mosses at the positive end (more recent samplings); except the intermediate grasslands where vascular plants, grasses and herbaceous species were found earlier in the succession (Fig. 6a). In the high-level grasslands the vascular plants were mainly graminoids/Poaceae and herbaceous species (Fig. 7a). In terms of clonality, there was a tendency for an increase in species with little vegetative spread in all experiments, plus species with shortly-creeping rhizomes in the high-level grasslands, extensively-creeping species in the intermediate grasslands, blanket bog and high-level bog and turf-forming species in both blanket bog and high-level bog.

The vascular plant life-histories showed some similarities in three experiments (intermediate grasslands, blanket bog, and high-level

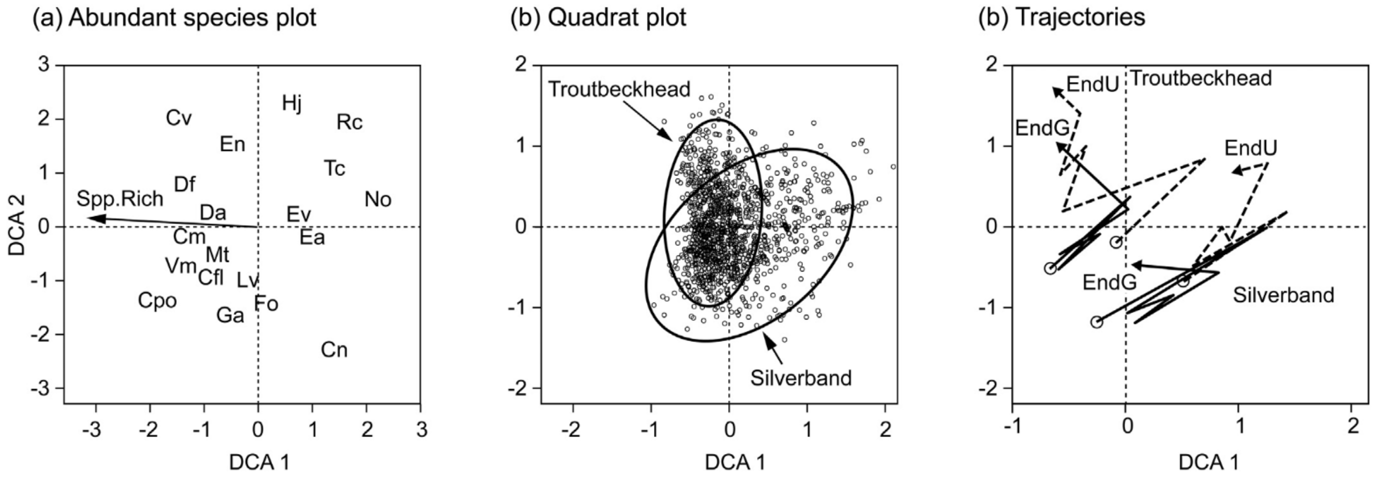


Fig. 4. Decorana plots from the grazed and ungrazed treatments from two high-level blanket bog sites (Silverband and Troutbeckhead) at Moor House NNR: (a) the most abundant species, (b) quadrat plot with sites displayed by standard deviational ellipses (95%CL) and (c) temporal trajectories through time. Species Key: Af = *Avenella flexuosa*; Cfl = *Campylopus flexuosus*; Cm = *Calypogeia muelleriana*; Cn = *Carex nigra*; Cpor = *Cladonia portentosa*; Cv = *Calluna vulgaris*; Da = *Diplophyllum albicans*; Ea = *Eriophorum angustifolium*; En = *Empetrum nigrum*; Ev = *Eriophorum vaginatum*; Fo = *Festuca ovina*; Ga = Green alga terrestrial; Hj = *Hypnum jutlandicum*; Lv = *Lophozia ventricosa*; Mt = *Mylia taylorii*; No = *Narthecium ossifragum*; Rc = *Rubus chamaemorus*; Tc = *Trichophorum cespitosum*; Vm = *Vaccinium myrtillus*. Start and end points of trajectories are illustrated with and open circles and diamonds respectively; dotted lines = ungrazed; solid = grazed.

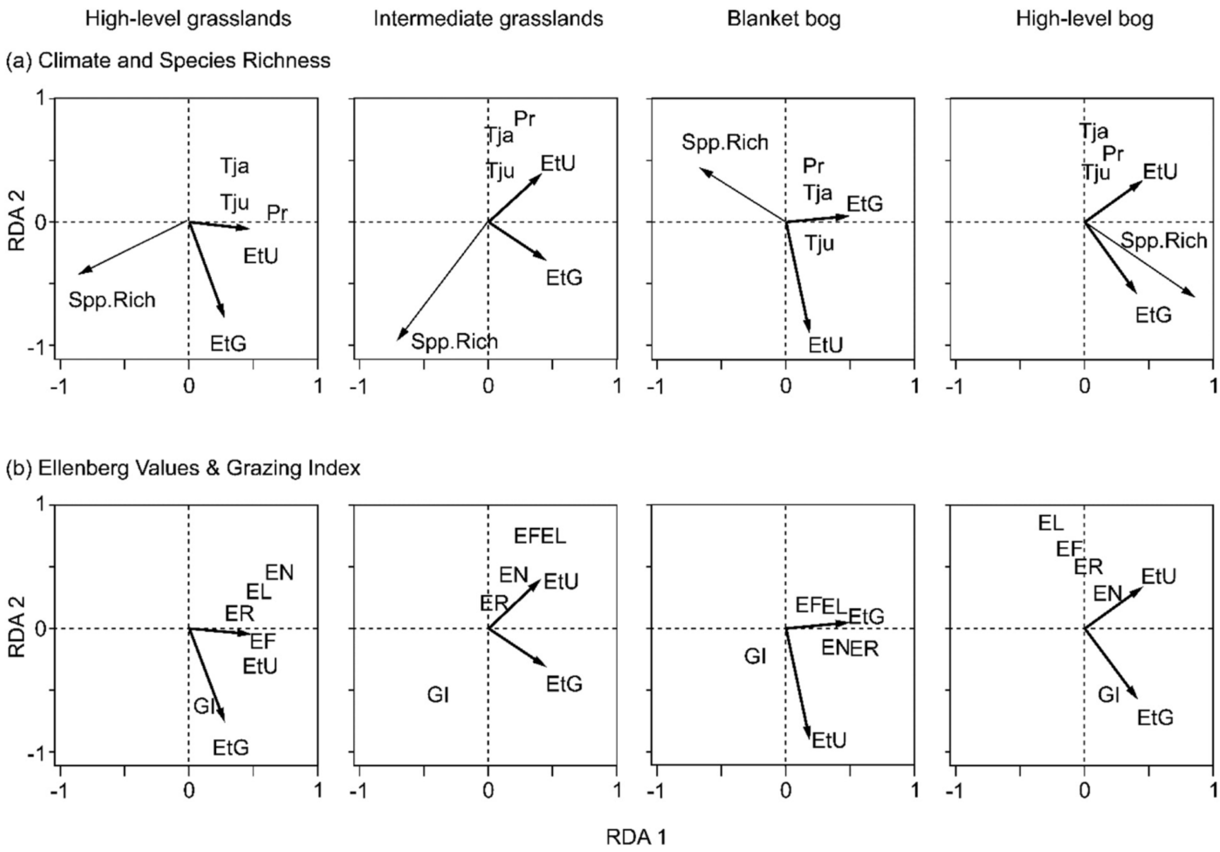


Fig. 5. Comparison of the changes in abundance–weighed traits derived from the redundancy analysis for (a) climate variables (mean annual January temperature, mean annual July temperature and precipitation), and (b) Ellenberg values and grazing index with respect to the temporal trajectories in the grazed, (EtG) and ungrazed plots, (EtU) for the four experimental groups at Moor House NNR. The species richness correlation was fitted over the climate variables plot (a): High-level grasslands $r^2 = 17.9\%$; Intermediate grasslands $r^2 = 54.9\%$; Blanket bog $r^2 = 12.1\%$; High-level bog $r^2 = 48.7\%$ (all $p < 0.001$). Variable codes are presented in Appendix A: Table S2.

bog) with hemi-cryptophytes placed at the negative end of the successional trajectories (older monitoring) and chamaephytes nearer the positive end (most recent samplings, Fig. 7a). No other life-history forms were significantly explaining species successional trends in these experiments. In the high-level grasslands, therophytes and chamaephytes were placed at the early part of the succession and hemi-cryptophytes in the later stages, geophytes being intermediate. The bryophyte life-histories showed a transition along the successional gradients with smooth and rough mats (high-level grasslands only), tufts and turfs at the negative end (older monitoring) and cushions, rough mats, turfs (blanket bog only) and species with little vegetative spread at the positive end (most recent monitoring, Fig. 7b).

4. Discussion

In this study, we compared the long-term (48–63 years) change in plant species composition of vegetation in the British uplands under experimental conditions comparing the effects of two grazing pressures, free-range sheep grazing versus no grazing pressure. We also investigated how the plant traits and life-history information might be responsible for detected differences, and hence could be used as potential indicators to inform conservation managers. Surprisingly, our results showed that the first hypothesis, related to quasi-equilibrium state of plant community composition maintained by grazing, was partially accepted because only two sites (Hard Hill high-level grassland, Silverband high-level bog) showed either cyclic or little change through time in vegetation composition of the grazed sites; all others experiments showed some directional change through time. Similarly, the second hypothesis, related to the positive effect of rewilding by grazing removal over vegetation composition, was also partially accepted because most sites showed a greater directional change of ungrazed plots than their grazed counterparts, nevertheless, this greater directional change was usually accompanied by a reduction in species diversity.

Our results did, however, highlight five important points. First, there has been no wholesale change in the composition of the dominant plant species (Grime, 1998) even though they have fluctuated in abundance (sensu Miles, 1979) during the last 48–63 years. However, sub-dominant species (Grime, 1998) have fluctuated and/or declined in abundance. Thus, part of the compositional differences were caused mainly by change in these sub-dominant species, some of them being more susceptible to management practices and environmental changes than the dominant ones, and this will obviously hamper their conservation. These results are in accordance with recent studies on synchrony and stability which highlighted that the dominant plant species was the main driver of community stability rather than species richness (Valencia et al., 2020). Second, different temporal responses in species richness were detected between the experiments which were dependent on species pools of the surrounding community types. For example, in three of the four experiments (high-level and intermediate grasslands and blanket bog) there has been a reduction in species richness through time, which is in agreement with successional trends described previously (Milligan et al., 2016). However, in the blanket bogs species richness was orthogonal to the trajectories and this may, in part, reflect differences in past site histories (legacy effects; Muurinen et al., 2019), Troutbeckhead being intact and Silverband recovering from frequent erosion damage (Rawes, 1983).

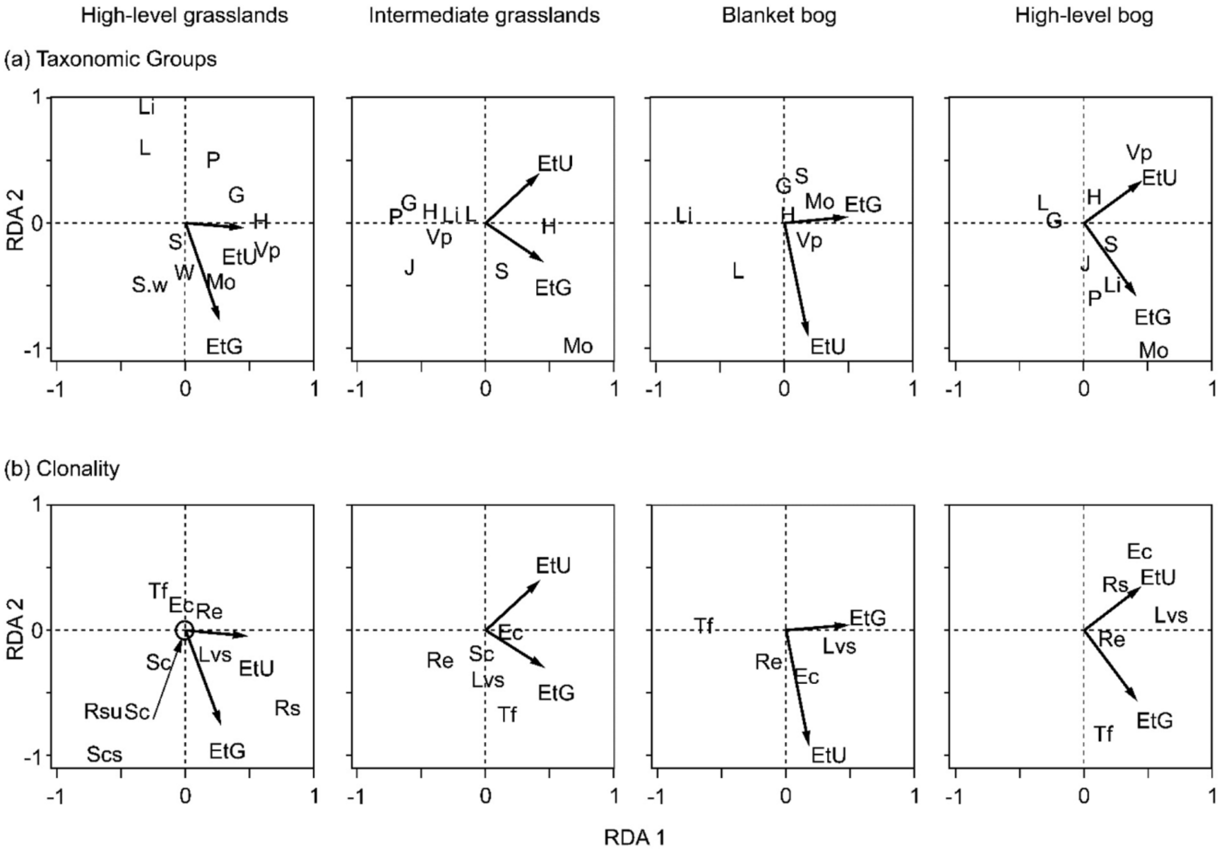


Fig. 6. Comparison of the changes in abundance–weighed derived from the redundancy analysis for (a) taxonomic and (b) clonality variables with respect the temporal trajectories in the grazed, (EtG) and ungrazed plots, (EtU) for the four experimental groups at Moor House NNR. Variable codes are presented in Appendix A: Table S2.

Third, the temporal trajectories for both grazed and ungrazed plots were moving in similar directions in most experiments (similar successional trends sensu Alday et al., 2011). The similarity of successional trends in each site between both plots was expected as local species pools are identical for both of them, and grazing was reduced across the experiment. The exception is the high-level grasslands, where site-dependent different responses were found between the grazed and ungrazed plots. For example, the species composition at Little Dun Fell changed the most through time with both grazed and ungrazed plots moving in similar directions comparable to previous sites, in contrast, Knock Fell showed an intermediate response with the ungrazed plot showing a similar trajectories to Little Dun Fell, but the grazed plot moving erratically less, whereas Hard Hill experiment showed remarkable stability with a small movement of both plots through time. It seems that these grasslands are more heterogeneous ecosystems than supposed, in view of these different successional responses (Seabloom et al., 2005).

Fourth, all of the blanket bog sites showed more or less similar trajectories for both grazed and ungrazed plots (compositional convergence sensu Alday et al., 2011), with site differences related to a combination of (a) elevation with the lowest Bog Hill being more species-rich than the higher-elevation Hard Hill plots, or (b) a reduction in species diversity in the Hard Hill plots associated with the burning treatment in 1954/55 (Milligan et al., 2018). Unfortunately, it is impossible to disentangle the real cause. However, the similarity in successional trends between both grazing treatments suggests that the initial effects of grazing exclosure have disappeared through time. Finally, where a reduction in species richness was detected, this was mainly due to a reduction in bryophytes, especially liverworts, and lichens. This is a common feature in the British uplands over the last century, being detected in a range of large-scale, repeat surveys (Britton and Fisher, 2009; Britton et al., 2009, 2018), almost certainly as a result of elevated pollutant impacts and/or increase vegetation growth (see below).

It is also important to consider those species that are producing the compositional changes through time. In the intermediate grasslands and two of the high-level grasslands, although the community composition in both grazing treatments were moving in the same direction with a general trend towards domination by graminoids, different dominants were detected in each experiment; *Avenella flexuosa* and *Carex bigelowii* at Little Dun Fell, *Agrostis capillaris*, *Deschampsia cespitosa* and *Festuca rubra* at Knock Fell, *Deschampsia cespitosa* at River Tees and *Eriophorum vaginatum* at Cottage Hill. The intermediate grasslands were considered transitional between grassland and blanket bog communities by Rawes (1981), however, these new data suggest that Cottage Hill plant composition is moving towards blanket bog, while River Tees plant composition is moving towards a grassland. Similarly, on the blanket bogs and high-level bogs, *Calluna vulgaris* and *Empetrum nigrum* increased through time along with the pleurocarpous mosses *Hypnum jutlandicum* and *Pleurozium schreberi*. These results are consistent with those from wider-scale, repeat surveys (Ross et al., 2012; Pakeman et al., 2019; Mitchell et al., 2017, 2018), indicating the importance of species pool heterogeneity in shaping grasslands composition (Questad and Foster, 2008).

In relation to successional speed, in both grassland experiments and the high-level bogs, the ungrazed plots moved a greater distance than the grazed ones during the same time frame, indicating greater compositional responses. This suggest that grazed impacts in these communities may be associated with increasing biomass and the reduction in light impinging on the bryophytes (van der Wal et al., 2005). Again, there were two exceptions, the first was at the high-level Hard Hill grassland, where this site showed a more or less-stable pattern through

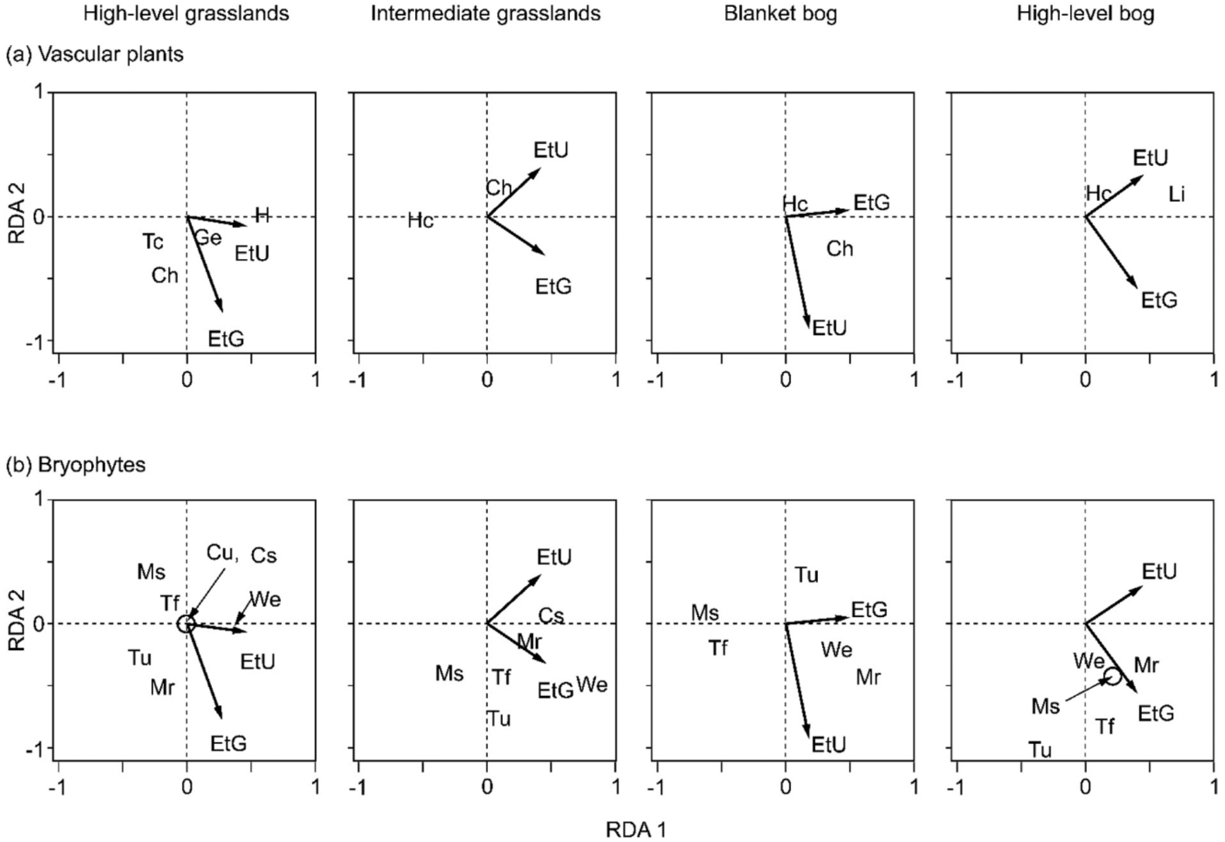


Fig. 7. Comparison of the changes in abundance–weighed derived from the redundancy analysis for life-history variables values with respect the temporal trajectories in the grazed, (EtG) and ungrazed plots, (EtU) for the four experimental groups at Moor House NNR: (a) vascular plants, and (b) bryophytes. Variable codes are presented in Appendix A: Table S2.

time with no evidence of the temporal trajectories at the other two sites. The other exceptions were the blanket bog; all sites showed similar trajectories through time but no consistency between the distance travelled between the grazed and ungrazed treatments. Part of the reasons for these inconsistences might be because of the differential grazing patterns across the reserve, in part controlled by interactions between the underlying geology/soil types interacting with the way the sheep are managed (by allowing them to freely range over a large area of differing vegetation types). The high-level grasslands occur on acid brown-earths and the other communities are on either peats or soils with a high surface organic content. The grazing unit is a “Common” under English law and the sheep are put onto the moor predominantly from the south-western edge of the reserve, where they gravitate to the best grazing (high-level grasslands) and when forage on these grasslands is depleted, they move to less-nutritious vegetation (Rawes and Welch, 1966, 1969). Hard Hill, is some distance (2.5 km) from the other high-level grasslands, it is separated by blanket bog, and had a much reduced sheep density in the early 1960s, averaging 2.1 sheep ha^{-1} over the season with an estimated annual herbage removal of 5.5 kg DM ha^{-1} compared to 3.3 and 4.2 sheep ha^{-1} and 7.4 and 7.6 kg DM ha^{-1} at Little Dun Fell and Knock Fell respectively (Welch and Rawes, 1964). In a similar vein, the Hard Hill blanket bog sites have a low sheep grazing density (Appendix A: Table S1), but they too are much closer to sheep entry point/good grazing than Bog Hill. However, these differential grazing pressures were measured in the 1960s before the two reductions in overall sheep numbers (Welch and Rawes, 1965, 1966; Rawes and Welch, 1966, 1969), but we would predict that the grazing pressure on the high-level grasslands would be reduced less than that of the blanket bogs because the sheep would tend to concentrate on them as the grazing there is most nutritious (Marrs et al., 2020). The importance of size and spatial distribution of species-rich grasslands within a grass-heath matrix has recently been shown to influence grazing impacts were red deer (*Cervus elaphus* L.) were the main herbivores (Moore et al., 2015). Here, the correlation of the grazing index with the grazed treatment in the high-level grasslands and high-level bogs confirms these hypotheses as these communities are closest to the sheep entry points and should have a greater grazing pressure. However, further studies on grazing patterns on these experiments are needed to confirm these predictions.

The analysis of the changes in plant traits provided to us some insight into the potential mechanisms involved in the successional trends and in the responses of grazed and ungrazed plots. For example, the positive association of all climate variables with vegetation temporal trajectories suggests that the species are responding to a warmer and wetter climate of the last years, which has been suggested as a major driver of vegetation change in the Scottish Highlands (Britton et al., 2017; Mitchell et al., 2018). At the same time, all the Ellenberg indices were also significantly correlated with the vegetation temporal trajectories. This suggest that through time there has been an increase in species that grow best in less acidic, more fertile, wetter and with more light habitats (Fig. 5b). This provides further tentative evidence for the suggestion damage to plant communities caused by interactions with atmospheric pollution are beginning to be reversed (Rose et al., 2016; Mitchell et al., 2018). Atmospheric SO_2 concentrations, a major cause of acidification since its peak in the 1970s had been reduced by 90% in 2008 and N emissions have also reduced over this period, but only by 50% (ROTAP, 2012; Monteith et al., 2016). The continuing increase in weighted N values suggests that elevated N may still be having an impact over these habitats. We accept that these conclusions are speculative and require further work is needed to unravel the exact mechanisms involved.

4.1. Limitations of this investigation

Like any long-term study, the experiment could have been improved with hindsight. Few of the experiments had appropriate baseline monitoring although all treatments were set up on "uniform vegetation" (Rawes and Hobbs, 1979). In some cases, one plot had a baseline sample taken but the other did not, hence, the variability of vegetation between some of the paired plots at the starting positions (Fig. 1). For the blanket bog sites, the current pin-quadrat monitoring started in 1972/3, ca. twenty years after the exclosures were erected, and there has been substantive changes in both atmospheric sulphur and nitrogen pollutant loads as well as overall sheep numbers which will almost certainly have impacted on the flora, and specially the bryophytes and lichens. Lastly, the monitoring methods were designed to assess species occurrence at a standardized detection level, therefore, species that are "new" or "disappear" may still be present at low frequency. In this regard, Milligan et al. (2018) argued that the recent appearance of *Sphagnum subnitens* might result from recent elevated nitrogen loads through a combination of colonization or increased abundance from an existing low population that was below the detections level in previous surveys. In any case, the analysis of long-term experiments simultaneously is a powerful tool to describe long-term vegetation trends to inform management choices (Alday et al., 2013b), as well as, to define some ecological indicators such as in our case the use of liverworts and lichens as indicators of grazing removal for these Upland habitats.

4.2. Conclusions and implications for conservation

Overall, the dominant plant species within these communities were rather stable, although lichens and bryophytes and some rare species were not. This suggests that the main vegetation is unlikely to change much over time if sheep numbers were to be reduced, or even removed, through wilding schemes (Monbiot, 2013; Sandom et al., 2013). One clear result is that plant community change takes a long time in these upland areas and wilding may take a very long time to produce compositional changes. The likely winners could be some of the sub-dominant species which might recover if grazing were to be removed, for example the seven focal species reported by Marrs et al. (2020), i.e. *Chamaenerion angustifolium*, *Dryopteris dilatata*, *Geum rivale*, *Narthecium ossifragum*, *Potentilla erecta*, *Rumex acetosa* and *Rubus chamaemorus* in a small-scale study of plant nutrition in some of these experiments. However, it took between 10 and 20 years in high-level bog and 60 years in the high-level grasslands for these focal species to increase (Marrs et al., 2020). As the seedbanks in these plant communities have been shown to be very depauperate (Lee et al., 2013, 2020), it is unlikely that additional species will colonize unless they are introduced by management, probably with some form of disturbance (Marrs et al., 2020). Moreover, in these experiments, and indeed across the entire grazing unit, there was no evidence of substantive tree invasion up to 2001 (24–45 years, Milligan et al., 2016) and this is confirmed here over a longer period (48–63 years). Restriction/control of tree invasion should be fundamental if these upland communities are to be conserved as they are or encouraged if succession to scrub woodland was deemed a desirable outcome. Irrespective, we predict that if sheep were removed at least in the short- to medium-term there would be a period of relative stability in plant composition. It can be argued that vegetation change might differ if grazing removal was implemented at larger scales than considered here (Ross et al., 2012); this is possible, but it remains to be tested.

CRediT authorship contribution statement

Josu Alday: Formal analysis, Writing - original draft, Writing - review & editing, Funding acquisition. **John O'Reilly:** Investigation, Writing - review & editing. **Rob J. Rose:** Data curation, Investigation, Writing - review & editing, Funding acquisition. **Rob H. Marrs:** Conceptualization, Data curation, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Funding acquisition.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Marrs is President of the Heather Trust, one of the funders. This is an ambassadorial position and has no decision-making authority. The funding was made by the Heather Trust to the University of Liverpool.

Acknowledgements

This work would not have been possible without the foresight and persistence of staff of the Nature Conservancy (Ken Park and M Rawes), its successor bodies (I. Findlay, C. McCarty, and M. Furness), the UK Environmental Change Network (J Adamson) and the Ecological Continuity Trust. This work was part-funded by (1) the Leverhulme Trust's award of an Emeritus Fellowship to RHM (EM-2018-073\2), (2) the Heather Trust and (3) a Ramon y Cajal fellowship (RYC-2016-20528) to JGA. The funders had no involvement in data analysis/interpretation of data, the writing of this manuscript or the decision to submit for publication. Ms. S. Yee produced the figures.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.143508.

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