Winners and losers in a long-term study of vegetation change at Moor House NNR: Effects of sheep grazing and its removal on British upland vegetation

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Abstract

In this paper, we analyse data from nine long-term experiments set up to assess the effects of sheep-grazing versus no-sheep-grazing at Moor House Ecological Change Network site. The experiments were set up between 1954-1972 across a range of vegetation types typical of upland Britain. Data from this type of experiment are often difficult to analyse and we describe the procedures undertaken to clean-up the data for analysis. We fitted the resultant data to the British National Vegetation Classification and used ordination techniques to assess the relative positions of the experiments with each other. Finally we used Generalized Linear Mixed-Effects Modelling within a Bayesian framework to model change through time in both sheep-grazed and ungrazed treatments; variables included species diversity, Shannon-Weiner index and derived data on occurrence and abundance of species guilds (based on taxonomy/physiognomy). Hurdle analysis, a technique commonly used in econometrics, was used to model the guild variables; this analysis separated the change through time on both probability of occurrence (binomial distribution) and abundance (Poisson distribution).

In the sheep-grazed plots (the control treatment) there was a reduction in species diversity, Shannon-Weiner index and a decrease in abundance of vascular plants, grasses, lichens, liverworts and mosses; only the herbs showed an increase. When probability of occurrence was considered the worrying result was a reduction in number of presences of both lichens and liverworts. Thus the status quo management of continuous sheep grazing, even though reduced since 1972, has resulted in a reduction in species composition of these plant communities, i.e. biotic homogenisation. It is, however, likely that some of these changes are driven by external factors such as elevated atmospheric al of sheep-grazing had nutrient deposition load. Removal had little positive benefit; only the shrubs benefitted.

Thus during the period that Moor House has been protected as a nature reserve the vegetation quality has declined in spite of reductions in grazing pressure. To reverse this trend probably requires some form of interventionist management.

1 Introduction

In order to manage our natural resources wisely, i.e. in a sustainable way, it is essential to have some understanding of how our ecosystems change through time, and how they respond to environmental drivers of change. Such drivers of change might include external factors such as climate change and pollutant loads and internal factors such as the management applied. Studies linking ecosystem change to environmental drivers are usually done using either a correlative approach, or by direct experimentation. The correlative approach is done most effectively when a large fraction of the available environmental resource has been surveyed and correlated directly to measured changes in the environmental drivers, or some proxy for them. A good example of this approach is the use of data from the Countryside Survey of Great Britain (Haines-Young *et al.* 2003; Firbank *et al.* 2003; Smart *et al.* 2003a; Maskell *et al.* 2010), where data of measured species change indicated that productive species, known to respond to atmospheric nitrogen pollution, were favoured (Smart *et al.* 2003a; Maskell *et al.* 2010). The second approach is where vegetation is monitored through time within either permanent plots/transects (Thomas 1960, 1963) or within experiments where management interventions are compared against an untreated control over a fairly long-period; such long-term manipulative experiments are particularly valuable for testing ecological hypotheses (Silvertown *et al.* 2010). There are many examples of such experimental studies, but there are two main types: the first are experiments that measure the effects of applied treatments in a single location, famous examples include the early Breckland grass-heath experiments of A.S. Watt (Watt 1957, 1960a, 1960b, 1962) and more recent ones such as the Buxton Climate Change Impacts Laboratory (Bates *et al.* 2005; Grime *et al.* 2008), Cedar Creek Ecosystem Science Reserve (Wilson *et al.* 1993; Tilman 1994), and the Park Grass Experiment at Rothamsted Experimental Station (Tilman *et al.* 1994; Silvertown *et al.* 2006). This type of experiment provides detailed information about the effects of manipulated factors on species change and ecosystem properties. The second type are experiments that consider the effects of similar treatment interventions on the same ecosystem type in a range of locations, extending the assessment of impacts over a greater range of variation of that ecosystem type are particularly valuable. These multi-site studies are less common than those on single sites and are more complex to analyse (Alday *et al.* 2013; Marrs and Alday 2014).

The Ecological Change Network site at Moor House National Nature Reserve (NNR) provides a third approach where a single treatment has been tested in a range of different plant communities over varying time periods from 28-44 years Adamson and Kahl (2003). This approach was pioneered by A.S. Watt in his studies on Breckland grass-heaths because he had similar experiments on the different plant communities he had described at Lakenheath Warren (Watt 1940), although he analysed them separately. At Moor House, it was perceived that there was a need for long-term information on the effects of both sheep grazing and its removal across the range of variation in plant communities typical of a large upland nature reserve (ca. 4000 ha). The vegetation at Moor House comprised a mosaic of different upland plant communities dominated by dwarf-shrubs, grasses or sedges. Moreover, these communities occurred on a range of soil types ranging from deep blanket peat through to brown-earth soils, and were subject to different sheep grazing pressures (Eddy *et al.* 1968; Rawes and Welch 1969; Heal and Smith 1978). Accordingly, between 1954 and 1972 a series of nine essentially identical experiments with similar designs, and monitored using the same methods (Marrs et al. 1986), were set up to compare the long-term effects on the vegetation of sheep grazing with the effects of sheep removal. In the early part of the time-series, detailed studies by Rawes and Welch (1969) estimated that there were 15,400 sheep on the Reserve in the summer months, assuming a grazing area of 3500 ha this was an average of 4.4 sheep ha^{-1} across all vegetation types.The formalisation of grazing rights under the Commons Registration Act (1965) was completed for Moor House in 1972 and grazing density was more than halved to a total of 2 sheep ha^{-1} or 7000 sheep. From a conservation point of view, it was hoped that this reduction would lead to an improvement in vegetation quality.

This suite of nine experiments covered the major moorland vegetation types that are found across the Moor House reserve, and are typical of many moorland ecosystems found in upland Britain. Some preliminary results have been published on species change in individual experiments, for example the high-level grasslands (Rawes 1981), two of the blanket bog experiments (Rawes 1983) and a *Juncus squarrosus*-dominated community (Marrs *et al.* 1988). However, one of the problems in analysing the data from these experiments is that each individual experiment is unreplicated, i.e. there is only one sheep-grazed plot and an equivalent ungrazed exclosure in each location. Moreover, the experiments have been monitored irregularly (between 3 and 8 times), but over a fairly long time period, 28-44 years (Adamson and Kahl 2003). One way to add power to the analysis is to assess change based on the combined data from all experiments; this approach should provide an overview of change with any significant result being a function of measured change across all experiments. Here, therefore, we provide a combined analysis of change across all nine long-term sheep-grazing versus no-sheep-grazing experiments at Moor House. There were two further complications, the first is that the grazed treatment is effectively the control in that it is the normal treatment applied to the vegetation and the removal of sheep grazing is the applied intervention treatment. But of course, there can also be changes in species composition in these control plots through time brought about by other environmental factors and there was a deliberate reduction in sheep grazing pressure in the early 1970s. The second is that some of the experiments were not monitored from the outset, rather they were set up on similar, visually-identical vegetation and comparisons in some experiments between grazed and ungrazed plots were not made for some years. Thus, here we use an approach that concentrates on detecting directional change within the control grazed plots, and then any additional change in direction associated with the intervention, i.e. grazing removal.

There were three parts to this analysis. The first was to provide a descriptive context for each of the experiments so that managers elsewhere could use the results in other locations. We did this by allocating the vegetation in each experiment to a community type within the British National Vegetation Classification (NVC; Rodwell 1992a, 1992b). The second was to analyse all of the data using multivariate analysis so that the relationships between experiments could be assessed. The third part considered the change in abundance of selected taxonomic/physiognomic groups (hereafter termed Guilds) through time. We used guilds rather than functional traits because they are more easily recognisable by conservation managers on the ground. The following hypotheses were tested: (1) the null hypothesis was that there would be no directional change in the sheep-grazed plots, i.e. under usual management conditions there was either a steady-state or any change could be described as a fluctuation (sensu Miles 1979), i.e. change in individual species around a notional mean; (2) if this hypothesis was rejected and directional change detected this would provide evidence for either (a) conservation enhancement (+ve relationship), or biotic homogenisation (−ve relationship). Biotic homogenisation has been reported in upland areas with losses in sub-dominant vascular plants, lichens and bryophytes (Smart *et al.* 2006; Britton *et al.* 2009). Identification of guilds that changed through time in the sheep-grazed plots (the usual situation on British upland moors) would provide sensitive measures that might be used elsewhere to monitor change. Hypothesis 3 tested whether there was an effect (+ve or −ve) with respect to the removal of sheep-grazing, and this might provide information to inform future conservation policy, which might involve reducing or stopping sheep grazing in selected upland areas, i.e. the proposed policy of Rewilding (Monbiot 2013; Sandom *et al.* 2013).

However, change in species composition within the plant community could occur in two ways; (1) a reduction in the number of occurrences within a plot, and (2) a reduction in abundance. As the datasets from all of these experiments contained a very large number of zeros, we used hurdle models to identify the effects of sheep grazing versus no sheep grazing through time on both (a) the change in the number of presences/absences (i.e. point occurrences), and (b) changes in abundance when the guild was present. Hurdle models are a class of two-component model combining a zero-hurdle model with a binomial distribution, and a left-truncated count data model with a Poisson distribution. They have been heavily used in econometrics (Mullahy 1986; Cameron and Trivedi 2005, 2013), but so far they have not commonly been applied to data from ecological experiments, despite their obvious potential.

2 Methods

2.1 Experimental Design

The nine experiments were located across the Moor House reserve to cover the range of variation in the vegetation across the area, i.e. from relatively productive *Agrostis-Festuca* grassland on brown-earth soils and a calcareous flush at the neutral end of the soil spectrum through grasslands dominated by *Festuca ovina* or *Nardus stricta*, to rush (*Juncus squarrosus*), sedge (*Eriophorum spp.*) and dwarf shrub *Calluna vulgaris-Empetrum nigrum*-dominated vegetation on blanket bog (least productive). Exact locations and plot details are shown in Table 1 and Supporting Information (Fig. S1).

All experiments consist of paired plots with one from each pair being fenced to exclude sheep and the other left open to allow free range grazing. Sheep grazing densities were estimated during the International Biological Program in the late 1960s (Table 1, Rawes and Welch 1969). Throughout, point-quadrats have been used to measure species abundance: in all experiments the point-quadrat frame was positioned using a permanently-marked reference system within the plot. The sampling positions were selected randomly at the outset. On many occasions height-stratified pins (0-10cm, 10-20 cm, 20-30 cm and >30 cm) were used to record vascular plants to provide information on canopy composition. The exact way in which the pin frame has been 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 a summary of the historical sampling information for each experiment is detailed in the Supporting Information Appendix (Table S1).

2.2 Data Preparation

The dataset are voluminous and complex and required a substantive clean-up, first to bring species nomenclature to the same standard: Stace (2010) for vascular plants, Atherton, Bosanquet and Lawley (2010) for bryophytes and Dobson (2000) for lichens, and secondly to combine some taxa that were recorded inconsistently. These changes are outlined along in the Supporting Information. (Table S2).

Whilst all data collection within each experiment was internally consistent there were differences in methods of stratified random sampling between experiments. Accordingly, the following procedure was adopted to achieve a common recording methodology and intensity across all experiments:

i. All species hits per pin from all height strata were summed to provide pin totals.

ii. These summed values were converted to presence/absence data using the decostand function in the vegan package (Oksanen, 2011). Taken together, these two steps reduced all data collected at a single pin to either 1 or 0.

iii. The sum of all presences was calculated at each sampling position; depending on experiment, this was either a pin-frame position or a 1m^2 quadrat where various positions were sampled. This provided an abundance score of between 0-10 for each sampling position for most sites and 0-5 for Moss Burn. These data were used in all analyses reported here.

The raw dataset had 139,619 data points, step 1 reduced it to 57,706 and step 3 reduced it to 7,830; there were 238 sample variables, 234 species/combined species groups e.g. *Luzula campestris*/multiflora and four environmental variables (bare rock, bare soil, litter and animal presence (dung/urine noted).

2.3 Data Analysis

In order to fit the vegetation within each experiment into a broader UK perspective, a species list for each experiment was collated along with a summed measure of abundance which was then converted to a percentage by dividing by the total number of samples. These data were then passed through TABLEFIT v1.1 (Hill 1996 [revised 2011]) to determine the best-fit community according to the National Vegetation Classification (NVC, Rodwell 1992a, 1992b). Usually, NVC allocation is done from species-abundance scores based on 4m^2 quadrats for this type of vegetation. This was not possible here so average species abundance

Table 1: Description of the nine monitored sheep-grazing exclosures at Moor House NNR in north-west England.

Site Name	British National Grid	Elevation (m)	Years Sampled	Vegetation Type (Eddy *et al.* 1969)	* Area of Vegetation (ha)	** Sheep Density (sheep ha^{-1})
Knock Fell	NY 71794 31267	750	1955 -2000	Limestone *Agrostos-Festucetum*	125	5.8
Hard Hill	NY 72576 33034	690	1954 -1998	*Festucetum*	180	2.6
Little Dun Fell	NY 70475 33104	830	1954 -1998	*Festucetum*	ND	5.8
Silverband	NY 71059 30975	690	1966-1997	*Eriophoretum* (eroding)	323	0.25
Troutbeck Head	NY 72236 31760	690	1966 -1997	*Eriophoretum*	419	0.5
Bog Hill	NY 76789 32869	550	1971-1999	*Calluna-Eriophorum*	1169	ND
Cottage Hill	NY 75801 33641	550	1967 -1995	*Juncus squarrosus* grassland	373	1.4
River Tees	NY 74796 34485	550	1967 -1995	*Nardus stricta* grassland	416	2.8
Moss Burn	NY 74553 31632	640	1972 -1996	Calcareous flush	14	ND

[*] The total area of these communities makes up 3019 ha, i.e. 79% of the reserve area of 3842 ha, the remaining vegetation comprised predominantly re-colonising peatland, Sandstone scree and mosaics of the above vegetation classes (Eddy *et al.* 1969); data were not available for one site (ND).

[**] Sheep grazing density was determined by dropping volume measurement (Rawes & Welch 1969); data were not available for two sites (ND).

over for the experiment over all years was used instead. It is accepted that this will be an approximation.

All other data analyses were performed using `R` version 3.1.2 (R Development Core Team 2011).

2.3.1 Multivariate Analysis

The dataset were analysed using Detrended Correspondence Analysis using the decorana function in the `vegan` version 2.0-2 package and Hellinger-transformed data; species that were present on only one occasion were removed before the analysis. The correlations between the ordination axes and the five environmental variables were then calculated using the envfit function (Oksanen, 2011) with 9999 permutations and plotted as passive variables. The distribution of experiments were visualized in ordination space as standard-deviational bivariate ellipses (SD-ellipses, 95% confident limits) using the ordiellipse function (Oksanen 2011) and centroids of grazing and sheep excluded treatments were then plotted through time for each site.

2.3.2 Univariate Analysis

The study design comprised nine sites each with a sheep-grazed and an ungrazed plot. Unfortunately, there was no within-site treatment replication, and hence no way of estimating treatment effects at the site level. Therefore, for each variable we tested for effects of grazing (sheep grazing versus no sheep grazing), time (with Year 0 set to 1955) and their interaction, essentially using the sites as replicates. A range of diversity measures were calculated, species richness and the Shannon-Weiner diversity index using the specnumber and diversity functions in vegan (Oksanen 2011). In addition the summed number of hits for each sampling position for eight guilds were computed, i.e. lichens, mosses, liverworts, graminoids (all sedges and rushes, i.e. *Juncus spp.*, *Luzula spp.*, *Carex spp.*, *Eriophorum spp.* and *Trichophorum cespitosum*), sedges (*Carex spp.*), herbs (all dicotyledons), grasses (Poaceae), shrubs (Ericaceae) and all vascular plants.

Except for vascular plants (no zero counts), the response of each of the vegetation functional types to grazing treatment, year and their interaction was modelled using mixed-effects hurdle Poisson regression. Hurdle models are a class of two-part, discrete mixture-models that operate under the assumption that zeroes in the data occur due to a single process whilst a different process drives the non-zero counts (Mullahy 1986). The first or hurdle part of the model estimates the probability of a non-zero count occurring (i.e. whether a guild was present or not), while the second or count part of the model relates to the non-zero count distribution (i.e. the response of a vegetation functional type if it is present). Hurdle Poisson regression was deemed a suitable approach because, (1) the data for all response variables except species richness and vascular plant abundance exhibited a high degree of zero-inflation, and (2) the models essentially allowed for the presence of each vegetation type in response to the predictors (grazing treatment, year and their interaction) to be investigated independently of the vegetation dynamics when that vegetation type is present. As we were interested in broad-scale patterns of change across the moorland, site was specified as a random effect in all models. The models were implemented using the `MCMCglmm` version 2.16 package (Hadfield 2010). Conducting the analyses in a Bayesian framework was deemed the most suitable approach because the data exhibited high levels of over-dispersion, which is readily accounted for during the sampling process, and additionally, robust 95% confidence intervals are calculated during posterior sampling, negating the requirement for post-hoc bootstrapping. Parameter expanded priors allowing for random slopes for site and assuming unequal variance and allowing for estimation of between site correlation in both the hurdle and the count parts of the models were incorporated into all models and the models were run for a 10 x 10^4 generation burn in with sampling of every 500th iteration for a further 2 x 10^6 iterations, giving an effective sample size for each parameter estimate of approximately 4 x 10^4 from the posterior distribution. Model convergence was assessed through inspection of the trace plots. Vascular plants, species richness and Shannon-Weiner diversity were modelled using GLMMs with the same fixed and random effects as the hurdle models.

3 Results

3.1 The individual experiments in the moorland context

The nine experiments covered eight NVC plant community types (Table 2) ranging from blanket bog mire communities (M19, M20), upland grasslands (U5, U6), an upland heath community (H19), calcareous grassland (CG10) and a flushed community (M38). All of the communities showed a high goodness-of-fit for compositional satisfaction but a lower value for mean constancy, implying that a reasonable number of the constant species were present, but the vegetation is relatively species-poor (Hill 1996).

The DCA analysis produced eigenvalues of 0.621, 0.457, 0.363, 0.222 and gradient lengths of 6.33, 5.42, 4.45, 3.96 for the first four axes. The distribution of species shows two clear gradients (Fig. 1a, b). On axis one the vegetation is dominated by dwarf shrubs (*Calluna vulgaris* and *Empetrum nigrum*) at the negative end, through dwarf-shrub and graminoid communities (*Vaccinium myrtillus*, *Deschampsia flexuosa*, *Festuca ovina*, *Eriophorum vaginatum* and *Agrostis capillaris* communities to vegetation with *Luzula spp.*, *Deschampsia cespitosa*, *Eriophorum angustifolium*, *Carex nigra* and *Carex demissa*). Axis two reflects a moisture gradient from grassland dominated by *Agrostis capillaris* and *Festuca ovina* through to vegetation dominated by *Empetrum nigrum* and *Eriophorum spp.*

The sites show four clear groupings (Fig. 1c, d): (a) Moss Burn flush which is clearly separated from the others, (b) the hilltop grasslands (Hard Hill, Little Dun Fell, Knock Fell), (3) blanket-bog communities (Bog Hill, Silverband and Troutbeck Head), and (d) the *Juncus*- and *Nardus*-grasslands (Cottage Hill and

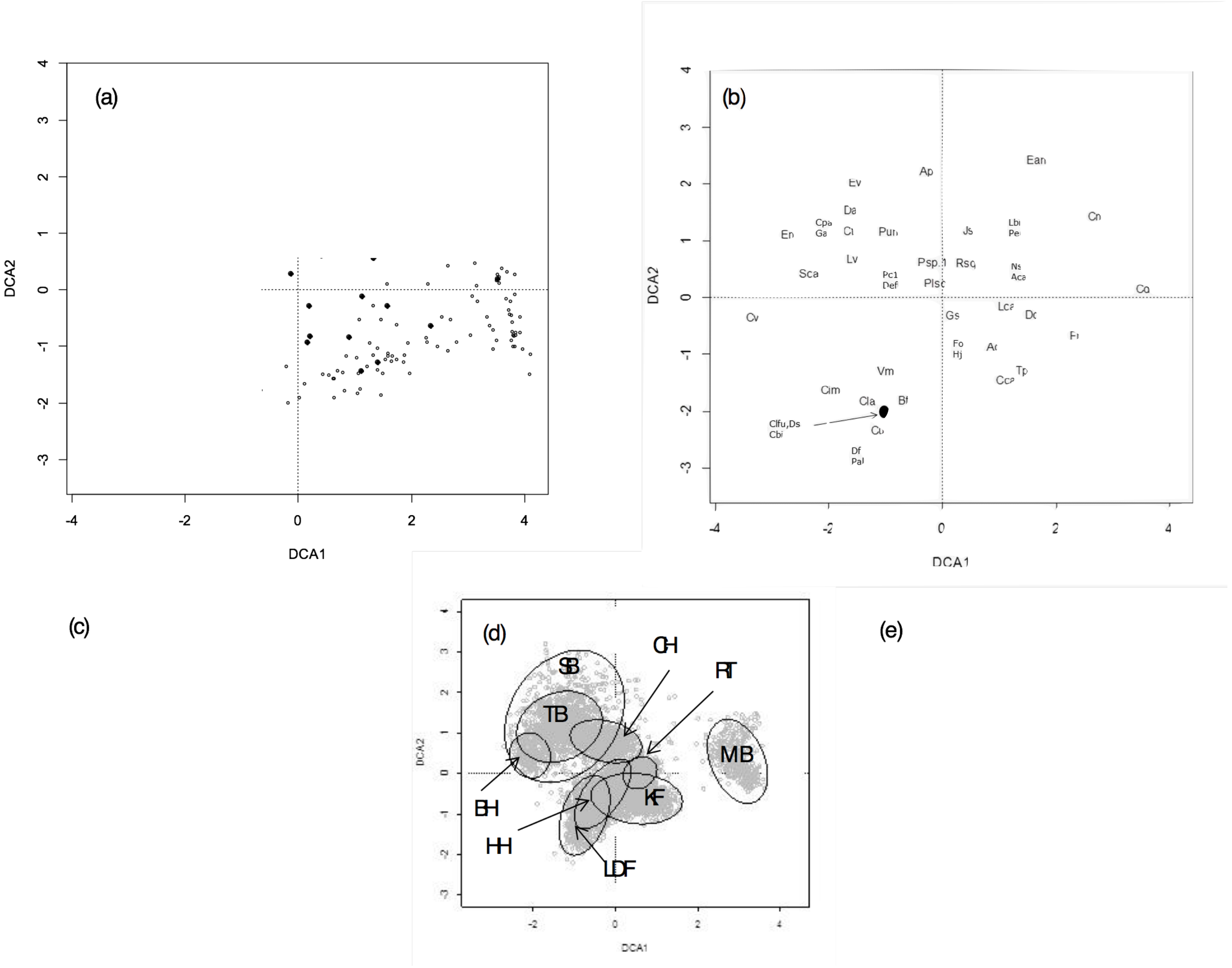

Figure 1: Plots derived from the DCA analysis of plant species composition data within nine experiments investigating the effects of sheep-grazing versus no sheep grazing at Moor House NNR, north-west England: (a) Species plot, all species are illustrated (large dots = the most abundant species); (b) Species plot showing only the most abundant species; (c) the distribution of sampling units; (d) the distribution of the nine experiments in ordination space illustrated using bivariate SD-ellipses (95%confidence limits) superimposed; (e) the significant environmental variables correlated with the ordination. Species codes for (b): Ac=*Agrostis capillaris*, Aca=*Agrostis canina*, Ap=*Aulacomnium palustre*, Bf=*Barbilophozia spp*, Cbi=*Carex bigelowii*, Cca=*Carex caryophyllea*, Cd=*Carex demissa*, Cim=*Cladonia impexa*, Cla=*Cladonia arbuscula*, Clfu=*Cladonia furcata*, Cn=*Carex nigra*, Cpa=*Campylopus paradoxus*, Ct=*Calypogeia spp.*, Cu=*Cladonia uncialis*, Cv=*Calluna vulgaris*, Da=*Diplophyllum albicans*, Dc=*Deschampsia cespitosa*, Defl=*Deschampsia flexuosa*, Df=*Dicranum fuscescens*, Ds=*Dicranum scoparium*, Ean=*Eriophorum angustifolium*, En=*Empetrum nigrum*, Ev=*Eriophorum vaginatum*, Fo=*Festuca ovina*, Fr=*Festuca rubra*, Ga=*Green algae*, Gs=*Galium saxatile*, Hj=*Hypnum jutlandicum*, Js=*Juncus squarrosus*, Lbi=*Lophocolea bidentata*, Lca=*Luzula campestris*/multiflora, Lv=*Lophozia spp.*, Ns=*Nardus stricta*, Pal=*Polytrichum alpestre*, Pc1=*Ptilidium ciliare*, Per=*Potentilla erecta*, Plsc=*Pleurozium schreberi*, Psp 1=*Polytrichum spp.*, Pun=*Plagiothecium undulatum*, Rsq=*Rhytidiadelphus squarrosus*, Sca=*Sphagnum capillifolium*, Tp=*Thymus praecox/arcticus*, Vm=*Vaccinium myrtillus*. Site codes for (d): BH=Bog Hill, CH=Cottage Hill, HH=Hard Hill, LDF=Little Dun Fell, KF=Knock Fell, MB=Moss Burn, RT=River Tees, SB= Silverband, TB=Troutbeck Head.

Table 2: The National Vegetation Classification (NVC, Rodwell 1991, 1992) communities found at each of the nine experiments at Moor House NNR in north-west England. The NVC classes were computed using TABLEFIT (Hill 1996); the best fit classes are presented along with the goodness-of-fit for compositional satisfaction and mean constancy, plus the overall means derived from four indices (G1-G4).

Site Name	NVC Class	Mean (G1-G4)	Compositional Satisfaction (G1)	Mean Constancy (G2)	Community Description
Bog Hill	M19	68	100	30	*Calluna vulgaris-Eriophorum vaginatum* blanket mire.
Cottage Hill	U6b	61	88	25	*Juncus squarrosus-Festuca ovina* grassland: *Carex nigra-Calypogeia trichmanis* sub-community.
Hard Hill	H19a	61	100	32	*Vaccinium myrtillus-Caldonia arbuscula* heath: *Festuca ovina-Galium saxatile* sub-community.
Knock Fell	CG10	55	91	16	*Festuca ovina-Agrostis capillaris-Thymus praecox* grassland
Little Dun Fell	H19a	63	100	30	*Vaccinium myrtillus-Caldonia arbuscula* heath: *Festuca ovina-Galium saxatile* sub-community.
Moss Burn	M28	57	96	44	*Cratoneuron commutatum-Carex nigra* spring.
River Tees	U5	73	100	28	*Nardus stricta-Galium saxatile* grassland.
Silver band	M20b	71	100	36	*Eriophorum vaginatum* blanket and raised mire: *Calluna vulgaris-Cladonia spp.* sub-community.
Trout beck Head	M20b	71	100	39	*Eriophorum vaginatum* blanket and raised mire: *Calluna vulgaris-Cladonia spp.* sub-community.

River Tees) that appear transitional between groups (b) and (c). There is little overlap between groups a, b and c, but group d overlaps with groups b and c. The sites show considerable intra-group overlap. The blanket bog sites are at the negative end of axis 1 with a relatively low species richness and this increases through the grasslands to the species-rich mire at Moss Burn at the positive end (Fig. 1c, d), whereas axis two reflects a gradient from the hilltop grasslands (Hard Hill, Little Dun Fell) at the negative end to the remaining sites which occupy positions around the centre of the axis to the positive end.

The correlations with the environmental variables had relatively low r2 values (Year = 3.1%, Bare rock = 9.2%, Bare rock =11.6%, Litter= 22.1%, Dung/urine = 0.2%) but all were significant ($P<0.001$) except for dung/urine ($P<0.01$). These variables show a gradient parallel to axis 2 (Fig. 1e), reflecting increasing amounts of bare rock and dung/urine on the hilltop grassland communities with greatest sheep grazing pressure (negative end) through the *Juncus*- and *Nardus*-dominated grasslands to the blanket bog communities (positive end) with greater litter and bare soil. Axis two was also correlated positively with through sampling year indicating a temporal positive movement.

The temporal trajectories based on the treatment x time centroids (Fig. 2) show relatively little overall movement away from the start position in most sites and considerable fluctuations. However, there was divergence over time between the sheep grazed and ungrazed plots in eight of the sites, the exception being the River Tees site where the two treatments intermingle. The largest movement from the grazed sites is in the *Juncus*-dominated grassland (Cottage Hill). At two sites the trajectories were in more or less the same direction (River Tees and Knock Fell), at all others there was either divergence (Bog Hill, Moss Burn and Little Dun Fell) or movement in opposite directions (Silverband, Troutbeck Head, Cottage Hill, Hard Hill and Little Dun Fell).

3.2 Change in species richness, diversity and abundance of guilds

The results from these analyses are complex, the outputs are presented in full in Table S.3 (Supplementary materials), and in summary form in Table 3. The results from both parts of the hurdle models need to be viewed in context of the modelled output (Figs 3 and 4). The estimates of interest here are the change in the measured variable with respect to time: where Year is significant then there is a significant increase (estimate is +ve) or decrease through time (estimate is −ve) in the sheep-grazed treatment (the intercept). Where there is a significant enclosed x year effect there is a significant increase or decrease in this rate of change with respect to sheep grazing and this represents a significant effect of no-sheep grazing.

3.2.1 Change in probability of occurrence (Hurdle model I)

The change in the probability of occurrence (binomial model, Table 3; Fig. 3) reflects a change in the point-sampled presences and shows that two types of temporal response were detected for all of the eight guilds tested here. In the sheep-grazed plots, the probability of occurrence of grasses, mosses, herbs and sedges all increased through time, whereas a decrease through time was found for liverworts and lichens. Removal of sheep grazing had: (1) no additional significant effect on the probability of occurrence of grasses, sedges and lichens, but (2) a significant additional effect on the rate of change in the probability of occurrence of mosses, herbs (both increasing faster), and liverworts (decreasing faster). Graminoids showed no change in time under grazing, but a significant decrease in the probability of occurrence within the exclosures. Shrubs showed no significant change in probability of occurrence through time in the grazed plots, but a small significant increase with no-grazing.

3.2.2 Change in abundance and biodiversity indices (Hurdle model II)

The change in the diversity measures and the abundance of the guilds (count model) are presented in Table 3 and Figure 4. Species richness decreased under sheep-grazing but there was no additional effect under the no grazing treatments, though the enclosed plots had a significantly lower starting value. There was no change in Shannon-Weiner diversity through time in the grazed treatments, whilst a small but significant increase though time was found in the ungrazed plots.

Three guilds showed an increase in abundance through time in the grazed plots (herbs, sedges and

Table 3: Summary results from the generalized linear mixed-effects models and mixed-effects hurdle models with two components: (1) a binomial one illustrating the effects of sheep-grazing (Intercept) versus no sheep grazing (Enclosed), time and their interaction on a range of measured variables (species richness, Shannon-Weiner index and abundance of a range of plant guilds) in a suite of nine experiments at Moor House NNR, north-west England. The full results are presented in Table S4 (Supplementary materials); here only the estimates are presented along with their significance. Positive and negative responses are denoted green and red respectively, and significance is denoted: *** = P<0.001, ** = P<0.01, * = P<0.05, - = no significant, NT = not tested.

Variable	Binomial Model				Count Model			
	Intercept	Enclosed	Year	Enclosed x Year	Intercept	Enclosed	Year	Enclosed x Year
Species Richness	NT	NT	NT	NT	2.124	-0.174	-0.004	0.001
					***	***	***	-
Shannon-Weiner Diversity	NT	NT	NT	NT	1.818	-0.177	-0.001	0.002
					***	***	-	***
Vascular Plants	NT	NT	NT	NT	2.915	0.064	-0.003	-0.001
					***	***	***	-
Grasses	6.951	-2.267	0.055	0.017	2.551	0.152	-0.007	-0.008
	*	***	***	-	***	***	***	***
Herbs	-0.379	-1.332	0.038	0.045	1.247	0.107	0.005	0.002
	-	***	***	***	***	**	***	-
Lichens	0.717	-0.670	-0.036	0.001	1.243	-0.128	-0.020	0.012
	-	***	***	-	***	**	***	***
Liverworts	1.060	-0.106	-0.059	-0.023	1.395	-0.098	-0.021	-0.006
	*	-	***	***	***	*	***	*
Mosses	1.080	-0.689	0.029	0.025	1.749	-0.281	-0.008	0.011
	-	***	***	***	***	***	***	***
Graminoids	5.234	-0.654	-0.001	-0.037	1.903	0.043	-0.001	-0.002
	*	***	-	***	***	-	-	-
Sedges	-1.236	0.238	0.032	0.004	1.012	0.085	0.007	0.005
	-	*	***	-	***	-	***	*
Shrubs	-0.035	-0.418	-0.003	0.016	0.865	0.277	0.004	0.005
	-	**	***	*	**	***	*	*

shrubs); removal of sheep grazing had no significant additional effect on the abundance of herbs but significantly enhanced the rate of increase of sedges and shrubs. All other guilds declined through time in the sheep grazing treatment, except for graminoids. Enclosure produced slower rates of decrease for lichens but faster rates of decreases for grasses, liverworts and vascular plants, whilst for mosses enclosure resulted in an increase in abundance through time.

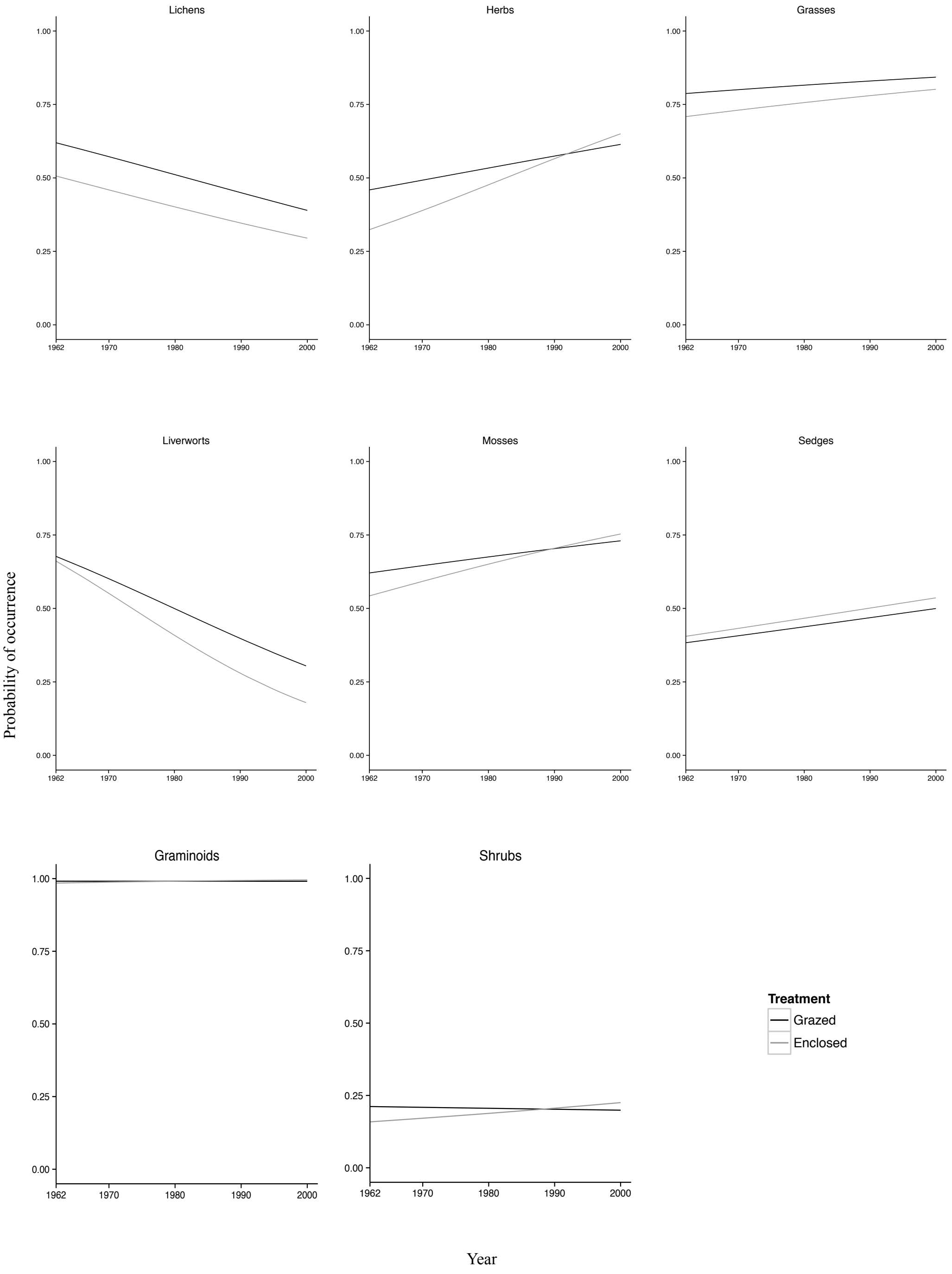

Figure 2: Fitted modelled responses of the probability of occurrence of selected guilds through time within nine experiments investigating the effects of sheep-grazing versus no sheep grazing at Moor House NNR, north-west England. Full outputs (Binomial part of the Hurdle models) are presented in Table S3 (Supplementary materials).

4 Discussion

4.1 Problems associated with the analysis of long-term plant community data

There are always problems in analysing data from long-term experiments where plant community data have been collected (Lee *et al.* 2013a). Part of this is because often the experiments did not begin as long-term

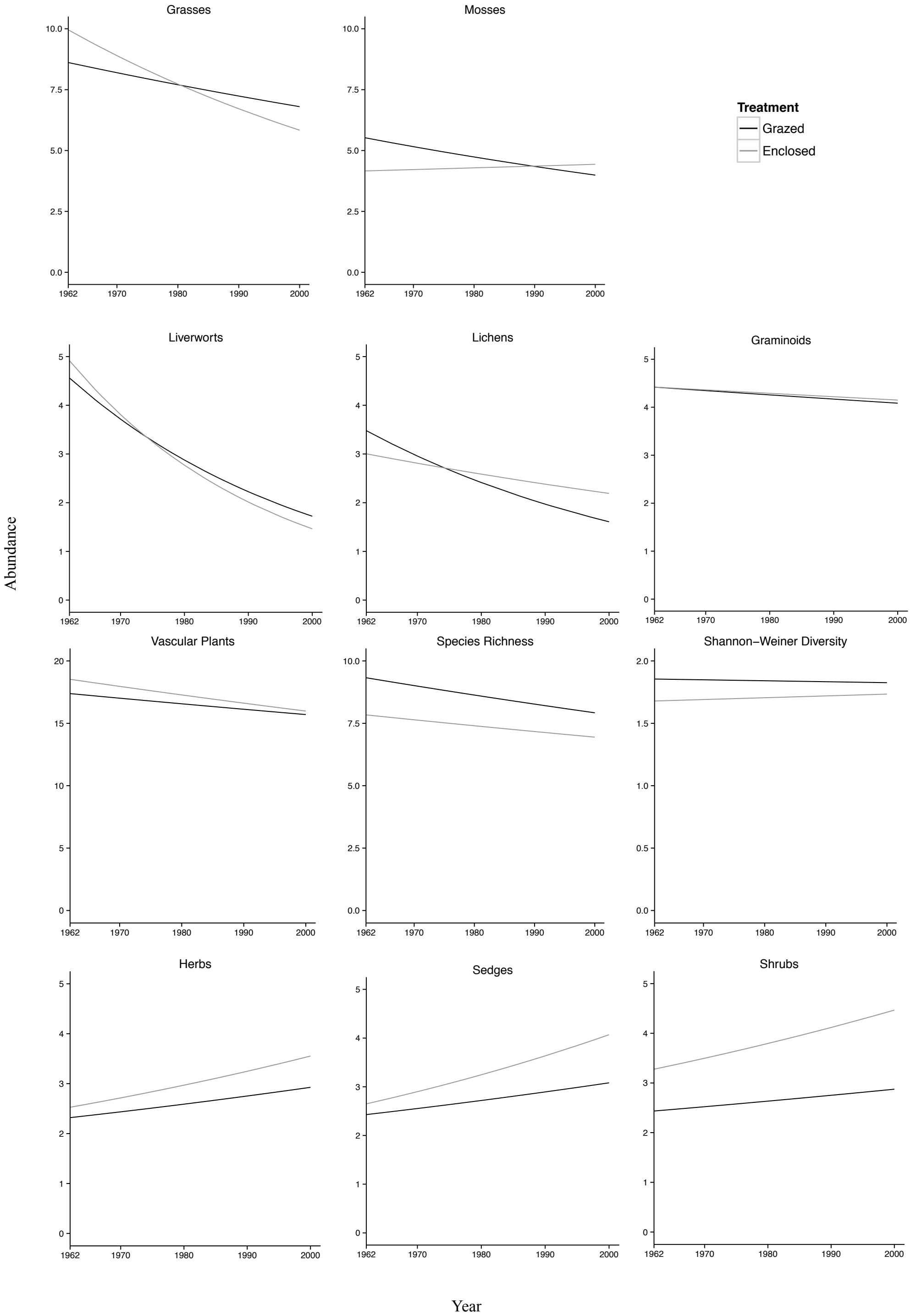

Figure 3: Fitted modelled responses of (1) the abundance of selected guilds, and (2) species richness and the Shannon-Weiner Index through time within nine experiments investigating the effects of sheep-grazing versus no sheep grazing at Moor House NNR, north-west England. Full outputs (Count part of the Hurdle models) are presented in Table S3 (Supplementary materials).

studies and not enough thought was given to their experimental design, recording methods and data storage at the outset. Here, even though the experiments all had the same experimental design (sheep-grazed-plot versus no-sheep-grazing) and the same basic monitoring methods (Marrs *et al.* 1986; Adamson and Kahl 2003), the experiments were started in different years and comparable measures were not always made simultaneously in both plots at the outset. Accordingly, some time elapsed between setting the experiments up and the first set of comparable data immediate changes in vegetation as a result of enclosure can only be inferred and probably explain the differences observed here between the intercept (sheep grazing treatment and the enclosed treatment). Accordingly, we have not discussed these differences here; rather we have concentrated on the rates of change through time.

In addition, two other issues needed to be tackled. The first was species nomenclature with respect to name changes through time and the likelihood of different recording teams identifying critical groups to differing standards. This was tackled using a clean-up procedure (Table S2, Supplementary materials), and for this study at least, the calculation of total abundance of high-level taxonomic/physiognomic guilds. Misnaming and mis-identification errors should, therefore, be relatively low at guild level. The second issue was that whilst the basic recording methodology was similar throughout, some measurements were made using counts of all species touches on height-stratified pins and some were first-touch species presences only (Marrs *et al.* 1986). Therefore, all of the data had to be converted to a single unit of currency, namely the number of presences on either a 10-point pin frame or within a series of pin positions within a 1m^2 quadrat.

4.2 The range of variation covered by the experiments

In any monitoring of species change within a given resource it is essential to encompass a reasonable range of the variation within the reserve. Here, the nine experiments were set up on eight different community types within the British National Vegetation Classification (Rodwell 1992a, 1992b), and accordingly they fulfilled their intention of providing information on species change across the spectrum of plant communities described at Moor House. The nine experiments were plots that were separated on two gradients, the first separating the base-rich flush (Moss Burn) from the other eight (x-axis, Fig. 1); these eight were then separated the on a climate-soil type gradient (y-axis, Fig.1). Surprisingly, within experiments there was relatively little change through time suggesting that the communities were relatively stable, although there was divergence between the sheep-grazed and ungrazed plots in eight of the nine experiments. The exception was the River Tees site which was noted as relatively stable in an earlier analysis (after ten years, Rawes 1981), and it is quite remarkable that this stability has been maintained over a 29-year period.

The distribution of sites within the ordination suggest that future, more detailed, analyses of these data might be better focussed around four main groups:

i. Blanket Bog sites (n=3: Bog Hill, Silverband, Troutbeck Head),

ii. Species-poor grasslands (n=2: Cottage Hill, River Tees),

iii. High-level grasslands (n=3: Hard Hill, Little Dun Fell, Knock Fell), and

iv. Base-rich flush (n=1: Moss Burn).

Each of these groups is, to a large extent, separated spatially within the ordination but there is a considerable amount of within-group overlap (Fig. 1). Future detailed analyses of species change within the first three of these groups will bring about a greater degree of statistical rigour as each experiment can be viewed as a replicate. This structure was to some extent planned, but previous analyses have considered change in vegetation at the individual experimental level in two groups (1) Blanket Bog: Silverband and Trout Beck Head, and (2) Grasslands: Cottage Hill, Hard Hill, Little Dun Fell, Knock Fell and River Tees. It is recommended that future analyses should be performed on the pooled data of the first three groups identified here which will provide an increase in statistical rigour, whereas Moss Burn, a relatively base-rich site (Marrs *et al.* 1989) should be analysed independently as a case-study.

4.3 Analytical methodology for assessing change in guilds through time

The application of mixed-effects hurdle models within a Bayesian framework presented here uses a new and seldom-used approach to assessing change in vegetation guilds through time. Whilst hurdle models have been used extensively in econometrics and the political sciences their use in ecological studies (Cameron and Trivedi 2005) is somewhat limited. This is most likely due to the difficulty inherent in assessing the providence of zero counts within the data. Here, it was reasoned a priori that zeroes within the counts were true zeroes due to the low taxonomic resolution at which the vegetation guilds were recorded, i.e. species misclassification would likely not occur at the taxonomic resolution used here. A Bayesian approach allowed for all data to be analysed without transformation (O‘Hara and Kotze 2010) whilst also accounting for over-dispersion. These analyses also allowed for two subtly distinct processes to be modelled; (1) the effects of grazing and time on the probability of a vegetation guild occurring, and (2) if a vegetation guild was present, the effects of grazing and time on the abundance of that guild. Thus, information was obtained on both the change in probability of a guild being present or not, and any changes in its abundance.

4.4 Changes in species richness, diversity and guilds through time

The null hypothesis of no change through time in the sheep-grazed treatment was partially rejected, as there was an overall decrease in species richness through time, though diversity was maintained and showed no change. Interestingly, whilst species richness was found to decrease at the same rate in both the grazed and unglazed treatments, diversity was actually found to increase in the unglazed exclosures. However, the ungrazed treatment started at a lower value for these variables than the sheep-grazed plots and this probably reflects a reduction in species in the period immediately after the start of the experiment and the first comparable dataset available for each treatment (see above).

Within the sheep-grazed treatment the changes in both the probability of occurrence (i.e. number of point sources on the ground) and abundance identified both temporal changes and potentially different effects between the guilds in how these changes occurred. In terms of the probability of occurrence, two guilds (lichens and liverworts) showed a reduction in point presences, i.e. these guilds were present at fewer points on the ground as time progressed, whilst except for graminoids, the other guilds all increased. However, when abundance was considered all groups except herbs, sedges and shrubs showed a reduced abundance through time. Taken together, these results suggest that directional change occurs (hypotheses 2 accepted) and that there is an overall reduction in plant community quality through time under background grazing conditions, i.e. the vegetation is getting worse and that biotic homogenization is occurring. Lichens and liverworts are particularly vulnerable as they are reducing in both occurrences and abundance.

The effects of removal of sheep-grazing led to additional increases in the probability of occurrence of herbs, mosses and shrubs, an increase in graminoids (no effect under grazing), and a greater reduction in liverworts. The abundance data showed the rate of decrease slowing for lichens and accelerating for many of the other guilds (grasses, liverworts and vascular plants). The only positive effect of exclosure was the increase in the abundance of mosses, though without data regarding the species composition of the mosses, it is difficult to quantify whether the increases in this guild can be construed as positive or not, i.e. abundance may be increasing at the guild level, but the composition of the species within the guild may be changing in a negative fashion, with the diversity decreasing and the abundance increases being driven by one or a few species. This would effectively show homogenisation within the guild. Of course, this could be said for any of the guilds exhibiting similar divergent dynamics, whether negative or positive in direction, between the two treatments. Overall, removal of sheep grazing had few positive effects and many negative ones (Hypothesis 3 rejected).

Previous analyses of these experiments have concentrated on species change within the enclosures and little attempt has been made to relate them to the ongoing, parallel changes occurring in the sheep-grazed enclosures (Rawes 1981, 1983). Rawes concentrated on changes in individual species and his general trends reflect those reported here for guilds, i.e. for blanket bog (increasing shrub cover, reduction in liverworts) and grasslands (increases in sedge cover and selected bryophytes, and a reduction in rushes, predominantly Juncus squarrosus). Reductions in bryophytes and lichens have also been detected in other studies of upland vegetation (Britton and Fisher 2010; Hall *et al.* 2011).

4.5 Implications for land managers and conservation

All in all, these results indicate a continuing decline in biodiversity value since Moor House was acquired as a nature reserve in 1952 specifically for scientific purposes. The long-term vision of the early conservation scientists who set these and other experiments up (Lee et al. 2013a,b) are now yielding important data to help guide nature conservation management. These long-term experimental datasets, and allied information, integrates well with the data collected within the UKs Ecological Change Network. The reserve has, over this period, been managed using minimal intervention apart from sheep-grazing and some relatively small-scale experimental treatments (Lee *et al.* 2013a,b). Even so, we have shown here a continued decline in species richness and changes in the probability of occurrence and abundance of several plant guilds. What is of particular concern are the reductions in (1) the probability of occurrence of liverworts and lichens and (2) the abundance of most guilds (exceptions being herbs, sedges, graminoids and shrubs). This implies a biotic homogenisation of these plant communities with a shift to dominance by herbs, sedges, and shrubs, with graminoids maintaining their abundance during this shift. Such biotic homogenisation has now been detected in Great Britain at the countrywide-scale (Smart *et al.* 2006) and within alpine communities (Britton *et al.* 2009), and it is possible that this reflects a continuing late-twentieth century impact of atmospheric pollution (Smart *et al.* 2003; Maskell *et al.* 2006; Britton and Fisher 2010; Hall *et al.* *2011*; Armitage *et al.* 2012). Irrespective, if there is a general wish to recover the plant communities that were present when the Moor House reserve was set up then clearly some restoration initiatives will be needed, and these will need to be determined by further experiment.

Interestingly, the effect of removal of sheep-grazing was on selected groups but generally the communities were rather stable. This implies that over the 28-44 years of this study the enclosed treatments have changed from their respective sheep-grazed control but not by all that much. One important result is an increase in shrub abundance but this was not reflected to the same extent in probability of occurrence, suggesting that measured change is through the growth expansion of individuals rather through recruitment of new plants; this was implied in a previous study of the Cottage Hill *Juncus squarrosus*-dominated grassland where one individual patch of *Calluna vulgaris* had expanded (Marrs *et al.* 1988). There has been no evidence of tree invasion and this is probably the for several reasons, such as the relatively large distances from potential seed sources, a lack of disturbance in the exclosures to provide safe-sites for germination (Harper 1977), the relative small size of the exclosures (maximum size = 900 m*2*), and altitude and soil type. Thus, any attempt to change the composition of the vegetation on this reserve by reducing sheep-grazing will on the basis of these results take a very long time, unless there is some intervention management. However, it could be argued that vegetation change might differ considerably from these small plot studies if the sheep-grazing pressure were to be reduced over a much larger geographic scale, i.e. the entire reserve. This is possible but remains to be tested.

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