Long-term effects of sheep-grazing and its removal on vegetation dynamics of British upland grasslands and moorlands; local management cannot overcome large-scale trends

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ABSTRACT

The upland and mountainous regions of northern Europe provide a wide variety of ecosystem services. However, these ecosystem services are highly vulnerable to environmental and land-use change. To ensure their future conservation, it is therefore, essential to understand whether upland plant communities will respond positively or negatively to a range of environmental factors such as grazing pressure and landscape-scale factors such as changes in atmospheric SO_2 and NO_x deposition. To understand this, here, we describe the long-term trends in four UK upland communities (high-level grassland, intermediate grassland, blanket bog, high-level bog) using four replicated long-term experiments examining the effects of sheep grazing compared to no-sheep grazing in Moor House (from 1954 to 2016). Our results showed that species richness and abundance recovered in grazed plots after 2000, with improvements in species richness and abundance of vascular plants, mosses, and liverworts. Unfortunately, no improvement was found for lichens. Species richness, vascular plants, and mosses recovered the fastest, and much faster than liverworts. There was no evidence of slower recovery of species richness and abundance in plots where sheep grazing was removed. These results are consistent with longitudinal studies suggesting recovery after 2000 as a result of reduced atmospheric deposition. Although trends in diversity and abundance in the grazed and ungrazed plots were not identical, they were not markedly different either. The similar richness and abundance trends in the grazed and ungrazed plots found in each plant community suggest that within-community dynamics may overcome initial differences between the grazing treatments over time. In contrast, differences in richness and abundance among plant communities over time suggest that some landscape-scale trends, such as those caused by a reduction in nutrient inputs, initiate community-dependent recovery.

1. Introduction

Upland and mountainous areas of Northern Europe provide a wide variety of ecosystem services ranging from provisioning (water), supporting (soil formation, carbon sequestration, oxygen production) and cultural services (aesthetic and recreational values; Ramchunder et al., 2009). However, these ecosystems have been demonstrated to be highly-vulnerable to environmental and land-use change (Clutterbuck et al., 2020). In this context, land-use change caused mainly by land abandonment is a contentious issue in these areas (Renwick et al., 2013). Land abandonment must, however, be considered a dynamic process, which is influenced by a complex range of socio-economic and environmental drivers that vary over time and space (Ustaoglu and Collier,

2018). The effects of land abandonment on plant communities and ecosystem services can be either positive or negative, depending on the conservation status of the area and the environmental drivers present (Ustaoglu and Collier, 2018). Currently, it remains unclear whether upland plant communities will respond positively or negatively in the face of a combination of further land abandonment/land-use-change inevitably associated with climate change (Alday et al., 2021). This is particularly important where change within plant communities is slow, for example, in the British uplands where a combination of high rainfall and cold temperatures prevail (Heal and Smith, 1978). This makes it difficult to predict the long-term effects of management or restoration efforts. Recently, there has been renewed interest in the management of upland vegetation in the United Kingdom, particularly with respect to

maintaining their conservation value and ecosystem services they provide (Renwick et al., 2013).

Many parts of the British uplands are grazed by sheep, but their densities have fluctuated markedly over the last 70 years (Anderson and Yalden, 1981; Ball et al., 1982). In the future, this sheep grazing pressure may be removed completely from some parts of the uplands as part of simple (re)-wilding schemes (Monbiot, 2013; Sandom et al., 2013) or reductions in agricultural practices (Ustaoglu and Collier, 2018). Long-term, top-down effects from herbivores have strong effects on plant communities and biomass dynamics, for example, spatial variation in herbivore distribution is well known to affect both the species composition and structure of plant communities within the landscape (Kok et al., 2020). However, there is a lack of knowledge about the long-term effects of grazing abandonment in upland plant communities, especially from an ecosystem conservation perspective.

One of the most important issues facing environmental monitoring is to be able to assess change accurately and ascribe it to environmental drivers (Millennium Ecosystem Assessment, 2005). Recent longitudinal monitoring studies in upland areas (Britton et al., 2017; Mitchell et al., 2017, 2018; Ross et al., 2012) has shown that upland vegetation composition has been influenced by a range of environmental factors, high grazing pressures and high atmospheric SO_2 and NOx concentrations. From these studies it appears that there are different short- to medium-term responses to environmental drivers between (1) plant communities, and (2) taxonomic groups, especially bryophytes and lichens (Milligan et al., 2016). However, in recent years there is evidence that the SO_2 and NO_x depositions have declined in these areas as a result of reduced emissions (RoTAP, 2012; Rose at al., 2016; Mitchell et al., 2017). At the same time, livestock grazing has been also reduced in some upland areas (Alday et al 2021). Therefore, for management based on conservation principles it would be informative to assess changes in upland plant communities over a longer time-scale, testing whether the temporal pattern of vegetation change is conditioned by local grazing or by large-scale trends produced by reductions in SO_2 and NO_x depositions (i.e. management vs. landscape environmental drivers). Here, we report long-term responses (48–63 years) of British upland plant communities using different long-term grazing experiments (Alday et al., 2021).

Recent studies have shown that information derived for short-term studies can be misleading with unforeseen consequences when viewed in the light of longer-term data (Chen et al., 2020). As a result, many studies are now highlighting that any conservation management should be validated using evidence derived from long-term, manipulative experiments (Stewart et al., 2005; Sutherland and Wordley, 2018). So far, long-term experiments analyzing vegetation changes due to combined long-term grazing and environmental changes are sparse (Zhumanova et al., 2021). In this context, considerable research efforts have been devoted to understand and predict the long-term mechanisms of change in upland vegetation at Moor House National Nature Reserve in the North Pennines of England (Milligan et al., 2016, 2018). Here, the vegetation comprises a mosaic of common upland plant communities dominated by dwarf-shrubs, grasses or sedges (Averis et al., 2004), occurring on soil types ranging from deep blanket peat through to brown-earth soils, and subject to different sheep grazing pressures (Milligan et al., 2016). A series of twelve long-term experimental sites each with a sheep-grazed plot and a comparable ungrazed one (surrounded by an exclosure) were started within four main plant communities between 1953 and 1967, the community types have been recently described as: (1) high-level grassland, (2) intermediate grassland, (3) blanket bog and (4) high-level bog (Milligan et al., 2016, 2018; Alday et al., 2021).

Our objective was to describe the long-term changes in species richness and abundance of main taxonomic groups, i.e. vascular plants, mosses, liverworts and lichens in these four plant community types comparing grazed versus ungrazed plots. This provided a generalized description of change in these facets of community dynamics to test the following long-term hypotheses:

1. In the grazing treatment there will be a post-2000 recovery of species richness and abundance of all four taxonomic groups, as a result of recent reductions in sheep grazing and pollutant loads (Alday et al., 2021). A balanced grazing pressure tends to maintain a more diverse plant species diversity (WallisdeVries et al., 1998; Lawrence et al., 2019).
2. In the ungrazed treatments where sheep-grazing has been removed for a long-time, species richness will have been reduced and any recovery after 2000 will be slower than in the grazed treatments.
3. In each of the four plant communities, the same diversity and abundance responses would occur for hypotheses 1 and 2, suggesting that upland plant communities will respond similarly to management/grazing drivers and large scale-trends such as nutrient deposition.

Thus, we evaluated the long-term effectiveness of sheep grazing for maintaining the original communities and the removal of livestock in (re)-wilding schemes as part of an ecological restoration strategy. These results will help define practices that prevent future negative impacts on these upland communities Based on these findings, we put forward recommendations for effective conservation and management of British upland plant communities and other areas of northern Europe where livestock removal may be implemented (Renwick et al., 2013).

2. Methods

2.1. Study sites

The experimental sites are located in the Moor House-Upper Teesdale National Nature Reserve in northern England (UK), where it was possible to conduct long-term manipulative studies (Supplementary materials, Table S1, Fig. S1). Between 1953 and 1967 a series of grazing exclosure-experiments were set up at 12 sites throughout the 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 towards the neutral end of the soil spectrum, to grassland dominated by *Festuca ovina* or *Nardus stricta*, and towards vegetation dominated by rushes (*Juncus squarrosus)*, and cotton-grass (*Eriophorum* spp.) or vegetation dominated by dwarf shrubs (*Calluna vulgaris, Erica tetralix* or *Empetrum nigrum*) - on blanket bog (least productive).

2.2. Experimental design

When these sheep exclusion studies were designed and set up, most of the 12 sites were considered independent, unreplicated experiments, with two plots in each; i.e. one was fenced to exclude sheep and the other was left open to allow free-range sheep grazing (Marrs et al., 1986). However, these 12 sites can be considered as four structured-experiments based on (i) the vegetation type present at each site, (ii) the length of time since the exclosure has been present and (iii) the sampling history (Supplementary materials Table S1, Milligan et al., 2016; Alday et al., 2021). The four groups were: (1) high-level grasslands starting in 1955/6 on the more-base-rich soils with three replicate sites, at the start, one site was mainly a mixture of *Agrostis capillaris* and *Festuca ovina* (National Vegetation Class (NVC) = CG10; for NVC descriptions see Rodwell (1991), 1992), and the other two were dominated by *Festuca ovina* (NVC class = H19a); (2) intermediate grasslands starting in 1967 with two replicate sites, one site dominated by *Eriophorum vaginatum* (NVC class = U6b) the other *Nardus stricta* (NVC class = U5); (3) blanket bog starting between 1953 and 1955 with *Calluna vulgaris* and *Eriophorum vaginatum as* the dominant species with five replicate sites (NVC class = M19), and (4) high-level bog starting in 1966 with two replicate sites; these two sites (NVC class = M20b) were dominated by *Eriophorum vaginatum* but one (Silverband) had been subject to severe erosion (Supplementary materials, Table S1).

At all sites, the point-quadrat method was used to measure the abundance of vascular plant, bryophyte and lichen species. In each plot the point-quadrat frame was positioned using a permanently-marked reference system with the sampling locations selected randomly at the outset. The detailed methodology has been published previously (see: Marrs et al., 1986; Milligan et al., 2016; Alday et al., 2021) and summarized in Supplementary materials, Appendix I.

We identified four major plant taxonomic groups; vascular plants, mosses, liverworts and lichens. The reason for considering these taxonomic groups was included in Hypotheses 1 and 2, i.e. to assess whether responses, recovery or lack of recovery, were evenly distributed among the different groups to suggest indicator groups that might prove valuable in future monitoring activities (Milligan et al., 2016). At the same time, this taxonomic level is recognized easily by non-specialists in the field.

With respect to grazing treatments, here, we define the sheep-grazing treatment as the "control" since it is the "business-as-usual" condition and the removal of sheep grazing as the "intervention" treatment. This is important because the sheep grazing pressure has changed over time and it is known to vary across the different plant communities. Before 1972, it was estimated that there were 15,400 sheep on the entire grazing unit during the summer months, i.e., 4.4 sheep ha^{-1} with an available grazing area of approximately 3500 ha (Milligan et al., 2016). In 1972, sheep numbers were halved to 7000 sheep or 2 sheep ha^{-1} after the formalization of grazing rights under the Commons Registration Act (1965). Following the Foot-and-Mouth outbreak in Great Britain in 2001 there was a further reduction to ca 1 sheep ha^{-1} as some of the common rights-to-graze were bought out by the landowners to hopefully improve conservation value. There is also a variation in grazing pressure between communities. The best grazing occurs on the high-level grasslands on brown-earth soils and it is much lower on the blanket bogs (Rawes and Welch, 1966; 1969), observations similar to those reported by Crawley et al. (2021) on St Kilda. Regarding the spatial distribution of the grazing pattern, sheep density was estimated to be lowest on blanket bog and greatest on the high-level grasslands, 0.25 and 5.8 sheep ha^{-1} respectively, a 23.2-fold difference (Supplementary Materials Table S1, Rawes and Welch, 1969).

2.3. Data preparation and analysis

All data preparation and analyses were performed in the R Statistical Environment (v.3.6.3, R Core Team, 2020) using the 'vegan' package (Oksanen et al., 2019) to determine species richness determination and the 'mgcv' package (Wood, 2017) to fit Generalized Additive Mixed Models (GAMM, Wood, 2017).

Within each plot measures of abundance for each species in the ten randomly-selected positions (each scored 0–10 based on the number of point-quadrat hits) were calculated. From these data, five response variables were derived: species richness (number of species per sampling point), and the summed total (abundance index) of all species within the four main taxonomic groups considered, i.e., vascular plants, mosses, liverworts and lichens.

For each of the four communities, the relationship of the five variables with respect to treatment and elapsed time were investigated with GAMMs (GAMM, Wood, 2017). This approach allowed for the fitting on non-linear patterns of each dependent variable with respect to elapsed time. As the experiments started at different times, the time variable (year) was transformed into "elapsed time", defined by Year 0 set to 1950 throughout, thus ensuring that all graphical outputs were displayed on the same timescale. Here, each of the five dependent variables was fitted with respect to elapsed time by site, i.e. fitting a separate smooth for each level of site factor. In addition, the site and grazing treatment variables were included as fixed parametric factors in each model to account for overall mean differences. The random factors in each model were elapsed time nested within sites by grazing treatment and elapsed time by grazing treatment structures were included to

account for hierarchical spatial and temporal correlation. Moreover, an autoregressive AR(1) structure was included to correct for error correlation in the time series (temporal random structure). Four knots were used for the elapsed time regression splines in order to avoid over-fitting the data, while still allow for unimodal or slightly more complex model fits (Wood, 2017). The results for all analyses are presented in Supplementary Table S2, and all responses discussed are significant ($P < 0.01$) unless explicitly stated).

Only two replicates were available for the intermediate grasslands and the high-level bogs; this is a function of history. We include the results from these analyses for completeness and because they will provide important information for land managers. However, we expect the models for these communities to be less reliable, and with greater confidence intervals than the high-level grasslands (n = 3) and the blanket bog (n = 5).

In the end, all the models developed and the collected graphical results were complex and extensive and we wanted to provide a coherent, and easy-to-understand summary that would be meaningful for conservation managers. Therefore, to test our hypotheses, we also evaluated each response curve for the "business-as-usual" grazed treatments using two simple criteria, i.e.:

1. was there evidence of an increase in the response curve at the end of the sample period, i.e., recovery after 2000 recovery, based on yes/no?
2. was the final value greater than the baseline value, i.e., was there an overall improvement irrespective of the fluctuations in the middle of the study period; this was based on a three-point scale, +ve increase, no effect, and -ve reduction.

The results of the summarization of the model information are reported in Table 1. This facilitates the interpretation of the results presented earlier.

3. Results

3.1. Change in overall species richness

In the high-level grasslands the grazed treatment showed significant differences between sites through time ($P < 0.02$) with the Little Dun Fell trajectory being relatively stable in richness through time (ca 6 species), albeit with fluctuations. Hard Hill richness was greater than Little Dun Fell (ca 8 species) but fluctuated in a similar manner, increasing after year 52 to the same levels as Knock Fell (ca 10 species). Finally, Knock Fell showed a dip around year 50 (lower than 10 species) followed by a recovery (Fig. 1). The ungrazed treatment also showed a significant temporal response ($P < 0.001$) with a very large species reduction at all three sites by year 30 followed by some recovery, with the Hard Hill and Little Dun Fell plots converging at ca 10 species (Fig. 1).

For the intermediate grasslands, species richness trends were slightly different between grazed and ungrazed plots ($P < 0.001$). In the grazed plots, species richness initially increased in both treatments ($P < 0.001$, Fig. 1). At Cottage Hill, this trend continued to year 45 after which there was a decline (ca 9 species), whereas species richness at River Tees peaked at year 30 (ca 13 species), after which there was a further decline and subsequent recovery (ca 9 species, Fig. 1). In the ungrazed plots, trends were also different between both sites ($P < 0.001$, Fig. 1). At Cottage Hill, there were fluctuations in species richness but it declined rapidly after year 50 down to ca 6 species, whereas at River Tees, species richness stabilized ca 5 species throughout (Fig. 1). However, in the ungrazed plots the initial differences in species richness were eliminated at year 20 (overlapping confidence intervals, Fig. 1).

The blanket bog sites had similar richness responses in both grazed and ungrazed treatments ($P > 0.05$), with the only differences in species richness reflecting to some extent the degree of site elevation. The
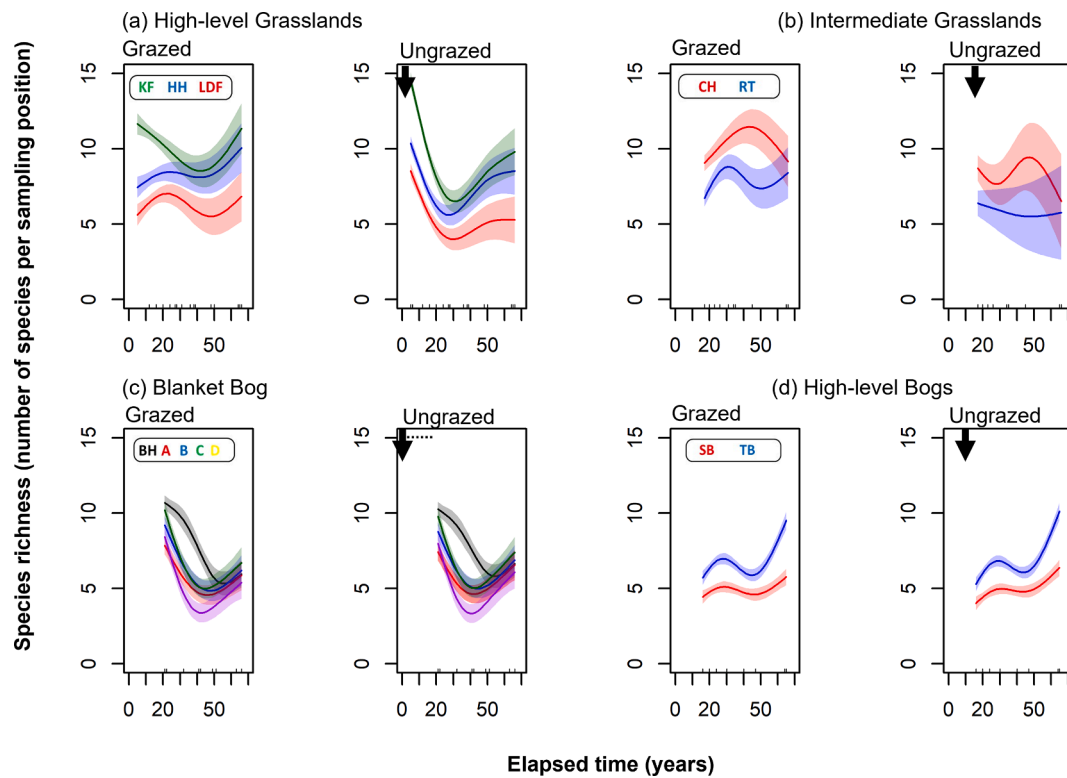
Fig. 1. Modelled responses (GAMM, ±95%CL) of species richness in grazed and ungrazed plots in four plant communities, each with replicate sites, over time at Moor House NNR in the northern Pennines, UK. For the two grassland communities and high-level bog, the bold arrows indicate both when the exclosures were erected and when recording began; for the blanket bog the bold arrow indicates the beginning of the record and the dotted line indicates the time since the exclosures were erected. Key to site codes (replicates): High-level grasslands: HH = Hard Hill, KF = Knock Fell, LDF = Little Dun Fell; Intermediate Grasslands; CH = Cottage Hill. RT = River Tees; Blanket Bog: BH = Bog Hill, A, B, C, and D (letters refer to blocks within the Hard Hill Burning Experiment); High-level bog: SB = Silverband, TB = Troutbeck Head. For details of the statistical analyses see Supplementary Materials: Table S2.

greatest species richness was at the lowest elevation (Bog Hill, ca 11 species) and the least at the highest elevation site (Block D, ca 8 species). In both treatments, and at all five sites, species richness showed similar trends over time (P < 0.001) with a decline until year 40 at Hard Hill and year 50 at Bog Hill (close to 5 species in both sites), followed by a slight recovery on species richness in both experiments (reaching 7 species, Fig. 1).

The high-level bogs showed significant site differences (P < 0.001; Fig. 1). There was no significant effect of grazing treatment or its interaction with sites on species richness.

(P > 0.05). Both sites showed a sinusoidal response in species richness over time (P < 0.001), but with Troutbeck Head having a consistently greater species richness than the Silverband site (ca 8 vs 5 species). Both sites showed a pronounced increase after year 40, which was particularly pronounced at Troutbeck Head, reaching up to 10 species (Fig. 1).

3.2. Changes in vascular plant abundance

Vascular plant abundance values in the high-level grasslands showed a site effect.

over time in both grazed and ungrazed plots (P < 0.001), especially early in the time-period. However, there was some convergence of abundance values after year 30 (P < 0.001, Fig. 2). In the grazed plots, Knock Fell showed an initial increase in abundance and a sinusoidal response through time; Little Dun Fell showed a similar abundance increase, sinusoidal response and a sharp increase after year 50, and at Hard Hill there was a continuous increase over the study period (Fig. 2). Abundance responses were similar in the ungrazed plots albeit at slightly greater values. The only difference was a marked abundance reduction at Hard Hill after year 45.

In the intermediate grasslands, vascular plant abundance was approximately the same in both grazing treatments at the beginning of the study (ca 25, Fig. 2). Thereafter, there was time × site interaction (P < 0.001) with a similar initial increase over time in both sites and grazing treatments (maximum ca 33–35), followed by a substantial decrease in abundance values at both sites (minimum grazed ca 18 River Tees vs. 25 Cottage Hill, minimum ungrazed ca 10 River Tees vs. 18 Cottage Hill), which was faster and more evident at River Tees (Fig. 2).

In the blanket bog community, there was a clear site effect (P < 0.001) between Bog Hill with a greater vascular plant abundance score (>20) than the four Hard Hill plots which showed little difference between them (<10, Fig. 2). This site effect remained between the two grazing treatments, showing little change in abundance in the Hard Hill sites, but a slight increase in abundance over time at Bog Hill (P < 0.001, Fig. 2), especially after year 40 (Fig. 2).

Finally, in the high-level bog community, although there was a site effect (P < 0.001) on vascular plant abundance in both grazing treatments, followed a similar upward trend up to year 30, followed by a decline and subsequent recovery (P < 0.001, Fig. 2). At the end of the study period, both grazing treatments at Troutbeck Head and the ungrazed treatment at Silverband had greater vascular plant abundance values than at the beginning, while the grazed treatment at Silverband was slightly lower (Fig. 2).

3.3. Change in moss abundance

The abundance of mosses in the high-level grasslands showed completely contrasting responses. (Fig. 3). In the grazed treatments at Hard Hill and Knock Fell moss abundance declined to year 30 and then recovered to values slightly above baseline (P < 0.001). In contrast, Little Dun Fell showed a completely different response with an increase
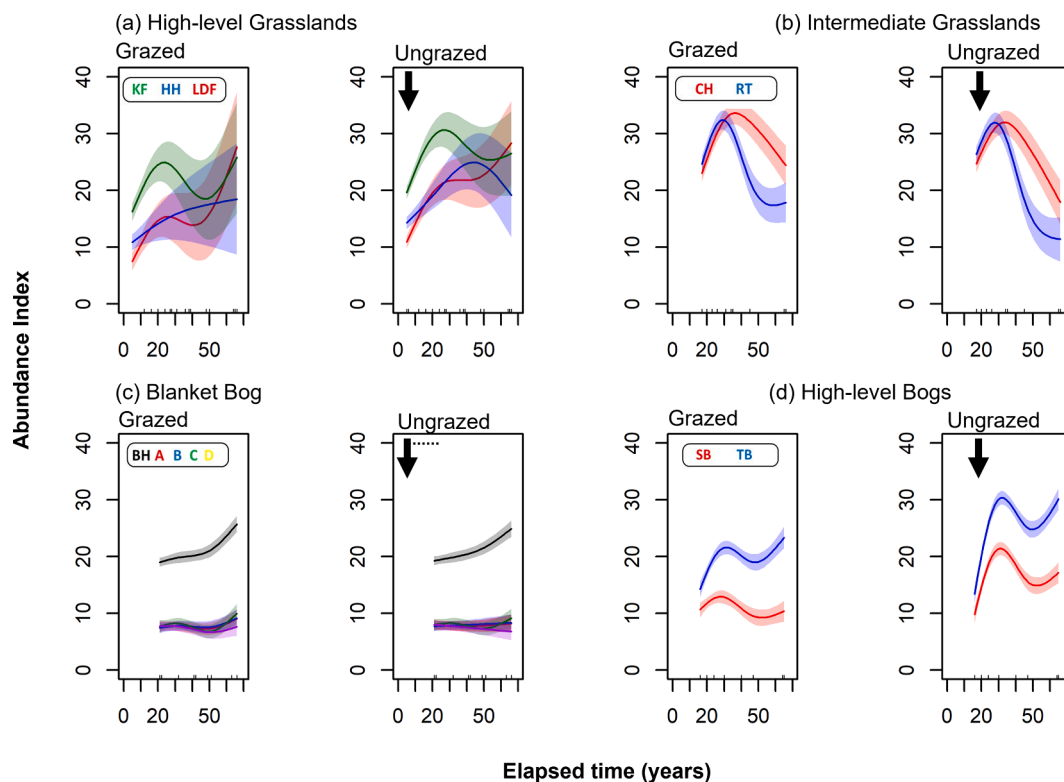
Fig. 2. Modelled responses (GAMM, ±95%CL) of vascular plant abundance in grazed and ungrazed plots in four plant communities, each with replicate sites, over time at Moor House NNR in the northern Pennines, UK. For the two grassland communities and high-level bog, the bold arrows indicate both when the exclosures were erected and when recording began; for the blanket bog the bold arrow indicates the beginning of the record and the dotted line indicates the time since the exclosures were erected. Key to site codes (replicates): High-level grasslands: HH = Hard Hill, KF = Knock Fell, LDF = Little Dun Fell; Intermediate Grasslands; CH = Cottage Hill. RT = River Tees; Blanket Bog: BH = Bog Hill, A, B, C, and D (letters refer to blocks within the Hard Hill Burning Experiment); High-level bog: SB = Silverband, TB = Troutbeck Head. For details of the statistical analyses see Supplementary Materials: Table S2.

to an asymptote at year 30 (ca 4, P < 0.001, Fig. 3). In the ungrazed plots, the responses in moss abundance were similar among the three sites over time (P < 0.01, Fig. 3), with a sharp decline to year 30 followed by a steep recovery to values above baseline moss abundance values. In the intermediate grasslands, abundance trends of the grazed and ungrazed mosses plots mainly showed an increasing abundance over time in both sites (P < 0.001, Fig. 3), albeit with greater fluctuations at River Tees.

In the blanket bog community, the mosses results were similar to those for vascular plants with Bog Hill having a significantly greater abundance of mosses than all four Hard Hill sites (P < 0.001), which showed no significant differences between them. Moss abundance in grazed and ungrazed plots was relatively stable over time at Bog Hill (grazed ca 8 vs ungrazed ca 9). In contrast, at Hard Hill, there was a significant increase in moss abundance increase after year 40 at all four sites (P < 0.001, Fig. 3).

Finally, in the high-level bog community, moss abundance was close to zero (Fig. 3). Interestingly, moss abundance increases over time in both grazing treatments (P < 0.001), with a smaller increase in Silverband compared to Troutbeck Head (Fig. 3).

3.4. Change in liverwort abundance

In the high-level grassland, there were no significant differences in liverwort abundance between sites or treatments, but there were significant temporal interactions among grazing treatments (P < 0.001, Fig. 4). In both grazing treatments, liverwort abundance was low (<5) and decreased over time in both grazing treatments time (values close to 1, Fig. 4).

In the Intermediate grasslands, there were significant differences in

liverwort abundance between sites (P < 0.001) with greater abundance at Cottage Hill than at River Tees throughout the study (Fig. 4). However, the trend at River Tees was stable with values less.

than 1, whereas at Cottage Hill liverwort abundance fluctuated between years 20 and 50 and then declines to values similar to those at River Tees (Fig. 4).

Liverwort abundance in the blanket bog showed a significant temporal decline over time at all sites (P < 0.001, Fig. 4), with Bog Hill starting at a greater value in both grazing treatments. Both the grazed and ungrazed plots showed a similar trend with a significant decline to year 40, after which there was some stabilization around a value of 1 (Fig. 4).

Liverwort abundance in the high-level bogs showed that Troutbeck Head consistently had greater liverwort abundance than Silverband at the beginning and end of the study (P < 0.01, Fig. 4). At both sites and in both grazing treatments, liverwort abundance was fairly stable until year 50, after which there was a slight increase (Fig. 4).

3.5. Change in lichen abundance

Lichens were not detected consistently in the intermediate grasslands and fits were generally poor for the other communities. There were also no significant differences detected between the two grazing treatments (P > 0.05). However, there was a consistent decline in lichen abundance over time in the high-level grasslands, blanket bog and high-level bogs (P < 0.001, Fig. 5), with no signs of recovery at the end of the study, and most communities approaching zero.
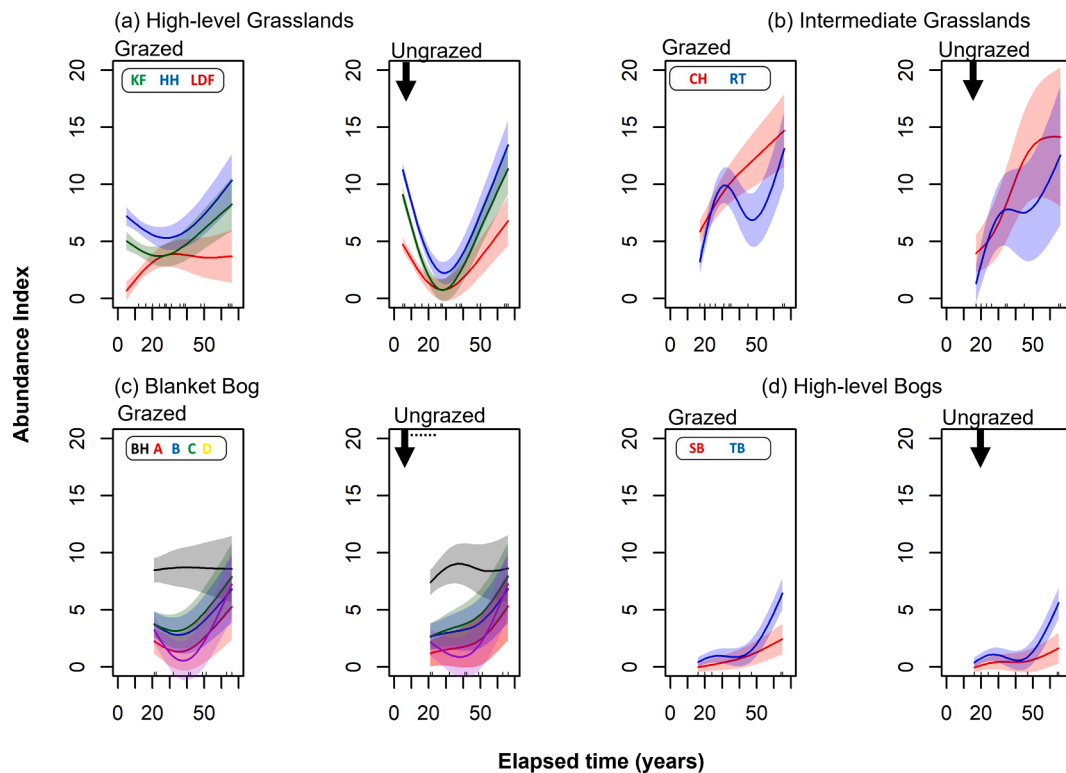
Fig. 3. Modelled responses (GAMM, ±95%CL) of moss abundance in grazed and ungrazed plots in four plant communities, each with replicate sites, over time at Moor House NNR in the northern Pennines, UK. For the two grassland communities and high-level bog, the bold arrows indicate both when the exclosures were erected and when recording began; for the blanket bog the bold arrow indicates the beginning of the record and the dotted line indicates the time since the exclosures were erected. Key to site codes (replicates): High-level grasslands: HH = Hard Hill, KF = Knock Fell, LDF = Little Dun Fell; Intermediate Grasslands; CH = Cottage Hill. RT = River Tees; Blanket Bog: BH = Bog Hill, A, B, C, and D (letters refer to blocks within the Hard Hill Burning Experiment); High-level bog: SB = Silverband, TB = Troutbeck Head. For details of the statistical analyses see Supplementary Materials: Table S2.

3.6. Summary of responses of conservation interest

In Table 1 several important results can be observed in the "business-as-usual" grazed treatment. After 2000, species richness increased at 11 out of the 12 sites, with Cottage Hill being the exception. Moreover, all of the high-level grasslands, and high-level bog sites along with River Tees had a greater species richness at the end of the time series than at the beginning of the sampling. Only, Cottage Hill and all of the Blanket bog sites had a lower species richness. It was also clear that there were substantive differences in abundance responses between the four taxonomic categories and community types. There was an increase in both vascular plants and mosses in 10 out of the 12 sites after 2000 but the intermediate grasslands showed no positive effect for vascular plants and Little Dun Fell and Bog Hill showing none for mosses.

However, there were differences in final abundance values compared to baseline positions. For vascular plants, the three high-level grasslands, Bog Hill and Troutbeck Head showed an increase in abundance relative to the baseline, and Silverband remained about the same value; all other sites were below their baseline values. For mosses, the result was much more positive: all sites had increased abundance above their baseline values, except for Bog Hill where values remained similar throughout. Liverwort abundance also increased after 2000 increase in all three high-level grasslands, both intermediate grasslands and both high-level bogs, but not in the blanket bogs. Only in the two high-level bogs was abundance greater at the end compared to the baseline. For lichens, there was no increase in abundance after 2000, and at all sites abundance was lower at the end of the experiment than at the start.

Interestingly, while there were some significant differences between the two grazing treatments in their temporal trajectories, in reality, many of the ungrazed treatment responses mirrored those in their respective grazing treatment to some degree (Figs. 1-5).

4. Discussion

In this work, we analyzed the long-term dynamics (48–63 years) of plant species richness and abundance in four plant communities typical of the British uplands; i.e. high-level grasslands, intermediate grasslands, blanket bog and high-level *Eriophorum*-dominated bog communities. In each community, we compared the effects of two grazing pressures, namely free-range sheep grazing versus no grazing pressure for species richness and abundance of four taxonomic groups that can be used as potential indicators to inform conservation managers (Milligan et al., 2016). Interestingly, our results showed that the first hypothesis, related to the recovery of species richness and abundance in the grazed plots was partially confirmed as species richness and abundance recovered to some degree at most sites after 2000, although lichens showed no trend. In contrast, our second hypothesis which related to a slower recovery of species richness and abundance in plots where sheep grazing was removed, could not be confirmed because there was no clear evidence to suggest that the removal of sheep grazing significantly altered the metrics of the grazed plots. Certainly, trends in the diversity and abundance trajectories were not identical in the grazed and ungrazed plots, but they were not markedly different either. Thus, considering that similar trends were found in grazed and ungrazed plots in each plant community, it suggests that internal community dynamics may overcome the effects of grazing. It also appears that landscape-level trends, such as reductions in nutrient deposition (Alday et al., 2021) influence community-dependent recovery.

4.1. Is there evidence of post-2000 recovery in the grazed plots? (Hypothesis 1)

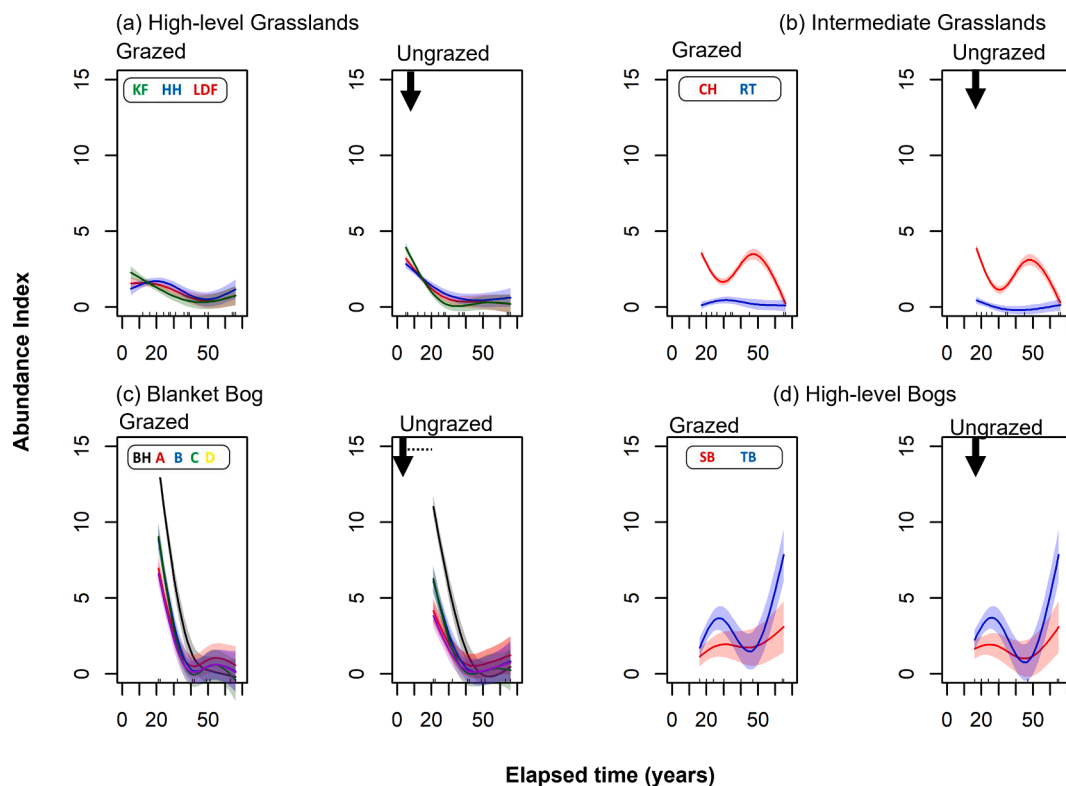Longitudinal monitoring studies have shown that species diversity

Fig. 4. Modelled responses (GAMM, ±95%CL) of liverwort abundance in grazed and ungrazed plots in four plant communities, each with replicate sites, over time at Moor House NNR in the northern Pennines, UK. For the two grassland communities and high-level bog, the bold arrows indicate both when the exclosures were erected and when recording began; for the blanket bog the bold arrow indicates the beginning of the record and the dotted line indicates the time since the exclosures were erected. Key to site codes (replicates): High-level grasslands: HH = Hard Hill, KF = Knock Fell, LDF = Little Dun Fell; Intermediate Grasslands; CH = Cottage Hill. RT = River Tees; Blanket Bog: BH = Bog Hill, A, B, C, and D (letters refer to blocks within the Hard Hill Burning Experiment); High-level bog: SB = Silverband, TB = Troutbeck Head. For details of the statistical analyses see Supplementary Materials: Table S2.

declined in the latter part of the twentieth century (Britton et al., 2017; Ross et al., 2012; Mitchell et al., 2017, although there are recent signs of reversal (Mitchell et al., 2017, 2018; Rose et al., 2016). For example, Mitchell et al. (2018) in a repeated study of vegetation plots across Scotland showed that calcareous, mesotrophic, *Nardus*- and wet-grasslands plots are recovering from the peak of SO_2 deposition in the 1970 s. Our results on grazed plots were consistent with these findings, with at least some recovery of plant species diversity at most sites and in most plant communities after 2000. For example, on grazed plots species richness recovered in 11 out of 12 sites, and abundance recovered for vascular plants in 10 out of 12 sites, mosses at 10 out of 12 sites and liverworts at 7 out of 12 sites (Table 1). While these results are positive for conservation, they are only part of the story. Defining recovery as final values being greater than the baseline values, the results are mixed with the best recovery results being found for moss abundance (11/12 sites) followed by species richness (6/12 sites), abundance of vascular plants (5/12 sites) and liverworts (2/12 sites). Overall, these results indicate that vegetation richness and abundance on grazed plots are recovering from past management and environmental impacts, albeit slowly. It appears the initial effects of grazing reported by Rawes (1981, 1983) have disappeared over time (Alday et al 2021).

Unfortunately, no recovery was observed for lichens in any experiment, or site, and only a slight recovery above baseline values for liverworts. These results are consistent with Mitchell et al. (2018), who found no recovery of lichens in acid or *Lolium*-dominated grasslands in a long-term vegetation monitoring program after nutrient deposition was reduced. Similar results were also found in moorland and alpine-heaths where specialist liverwort and lichen species continued to decline (Britton et al., 2017, Britton et al., 2018). This poor recovery of liverworts and lichens suggests that special attention should be given to

develop intervention approaches to restore liverworts, and especially lichens in these communities.

The evidence that there is a sequence of recovery phases in which species richness, vascular plants and mosses recover faster than liverworts and lichens, with lichens showing almost no detectable recovery, is important for planning management programs and restoration efforts (Marrs et al. 2020). In this context, moss cover is known to be affected heavily by atmospheric pollution, especially SO_2 (Caporn and Emmett, 2009; Tallis, 1998) and NO_x (Britton et al., 2018) so it is encouraging that overall moss abundance has improved in most communities here. Information on mosses and liverworts is collected rarely, but it appears that they are susceptible to a similar suite of environmental pressures as lichens, including climate change (Evju and Bruteig, 2013, de Guevara et al., 2018; Colesie et al., 2018), grazing and trampling pressures and atmospheric pollutants (Britton and Fisher, 2010; Evju and Bruteig, 2013; Heggenes, et al., 2017), all of which may be affected by increasing vegetation biomass (Chagnon and Boudreau 2019). Interestingly our results for mosses and liverworts lead to similar conclusions to those of Outhwaite et al. (2020), who in a nationwide assessment of presence-only records of bryophytes (mosses and liverworts) in the UK showed a slight decline between 1970 and 2000 followed by a recovery to 1970 values in 2000 with a subsequent increase through to 2013. Thus, it appears mosses and liverworts can recover naturally if deleterious environmental and management influences are removed or reduced. However, ecological restoration programs could be used to accelerate this recovery (Letendre et al., 2019).

In contrast, our results for lichens in grazed plots show completely opposite trends to those of Outhwaite et al. (2020); they showed a steady increase between 1970 and 2000 followed by a slight decrease to a more or less stable high value, whereas in our case no trends were observed.
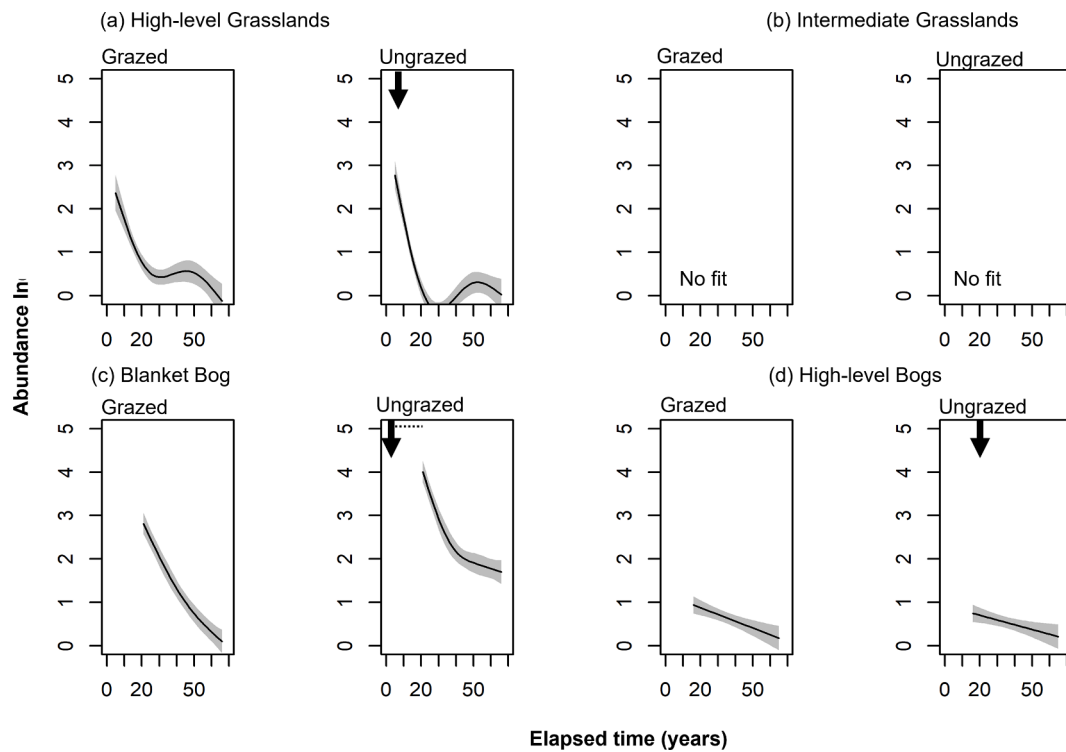
Fig. 5. Modelled responses (GAMM, ±95%CL) of lichen abundance in grazed and ungrazed plots in four plant communities, each with replicate sites, over time at Moor House NNR in the northern Pennines, UK. In this figure the replicated sites did not show significant differences so pooled responses are shown. For the two grassland communities and high-level bog, the bold arrows indicate both when the exclosures were erected and when recording began; for the blanket bog the bold arrow indicates the beginning of the record and the dotted line indicates the time since the exclosures were erected. For details of the statistical analyses see Supplementary Materials: Table S2.

Table 1
Summary of responses derived from graphical and statistical results of the grazed "business-as-usual" treatment. Two metrics were derived for each of the five biodiversity variables at each site: (a) evidence of an increase in response after 2000, scored "✓" for a positive response and "X" for a negative or no response, and (b) evidence that the variable was greater at the end of the monitoring period compared to the baseline, it scored "+" if the endpoint > baseline, 0 if the endpoint ≈ baseline, and "-" if the endpoint < baseline. Sites that showed an increase after 2000 and a greater endpoint relative to their baseline are shaded grey.

Plant community	Site	Species richness		Vascular plants		Mosses		Liverworts		Lichens	
		Post-2000 recovery	Endpoint position relative to baseline	Post-2000 recovery	Endpoint position relative to baseline	Post-2000 recovery	Endpoint position relative to baseline	Post-2000 recovery	Endpoint position relative to baseline	Post-2000 recovery	Endpoint position relative to baseline
High-level grasslands	Hard Hill	✓	+	✓	+	✓	+	✓	–	X	–
	Little Dun Fell	✓	+	✓	+	X	+	✓	–	X	–
	Knock Fell	✓	+	✓	+	✓	+	✓	–	X	–
Intermediate grasslands	Cottage Hill	X	–	X	–	✓	+	✓	–	X	–
	River Tees	✓	+	X	–	✓	+	✓	–	X	–
Blanket Bog	Bog Hill	✓	–	✓	+	X	0	X	–	X	–
	Hard Hill-A	✓	–	✓	–	✓	+	X	–	X	–
	Hard Hill-B	✓	–	✓	–	✓	+	X	–	X	–
	Hard Hill-C	✓	–	✓	–	✓	+	X	–	X	–
	Hard Hill D	✓	–	✓	–	✓	+	X	–	X	–
High-level Bog	Silverband	✓	+	✓	0	✓	+	✓	+	X	–
	Troutbeck Head	✓	+	✓	+		+	✓	+	X	–

We suspect that changes in lichens are highly-dependent, on plot size and they are influenced by changes in other members of the plant communities and the environmental pressures to which they are exposed. It is also possible that the decline in lichens is influenced by an increase in vascular plants, which make up most of the structure of these communities (Alday et al., 2021). Competition with vascular plants has been cited as a possible reason for the decline in lichen species diversity, perhaps due to elevated N deposition (Wieder et al. 2019). In any case, research to restore liverworts and lichens in these communities appears to be a priority, but little is known about how to increase their species richness or abundance.

4.2. Recovery will be slower where sheep-grazing is removed (Hypothesis 2)

In testing our second hypothesis, relating a slower recovery of diversity and abundance in plots where sheep-grazing was removed, our results showed that the long-term trends in the ungrazed treatments often showed many similarities in the general direction and shape of the response compared to their grazed comparators. It appears that there was no clear evidence that the removal of sheep grazing made much difference to the metrics in the ungrazed plots without a marked decrease in recovery. Thus, there was no evidence to accept the second hypothesis based on the metrics assessed here. Certainly, the trajectories in the grazed and ungrazed plots were not very different and the long-term recovery rates were similar. These results are consistent with the observations of Pakeman and Fielding (2021) where they did not observe a clear separation of plant community responses when considering plant functional attributes in a long-term, large-scale grazing experiment in upland Scotland. It is, however, true that this approach, which is useful for policy makers and managers in devising landscape management plans, hides much detail at the level of individual species and functional groups (Alday et al., 2021).

We monitored the change of a reduced "business-as-usual" grazing pressure enforced by management decisions and improvements in atmospheric pollutants deposited at the site. Overall, however, the results indicate the vegetation in ungrazed plots is responding positively over time with some taxonomic groups and richness recovering. These changes may be due to a reduction in pollutant deposition levels (Tipping et al., 2019), and possibly also to recent temperature increases (Monteith et al. 2016). In any case, further studies are needed to unravel the true significance of each of these landscape drivers influencing long-term plant community responses to prevent future negative impacts on upland plant communities.

It would be expected that changes in weather would play at least some part in controlling species dynamics. Unfortunately, we only have weather records available only at the Moor House catchment and not for individual sites or at temporal scales that link to our sampling dates, making inclusion of weather variables in our models difficult. However, annual temperatures have increased over the period of our study from 4.6 to 6.4 °C between 1930 and 2006 (Holden and Rose, 2011) and there was a linear increase in both mean annual temperature (0.002 °C yr^{-1}) and rainfall (0.183 mm yr^{-2}) between 1993 and 2012 (Monteith et al. 2016). Over the same period there was also a reduction in most element precipitation inputs through time (Monteith et al. 2016). Indeed, between 1993 and 2015 recent results from four Long-Term Monitoring Sites (including Moor House) suggest that there has been a shift from anthropogenic sources of elements in rainfall to ones derived naturally (e.g. sea salt) (Tso et al., 2022). So results from Moor House appear to follow these national trends, in that the conditions are getting warmer, possibly wetter and with reduced pollutant inputs.

4.3. Do the same responses for hypotheses 1 and 2 occur in each of the four plant communities (Hypothesis 3)?

The third hypothesis that the four plant community types respond in a similar manner with respect to species richness and species abundance over the long-term in response to management/grazing drivers and some large scale-trends such as nutrient deposition, is partially accepted. Overall, there were similar trends in grazed and ungrazed plots within each plant community for the various metrics analyzed, although there were differences in long-term trends over time among the plant communities. Clearly, the different communities did not respond in parallel, highlighting at least some part of the differences in temporal response between communities (Britton et al. 2017; Milligan et al., 2016, 2018). These results suggest that some within-community processes can overcome the impacts of management-grazing drivers, but not the large-scale landscape trends such as those caused by a reduction of nutrient

deposition (Alday et al. 2021), resulting in different between-community responses.

In the grazed plots, the main trends differed significantly among plant communities, suggesting that the long-term response to landscape drivers are plant-community dependent. These results are consistent with the findings of Alday et al. (2021) who showed in a multivariate community analysis of these experiments that long-term community dynamics for most sites moved in the same directions at most sites but at different rates. These results are important in defining practices to prevent future negative impacts on upland habitats especially considering that elimination of sheep grazing has been suggested as a potential (re)-wilding strategy for the management of UK upland vegetation (Monbiot, 2013; Sandon et al., 2013). Our results suggest that management/restoration programs in these upland areas should be dependent on the plant community, especially when management/restoration aims to preserve species richness. Here, species recovery was limited to local species pools, possibly because these plant communities had a very depauperate soil seed bank (Lee et al., 2013; Lee et al., 2020). Therefore, restoration efforts should focus on maintaining and indeed increasing these local species pools and preventing the ingress of additional negative species that may alter the functioning of these plant communities (Warner et al., 2021). For example, if these upland communities are to be maintained in their present state some management will eventually be needed to prevent shrub and tree encroachment. An alternative management decision might be to allow the invasion of shrubs and trees which will eventually develop into upland woodland (Alday et al. 2021). This would inevitably lead to changes in biogeochemical cycling which is important as large parts of the Moor House catchment is deep peat and are, therefore, important for carbon sequestration (Bain et al., 2011).

5. Conclusions

Overall, our results based on manipulative experiments reflect the results from long-term longitudinal monitoring studies, i.e., some plant groups (e.g. plants and mosses) have recovered after 2000, in part related to reduced sheep grazing and atmospheric pollutant deposition. However, there were also some important differences in long-term trends within- and between-communities suggesting that local management cannot overcome large-scale trends in community dynamics in these uplands. For example, the similar dynamics of change in grazed and ungrazed treatments suggest that some within-community processes are overcoming these management drivers. In contrast, our results also showed that the long-term response to landscape factors is plant community dependent. These results are extremely important for ecological restoration and management plans because they suggest suggesting that different management actions may need to be developed for each plant-community. At the same time, our results showed that in both grazing treatments and all four plant communities there was limited recovery in liverworts and, none in lichens. Research to restore liverworts and lichens appears a priority but almost nothing is known about how to increase the number of their species or their abundance (Letendre et al. 2019). Regardless., more longer-term research is needed to confirm the rate at which liverworts and lichens recover.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Rob Rose, John O'Reilly reports financial support, administrative support, and travel were provided by UK Environmental Change Network, institutional support via UKCEH. Rob Marrs reports article publishing charges and travel were provided by Leverhulme Trust. Rob Marrs reports travel was provided by The Heather Trust. Josu Alday reports financial support was provided by Ramon y Cajal fellowship. Rob Marrs reports a relationship with Heather Trust that includes:. RHM is the President of the Heather Trust (ambassadorial role) and sits on the Game and Wildlife Conservancy Trust's uplands scientific committee and NatureScot's Scientific Advisory Committee Expert Panel, both in an advisory capacity only. None of these organizations has had sight of the results in this paper.

Data Availability Statement

All data generated or analyzed during this study are included in this published article and are available in Rose et al. (2018), 2020).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.108878.

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