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**EFFECTS OF ROTATIONAL PRESCRIBED BURNING AND SHEEP-GRAZING ON MOORLAND
PLANT COMMUNITIES: RESULTS FROM A 60-YEAR INTERVENTION EXPERIMENT**

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ABSTRACT

The effect of prescribed burning for conservation management of plant communities is controversial for moorlands growing on peat. These ecosystems provide many services which may be damaged by fire, hence it is important to fully assess its impact on all aspects of ecosystem structure and function experimentally over relatively long time-scales. This paper describes change in community composition, major plant species and plant functional types on moorland on peat in upland Britain over 60 years subject to three burning treatments after an initial burn in 1954/5: no further burn, and burning at 10 and 20-year intervals (all \pm sheep-grazing). Data were analysed using multivariate and univariate methods. Vegetation composition and individual species abundance reflected the degree of disturbance. The least-disturbed was dominated by *Calluna vulgaris* and pleurocarpous mosses whereas the most-disturbed treatment (burned every 10 years) had greater *Eriophorum vaginatum*, *Sphagnum* spp., acrocarpous mosses, liverworts and lichens. The 20-year treatment was intermediate in response disturbance. Repeated burning increased species-abundance-weighted-Ellenberg values for moisture, reaction, light through time, and fertility; the exception was the 10-year rotation for fertility. These confirm that prescribed burning is not deleterious to peat-forming species (*Eriophorum* spp. and *Sphagnum* spp.) indeed these species were found in greater abundance in frequently-burned treatments. It also confirms that a no-burn policy will lead to increasing dominance of *C. vulgaris*, a flammable, fire-adapted shrub, which increases summer wildfire risk. These results inform conservation management policy for moorland vegetation growing on peat; for this site, a 20-year prescribed burning rotation is recommended.

KEY-WORDS: conservation, Ellenberg values, fire, functional types, blanket bog

INTRODUCTION

The use of prescribed burning for conservation purposes is controversial wherever it is practiced worldwide, such as Australia (Murphy et al., 2015), Africa (Johansson & Granstrom, 2014; Cowell & Cheney, 2017), Mediterranean areas (Paniw et al., 2015) and the boreal region (Velle et al., 2014). Part of this is down to the fear that the use of an intervention like fire, which is bound to cause some initial damage to the ecosystem, will provide long-lasting and irrecoverable damage and vegetation change (Cowell & Cheney, 2017). Where fire is used, therefore, it must be accepted that there will be a cyclical post-fire recovery that will at best maintain the biodiversity of the community and if possible enhance it (ecological resilience *sensu* Lepš et al., 1982; Mitchell et al., 1999; Alday et al. 2013). The ideal scenario is to maintain this cycle and avoid severe fires, which could lead to vegetation change.

This is particularly true for dwarf-shrub communities such as heathland and moorlands. These communities occur across the globe and are often composed of at least some fire-adapted, flammable plant species (Måren et al., 2012; Santana & Marrs, 2014), and in some cases the communities have been created and maintained by human action (Gimingham, 1972). However, whilst any fire-adapted community can be managed by prescribed burning they are by definition a high risk for wildfires; these can be created naturally by lightning, accidentally through fires escaping from a prescribed burn or recreational use, or by vandalism (Albertson et al., 2009; Log et al., 2017). In the UK, lightning-induced fires are rare, escapes from prescribed burns should be confined to the legal burning period (1 October-15 April depending on location and altitude, DEFRA, 2007), whereas escapes from recreational use and vandalism fires are concentrated in spring and summer. Irrespective of the cause of the wildfire, prescribed burning is often viewed as an important tool for minimizing wildfire damage (Cowell & Cheney, 2017; Davies et al., 2016a).

The plant communities in the north-temperate and boreal regions are of particular interest because many of them are peat-forming and are an important resource for meeting carbon sequestration targets (IPCC, 2014). The aim should be to manage them so that they are maintained as carbon sinks rather than sources. In spite of its importance, there are relatively few long-term experiments to provide information on the impact of prescribed burning on such ecosystems; this is partly because their slow growth-rates and long-term management cycles means that experiments must run over decades rather than years. In this paper, we

report the results of one intervention experiment where prescribed burning rotations have been compared over a 60-year period on moorlands growing on peat in upland Britain.

Prescribed burning on British moorlands

Moorland vegetation on peat in upland Britain is deemed to be degraded because of historic pollution, overgrazing and inappropriate burning regimes (Bain et al., 2011; Harper et al., 2018). The current land use in many areas involve the use of prescribed fire coupled with low-intensity sheep grazing. This prescribed burning is used primarily to increase red grouse (*Lagopus lagopus scotica* Latham) productivity for sporting purposes and to a lesser extent sheep grazing. This management is implemented over relatively large areas Great Britain, being present in 8551 1-km squares with one-third of these squares on peat ≥ 0.5 m in depth Douglas et al. (2015).

The role of prescribed fire is currently the matter of contentious debate both in the popular press (RSPB, 2014) and in the scientific literature (Bain et al., 2011; Davies et al., 2016a,b; Brown et al., 2016, Douglas et al., 2016; Harper et al., 2018). The central issue is the degree of damage that the prescribed fire does to the peatland ecosystem and associated ecosystem services relative to the damage that could occur through wildfire (Allen et al., 2013; Santana et al., 2016). That prescribed fire damages the ecosystem is not under dispute. Once a decision is made to burn it must be accepted that there may be: (a) loss of carbon and other nutrients in smoke and run-off (Allen et al., 2013), (b) damage to the underlying peat with reduced C accumulation (Garnett et al., 2000), and (c) differential effects on species abundance at least in the short-term. The effects on species abundance may be short-term with relatively rapid recovery within a post-fire succession; in Britain, this recovery is often controlled by the response of *C. vulgaris* via seed germination or resprouting (Gimingham, 1972; Harris et al., 2011).

There is also no doubt that damaging impacts of fire occur across a continuum from those that have a very high intensity and severity (*sensu* Keeley, 2009) through to ones where the severity is rather light with only a small fraction of the surface vegetation removed. As a crude generalization, we would expect that prescribed burning on British moorlands would produce fires that are likely to be at the less severe end of the continuum and summer wildfires are likely to be more severe. Wildfires are common in upland Britain (Albertson et al., 2009, 2010) and they can be particularly damaging, especially in drought years, when the soil and

vegetation become extremely dry (Maltby et al., 1990) or when a summer wildfire is followed by severe autumn rainfall (Anderson, 1997). Where fire burns into the peat it can smoulder for months (Maltby et al., 1990; Davies et al. 2013), and as such peatlands can contain substantive quantities of heavy metals (Rothwell et al., 2007; Turetsky et al., 2006) burning can release these metals into the atmosphere (Turetsky et al., 2006).

The rationale behind confining the UK legal burning season to winter and early-spring is to minimize ecosystem damage, i.e. to (a) protect ground-nesting, breeding birds, and (b) produce fires that have a lower intensity and are less damaging than late-spring, summer and early-autumn fires. When the fires are lit in the burning season the soil and surface vegetation should retain a greater moisture content than in other seasons (Harris et al., 2011).

The use of prescribed burning has important economic consequences. It is deemed essential for driven-grouse shooting, estimated as worth £90 million of direct income to sporting estates and £750 million of Gross Added Value between 2004

and 2006 (PACEC, 2006). However, upland catchments with a high moorland component are used to collect potable drinking water and prescribed burning has been attributed as a contributory factor to the recent increased colouration of the water. To purify this water for human consumption is costly (Yallop & Clutterbuck, 2009). For carbon management, less information is available, but initial modelling studies of above-ground carbon (peat was not included) in relation to both rotational prescribed burning frequency and wildfire indicate that the prescribed fire frequency that minimizes carbon loss varies markedly across Great Britain (Allen et al., 2013; Santana et al., 2016).

In a recent review of prescribed burning, Davies et al. (2016a) identified a series of contentious issues that need to be tested for British moorlands. Two of these are tested here; we hypothesised that regular prescribed burning:

1. Increases the dominance of the shrub *Calluna vulgaris*, presumably to the detriment of other species.
2. Kills or significantly damages *Sphagnum* spp.

These hypotheses are consistent with the current conservation objective for this type of vegetation, which is primarily to maintain and enhance the peat system and its associated ecosystem services. Hence, the target vegetation should ideally have more peat-forming species such as *Sphagnum* spp. and *Eriophorum* spp. and a lesser amount of *C. vulgaris* (Bain

et al., 2011). Therefore, the vegetation produced during the use, or not, of prescribed burning is likely to differ and the balance of peat-forming/no-peat-forming species present in the resulting vegetation will impinge on C sequestration (Bain et al., 2011). Moreover, from a biodiversity perspective, it is also important to consider impacts of burning on the balance between all the component species within the vegetation. Therefore, here we also assessed impacts of burning on both the plant community and other component species.

We test these hypotheses using a long-term experiment on Hard Hill at Moor House National Nature Reserve (NNR) in northern England. The experiment was set up in 1954 to test the effects of different burning rotations (every 10- and 20-years) against a single burn at the start, all with and without low-intensity sheep grazing. Early assessments of change within this experiment produced excellent initial summaries even though not all the treatment effects could have been detected at that time (Rawes & Hobbs, 1979; Hobbs, 1984). A further analysis (Lee et al., 2013a) produced analyses of all treatments, but not all parts of the burning cycles had been completed. It is only now after new data collection in 2013 that it is possible to compare all the treatments at similar stages of their development, i.e.:

- (a) The 10-year rotation has had six burn cycles – most intensively-burned,
- (b) The 20-year rotation has had three burn cycles – intermediate disturbance, and
- (c) The unburned since 1954/5 has had sixty years of recovery after burning – least intensively-burned.

Here, we report the effects of these three long-term, burning-rotation treatments with and without sheep grazing on plant communities, individual species and species functional groups over a 60-year period. We aimed to inform the debate on the use, or not, of repeated prescribed burning within a conservation setting that aims to maintain or improve the conservation value of these degraded ecosystems.

METHODS

Site details

The experiment is located at Hard Hill (Latitude 54°41.5'N, Longitude 2°24.6'W); on a gently-sloping, high-level plateau at an altitude of 600-650m within the Moor House National Nature Reserve in the northern Pennines, England Heal & Smith, 1978). The vegetation overlying the experimental areas is dominated by *Calluna vulgaris*, *Eriophorum vaginatum* and *Sphagnum* spp., and would be classified as M19 (*Calluna vulgaris*-*Eriophorum vaginatum* blanket mire) in the British National Vegetation Classification (Rodwell, 1991). The vegetation grows on peat (1.5-2.5 m deep) overlying almost horizontal beds of limestone, sandstone and shale (Heal & Smith, 1978). The peat is dissected by natural gullies but there has been no activity to improve drainage. The climate is cold and wet with January and July mean temperatures of 0.9°C and 12.2°C respectively and an average annual precipitation of 2054 mm (ECN, 25-year means, www.ecn.ac.uk).

The full experimental design and sampling methodology is detailed in Marrs et al. (1986), Lee et al. (2013a) and Methods S1.

Experimental Design

The experiment was set up in 1954 on vegetation considered to have remained unburned or at least 30 years (Rawes & Hobbs, 1979). Four replicate moorland blocks (A-D), each contain two main-plot treatments: (a) grazed, sheep-grazing allowed, and (b) Ungrazed, no sheep-grazing. Within each main plot, three burning rotation treatments were allocated randomly to sub-plots: (i) Short-rotation burning (S, approximately every 10 years), (ii) Long-rotation burning (L, approximately every 20 years, (iii) unburned since year 1954/5 (N, one burn at outset). Species composition was recorded five times between 1972/3 and 2013 using point quadrats, seven years after the 1965 burn (the second short rotation burn) and then at approximately decadal intervals to maintain the same post-burn vegetation age for the short-rotation burn at each survey date. For 1972 and 2013, complete data on vertical stratification for vascular plants were available and it was possible to test for changes in vegetation structure (Methods S1 for recording details).

Statistical analysis

All analyses were performed in R v.3.0.2. (R Core Team, 2013), the 'vegan' package was used for all community analyses (Oksanen, 2011).

The relationship between the species community data was explored using Non-metric Multi-Dimensional Scaling (NMDS) using the 'metaMDS' function (mean stress value of 0.23 over 50 runs). Significance of treatment effects was assessed using Permutational Analysis of Variance using the 'adonis' function where the input was a Bray and Curtis distance matrix created by the 'vegdist' function' and the experimental design defined using the 'how' function and the maximal possible number of permitted permutations. Treatment effects were visualised with 2-dimensional standard deviational ellipses fitted using the 'ordiellipse' function.

Thereafter, a Principal Response Curves analysis (PRC, van den Brink & ter Braak, 1999) was performed to quantify the interaction between grazing x burning treatments through time ('prc' function). PRC plots the temporal changes in species composition (Hellinger-transformed) for selected treatments as deviations from a "designated control" treatment represented as a zero line. Here, the "designated control" treatment was the sheep-grazed (G) no burn since 1954 (N) treatment. The model and first axis of the PRC were assessed using randomization tests with the reduced model and 999 permutations, stratified within block per year. The species weights represent the affinity of each species with the treatments analysed.

Univariate analyses

Twenty three response variables were analysed, including the abundance of 11 of the most common species: the four dominant species identified in previous analyses of these data (*C. vulgaris*, *E. vaginatum*, *Hypnum jutlandicum* and *Sphagnum* spp., plus seven sub-dominant species, two vascular plant species (*Empetrum nigrum*, *Rubus chamaemorus*), two mosses (*Campylopus paradoxus*, *Pohlia nutans*) and three liverworts (*Calypogeia muelleriana*, *Cephalozia bicuspidata*, *Lophozia ventricosa*). In addition, ten derived variables were also calculated for each quadrat, these were: four taxonomic groups (vascular plants, liverworts, mosses and lichens), species richness, Shannon-Weiner diversity index and abundance-weighted Ellenberg values for; moisture (F), light (L), soil fertility (N) and acidity (R) abstracted from Hill et al., 2004 for vascular plants; Hill et al., 2007 for bryophytes.

Each univariate analysis consisted of one continuous predictor (elapsed time since the first burn) and burn [N, L, S] and grazing [G, UG] treatments in factorial combination. The intercept was the “business-as-usual” scenario of sheep grazing (G) with the no burning since 1954 (N) treatment. Goodness-of-fit for all models was compared using AIC values and graphical assessment of observed *versus* expected proportion of zeros, and the sample mean-variance relationship (Warton, 2005). Preliminary analyses on almost all the datasets showed that for the species data, there was no additional benefit for employing mixed-effects models to account for block and main-plot effects. Four different analyses were performed:

1. The abundance of *C. vulgaris* and *E. vaginatum* were modelled using the ‘glm’ function using a Poisson error structure.
2. As the abundance of *Sphagnum* spp. proved difficult to fit and would not converge, the probability of *Sphagnum* spp. occurrence was modelled using the ‘glm function’ with a binomial error structure.
3. The abundance of *H. jutlandicum*, all of the sub-dominant species and the total Lichen spp. had a large number of zeroes so a zero-inflated modelling approach was used; here only the count part of the model is presented, both were fitted with a Poisson distribution.
4. The total number of species and the weighted Ellenberg score were analysed using the ‘lm’ function.

Results for total abundance of liverworts and mosses are not reported as they were better represented by the dominant contributing species.

Effects on vegetation structure (pin hits per strata) was modelled in response to the interaction of vegetation strata height (four strata; >30 cm, 20-30 cm, 10-10 cm and 0-10 cm), burning treatment, grazing treatment and elapsed time using a GLMM with Poisson error distribution and block as a random effect. The model was run using the lme4 package (Bates et al., 2015).

Detailed outputs of these univariate analyses are provided (Tables S1-S5) with a summary table on all Figures to aid interpretation.

RESULTS

Community Analyses

The four dominant species within the communities are distributed along axis 1 on the NMDS biplot (Figure 1a,b), centred around the origin but producing a sequence from *C. vulgaris* with a negative score of -0.32; *Sphagnum capillifolium* with -0.11 through to the two *Eriophorum* spp. with positive scores of 0.27 and 0.17. Species that were associated with the negative end of axis 1 were pleurocarpous mosses (*Aulacomnium palustre*, *H. jutlandicum*, *Plagiothecium undulatum*, *Pleurozium schreberi*) whereas at positive end the main species were acrocarpous mosses (*C. paradoxus*, *P. nutans*), liverworts (*C. bicuspidata*, *C. connivens*, *L. ventricosa*) and green algae.

Permutational anova showed only significant effects of the three main factors (Grazing, $F=22.68$, $P<0.001$), Burning, $F=146.34$, $P=0.005$, Elapsed Time, $F=134.26$, $P=0.005$) plus the interaction between burning x elapsed time ($F=32.98$, $P<0.005$); all other treatment interactions were not significant ($P>0.05$). The effects of grazing (Figure 1c) were relatively minor with a great deal of overlap between grazing treatments. However, removal of sheep grazing moved the community in a negative direction, i.e. away from *E. vaginatum* towards *C. vulgaris*.

The burning x elapsed time interaction produced clear different treatment trajectories (Figure 1d-e). All treatments started more or less in the same position in 1972, thereafter there was considerable divergence in trajectories. By 1982, the N treatment moved in a negative direction towards *C. vulgaris* and *H. jutlandicum* and remained in the same area until 2013 (Figure 1d). The S treatment remained mainly at the negative end of axis 1 associated with *Eriophorum* spp. (Figure 1f), whereas the L treatment was intermediate in position, straddling the origin (Figure 1e). Both S and L burning treatments showed considerable changes between-samplings, almost showing cyclic changes.

The PRC analysis for the burning x grazing interaction was significant ($P<0.001$, pseudo- $F = 302.4$ Figure 2). The N treatment showed almost no difference between grazing treatments and they were situated at the mid-point of the species-weights axis. After 60 years the S treatment had the largest negative effect relative to the N treatment (i.e. towards *Eriophorum* spp.), with the L treatment having a lesser effect. In the S treatment the grazed treatment was almost linear but the ungrazed treatment showed a slight zig-zag

trajectory associated with timing of burn application. This zig-zag effect was more pronounced in the L treatment which resembled the S treatment in the early part of its rotation (i.e. seven years after both the S and L treatments were last burnt) but was closer to the N treatment towards the end of its rotation (17 years after burning). Removal of sheep grazing slightly enhanced the move towards *Eriophorum* spp. in both S and L treatments

Response of Community Properties, Major Species and Functional Types

Community properties

Overall diversity (Shannon-Weiner index) reduced through time in the N treatment; there was no effect of grazing treatment (Figure 3a). Both S and L treatments had a greater diversity index than the N treatment; both also increased with time in the grazed treatment but decreased when grazing was removed. The S treatment had the greatest diversity index. The number of vascular plants showed no temporal change in the N treatment (Figure 3b), but significant increases through time in both the S and L treatments with the rate of change increasing with increasing burn frequency. Grazing treatment had no effect through time, but there was a significant grazing x burning interaction (Figure 3c) with a decrease in vascular plant abundance in the ungrazed N treatment compared to the grazed treatment and the opposite in the S-treatment; there was no difference between sheep grazing treatments in the L-treatment.

Vascular plants

C. vulgaris abundance was greatest in the N treatment and there has been a slight increase through time and no significant difference between the grazing treatments (Figure 4a). At the start, S and L treatments had lower *C. vulgaris* abundance than the N one, with the S treatment having the lowest; both the S and L treatments increased through time but the linear models fitted masked considerable fluctuations associated with the reduction of this species immediately after burning followed by recovery. There was little difference between grazing treatments in the L treatment but a significantly greater abundance in the ungrazed S treatment.

E. vaginatum abundance only showed significant effects in response to grazing and burning treatments; there were no significant temporal effects (Figure 4d). Abundance was increased

in the ungrazed treatments and by increasing burning frequency (Fig, 4d). *E. nigrum* showed opposing responses in the N treatment, decreasing where sheep-grazed and increasing where there was no grazing (Figure 4b). In the L-treatment, *E. nigrum* had a low abundance where sheep grazed, and a greater abundance when ungrazed; both declining through time. In the S treatment there was low abundance in the sheep-grazed plots and a much greater abundance when ungrazed; this species increased slightly in the former and decreased significantly in the latter. *R. chamaemorus* only showed significant effects in the S treatment, where abundance was generally greater than the other treatments at the start but this was followed by a subsequent decline (Figure 4c). There were no effects of sheep grazing.

Mosses

The probability of occurrence of *Sphagnum* spp. in the N treatments remained constant through time (Figure 5a); the probability of occurrence in the grazed S and L treatments started at the same order of magnitude as the N one, but both increased through time. In the ungrazed S and L plots the probability of occurrence for *Sphagnum* spp. was greater than their grazed counterparts, especially in the S treatment, but the rate of increase through time was less. *H. jutlandicum* showed a massive increase through time in the N treatment from the 20-year mark (Figure 5b), and removal of grazing enhanced this increase. In the L treatment, there was an approximate 20-year delay before this species increased, and there was no increase in the S treatment. *C. paradoxus* showed an increasing abundance with increasing burn frequency (Figure 5c) but differing responses through time, a reduction through time in the N treatment but increases in both S and L treatments. Removal of sheep grazing reduced the decline in the N treatment but produced a reduction in both S and L treatments. *P. nutans* showed a decline in all three burning treatments but the greatest decline was in the S treatment, and this is partly because of its much greater starting value (Figure 5d). Removal of sheep grazing accelerated these declines.

Liverworts and lichens

The three species of liverwort tested (*C. muelleriana*, *C. bicuspidata*, *L. ventricosa*) showed similar declines through time in the N grazed treatment (Figure 6); the ungrazed comparison also showed similar responses although they started at a slightly lower abundance. The abundance of all three species was greater in S and L treatments, but *C. muelleriana*

increased through time (Figure 6a) and the other two species declined (Figure 6b,c). In the burn rotations removal of sheep grazing usually produced a more negative slope compared to their grazed comparators. Total lichen cover reduced in all treatments but at differing rates; fastest in the N treatment, intermediate in the L and slowest in the S treatment (Figure 6d). Removal of sheep grazing slowed this decline with increasing burn frequency.

Plant functional groups

The weighted mean Ellenberg values show that in the N treatment there is either no change in light or fertility, or a reduction in moisture and reaction scores; there was no effect of sheep grazing in this treatment (Fig. 7). The L treatment showed an increase in all four Ellenberg values through time; removal of sheep grazing either had no significant effect (L=light, N=fertility, Fig. 7a,c), or there was a slightly reduced rate of increase (F=moisture, R=reaction, Fig. 7b,d). The S treatment showed an increase in moisture, light and reaction (Fig. 7a,b,d) but a reduction in fertility (Fig. 7c); removal of sheep grazing reduced the rate of increase of moisture, light and reaction but completely reversed the response of fertility with a large increase through time. The modelled responses concealed large fluctuations in all treatments with the means of the raw data indicating reductions in the middle of the sample period followed by recovery (Fig. 7).

Vegetation structure

The height profiles of the vegetation show clear differences between the S treatment and both the L and N ones (Figure 8). The S treatments had a height profile that was greatest in the bottom two layers (0-20 cm) with a marked reduction above 20 cm ($P < 0.001$) (Figure 8c). The vegetation in L and N treatments produced a vegetation with curvilinear height profile (Figure 8a,b); here there was a lower number of hits in the bottom (0-10 cm) and top (>30 cm) layers and a greater number of hits in mid profile (10-30 cm). The number of hits in the surface profile of the L treatment was significantly lower in the ungrazed compared to the grazed treatments ($P < 0.01$, Fig. 8c). It should be noted that dead material was not counted systematically at each pin position and the profiles for N and L treatments reflect living plant material overlying a dense layer of litter.

DISCUSSION

Effects of burning and grazing on the moorland vegetation

The aim of this paper was to determine the relationship between three prescribed burning rotations in interaction with, and without, sheep grazing on the dynamics of moorland communities growing on peat along with their component species within a 60-year experiment. The cessation of burning and two burning treatments represent the extremes of management suggested for these ecosystems in upland Britain for both conservation (less burning) and grouse moor management (more burning). Experimentally, they reflect increasing levels of disturbance (N = least-, L = intermediate-, S = most-frequently burned).

We tested two hypotheses based on Davies et al. (2016a), that prescribed burning:

1. Increases the dominance of the shrub *C. vulgaris*, presumably to the detriment of other species.
2. Kills or significantly damages *Sphagnum* spp.

Both of these hypotheses were rejected. The first because *C. vulgaris* became dominant in the least-frequently burned (N) treatment and had the lowest abundance in the most frequently-burned (S) treatment. This result is reinforced by the high *C. vulgaris* cover detected in plots unburned since ca. 1923 adjacent to this experiment (Lee et al., 2013a). The second hypothesis was rejected because the *Sphagnum* spp. component showed a reverse trend, being most abundant in the most-frequently burned (S) treatment, and least abundant in the least-frequently burned (N) treatment.

Removal of sheep grazing had a lesser overall impact than the burning treatments, but there were a few minor impacts on individual species.

Effects of increasing disturbance on the balance of species

In all treatments the main component species of the typical moorland communities that would be expected on this site to meet its conservation objectives were present; i.e. either a M19 (*C. vulgaris*-*E. vaginatum* blanket mire) or a M20 (*E. vaginatum* blanket and raised mire) community (Rodwell, 1991). However, the treatments imposed important differences in both the relative abundances and the change in abundances through time.

Increasing the burning frequency increased the species richness of vascular plants with time, whereas a reduction in grazing reduced richness of vascular plants. This increased

biodiversity after prescribed burning is consistent with other results from the British uplands (Harris et al., 2011), and elsewhere (Johansson & Granstrom, 2014; Murphy et al., 2015; Paniw et al., 2015; Velle et al., 2014). We can speculate that both these results are a function of either the increasing light levels through the canopy or the creation of suitable substrate or microclimatic conditions for seed germination and subsequent establishment (*sensu* Harper, 1977); both being greatest in the most-disturbed, i.e. the frequently-burned (S), grazed treatment.

The multivariate analyses showed that although all treatments were similar at the start they diverged through time. The least frequently-burned (N) treatment was associated with pleurocarpous mosses whereas the most-disturbed (S) treatment was associated with *Eriophorum* spp., *Sphagnum* spp., acrocarpous mosses and liverworts; the intermediate (L) treatment was in-between. Removal of sheep grazing moved the community in a similar direction as the least-disturbed (N) treatment. Both NMDS and PRC analyses highlighted marked fluctuations in community response associated with the timing of fires and subsequent post-fire recovery.

The results are best discussed by considering the two extreme disturbance treatments (S and N treatments).

The least-disturbed (N) treatment: no-burn since 1954

In this least-disturbed treatment, there was an increased abundance of two species, *C. vulgaris* and *H. jutlandicum* compared to the other burning treatments; both also increased through time. In contrast, *E. vaginatum* and *Sphagnum* spp. showed a lower abundance, and *Sphagnum* spp. reduced through time. This is in contrast to widely-held beliefs that a no burning policy will lead to greater *Sphagnum* cover (Bain et al. 2011).

Removal of grazing changed the response of *E. nigrum* and *Sphagnum* spp. from a negative to a positive one indicating that these two species might be very sensitive to the sheep grazing-intensity.

This unburned vegetation is probably moving in the direction of an H12 upland heathland community (Rodwell, 1991) with a *Calluna vulgaris*-dominated canopy layer and a ground flora dominated by pleurocarpous mosses; this change would not meet conservation objectives.

The most frequently-disturbed (S) treatment: 10-year burn cycle

In this most disturbed treatment, *C. vulgaris* had the lowest abundance, and although it was increasing slowly through the study period it was always lower than the less-disturbed treatments. *H. jutlandicum* remained low, whereas *E. vaginatum* and *Sphagnum* spp. had the greatest abundance compared to other burning treatments and *Sphagnum* spp. was increasing through time. Interestingly, *Sphagnum* spp. had a much greater probability of occurrence in the ungrazed treatment throughout, and assuming that there were no inherent distributional differences within this randomized design at the start of the experiment, suggests that there was a very rapid expansion in the first twenty years of the study. These are important results because it suggests that *Eriophorum* and *Sphagnum* spp., both considered peat-forming species (Bain et al., 2011) can respond positively after prescribed burning, probably because of the reduction in canopy competition from *C. vulgaris*. Amongst conservation bodies, there is a fear that prescribed burning damages peat-forming species (RSPB, 2014); our results suggest that this will not necessarily occur.

R. chamaemorus had the greatest abundance in this treatment, but there were no grazing or temporal effects. The responses for burning are consistent with those of Taylor and Marks (1971), who showed a tenfold increase in *R. chamaemorus* biomass after burning, but not with their reported five-fold increase in the absence of sheep-grazing. Longer-term, more-detailed studies of this species are needed, therefore, to investigate these inconsistencies. The liverworts maintained their presence in this treatment, or increased (*C. mulleriana*), and the reduction in lichens slowed. Removal of sheep grazing increased *C. vulgaris* and *Sphagnum* spp. and lichen abundance but reduced *C. paradoxus*, and most liverworts.

This ten-year cycle of burning is moving the plant community towards the M19 conservation target plant community (M19b, *Calluna vulgaris*-*Eriophorum vaginatum* *Empetrum nigrum* ssp. *nigrum* blanket mire community, Rodwell, 1991).

Effects of increasing disturbance on vegetation structure

Vegetation structure was altered considerably by burning treatment. Most of the living plants are in the lowest vegetation layers in the most-frequently burned (S) treatment but in mid-layers in the later years of the intermediate (L) burn cycle and single burn (N) treatment. As dead material was not counted, this suggests that in the L and N treatments the living material

lies on a bed of dead material (plant litter), whereas in the most-disturbed (S) treatment the living material was concentrated nearer to the peat surface. This drier litter surface may be the reason why the pleurocarpous mosses increased in abundance in the least-disturbed treatments as their straggling growth form allows them to grow through and over the litter and developing vegetation, whereas most acrocarpous mosses and liverworts require more open conditions (Atherton et al., 2010). As vegetation structure is an important factor in determining the intensity and severity of a fire (Davies et al., 2009), the different vegetation structures produced here implies that the burning treatments will increasingly affect fire behaviour with possible feedback effects. The regularly burnt treatments are likely to be less severely affected by wildfire due to the maintenance of a reduced fuel load in the form of living plant and litter material.

Effects of increasing disturbance on mosses, liverworts and lichens

The mosses, liverworts and lichens are key components of moorland plant communities (Rodwell, 1991), but there is very little information about the impacts of land management on these taxonomic groups. Here, the abundance of lichens and liverworts was reduced in the least disturbed (N) treatment, suggesting that the reduced light and lack of gaps under the increasingly dense *C. vulgaris* canopy might be important constraints. This result is in accord with some reported responses elsewhere; i.e. a pulse in the immediate post-fire period after prescribed burning (Burch, 2008; Harris et al., 2011), and in comparisons of bryophyte richness along a sheep grazing intensity gradient where richness was reduced at the high litter and biomass values associated with low grazing intensities (Virtanen & Crawley, 2010). However, our results for *Sphagnum* spp. decreasing in abundance in the plots with the greatest *C. vulgaris* cover conflicts with responses from studies of cryptogams in relation to red deer grazing pressure in wet heath and blanket bog vegetation in north-west Scotland (Moore & Crawley, 2014, 2015b; Moore et al. 2015). In this study, where grazing pressure was reduced, *C. vulgaris* as well as *Sphagnum capillifolium* ssp. *rubellum*, five other bryophyte and two lichen species all increased (Moore and Crawley, 2015a). Clearly, much more experimental work is needed to ascertain the relationship between mosses, liverworts and lichens in relation to the direct effects of management and the indirect effects brought about through modified vegetation structure, including both living and litter components.

Effects of increasing disturbance on plant functional types

The changes in plant functional types are important because they give an indication as to the possible environmental drivers involved in controlling species presence/abundance. The positive responses to moisture and reaction (Ellenberg-F and R) indicated that the treatments were producing a vegetation composed of species that preferred moister and less acidic conditions. Species in the most-frequently burned (S) and intermediate (L) treatments also increased with respect to light requirements (Ellenberg-L) suggesting that the species were responding to canopy opening through disturbance allowing more light in. Conversely, the lack of response to light in the least disturbed (N) treatment suggests that the dense canopy cover is restricting species with greater light requirements. This is in keeping with the responses about individual species noted earlier, and especially the bryophyte and lichen responses (Burch, 2008; Virtanen & Crawley, 2010; Harris et al., 2011, Moore & Crawley, 2014, 2015b; Moore et al. 2015).

The results for acidity and fertility, Ellenberg-R and –N respectively, must also be viewed against the changing atmospheric depositions patterns occurring over Great Britain over the last 60 years. In the UK, sulphur emissions peaked in 1970 and have been reduced by a factor of ten since then; this has translated into reductions in both dry and wet sulphur deposition of 92 % and 67% respectively between the mid 1980's and 2008 (RoTAP, 2012). The observed increases in Ellenberg-R values found here for the L and S-burning treatments suggests that disturbance has increased the abundance of species that grow in slightly less acidic conditions, and is consistent with reduced acidification. Similar signals have been detected in other long-term studies in upland Britain (Rose et al., 2016; Mitchell et al., 2018). Here, in the least disturbed (N) treatment, there was no significant recovery.

Nitrogen deposition has also varied over the study period, peaking in 1990 and reducing by about 70% by 2010 (RoTAP, 2012). Ellenberg-N values again showed no effect in the least-frequently burned (N) treatment, an increase in the intermediate (L) treatment (i.e. species of greater fertility), but a decrease in the most frequently burned (S) one (species of lesser fertility). This suggests that increased burning frequency produces a tipping point between the twenty-year rotation (L) and ten-year (S) one, with the shorter rotation negating any effects of atmospheric nitrogen deposition. Essentially, these communities are very finely-

balanced with respect to atmospheric nitrogen deposition. Importantly, the least-disturbed (N) treatment showed no response.

The Ellenberg-R and –N responses are consistent with the changing impact of atmospheric sulphur and nitrogen deposition and the consequent impacts that have been reported in a range of British ecosystems (Maskell et al., 2010; Armitage et al., 2012; Rose et al., 2016; Mitchell et al., 2018). Again, these responses are speculative and require testing by further monitoring and additional experiment.

Limitations of this investigation

Like any long-term study, the study could have been improved with hindsight. The experiment did not have baseline monitoring although all treatments were set up on “uniform vegetation” (Rawes & Hobbs, 1979). The current monitoring with pin quadrats started in 1972/3 and there is no comparable information before then. There also is no formal control because there is no unburned treatment. Some grazed, unburned plots are available adjacent to each block, but there is no ungrazed comparator and they have been sampled sporadically using different methods to the main experiment (Lee et al., 2013a). Moreover, our analyses use simple linear models to detect direction of change; more complex models would be counter-productive with data from only five time-points available.

One problem that could not have been foreseen is that conditions at the site has changed through time. The sheep grazing pressure has, for example, changed as a result of national and local grazing policies, reducing from ca.15,400 to ca. 7000 sheep in the early 1970s, and to 3500 sheep ha⁻¹ in the early 2000s (Milligan et al., 2016). As blanket bog vegetation has the lowest grazing pressure on this reserve (Rawes & Welch, 1969), the experimental grazing pressure has gone from low to very-low. Moreover, the changing pollutant load noted above will almost certainly also have contributed to vegetation change.

Burn characteristics; burn intensity and severity (*sensu* Keeley, 2009) will also vary depending on a range of factors including fuel load, pre-burn and prevailing weather conditions such as wind speed, as well as the vegetation type including the amount of fine fuels within the canopy. Subsequent vegetation post-fire will vary depending on post-burn climate, summer temperature and rainfall and the occurrence of very severe winters as well as pollutant load, all of which are known to vary at this site (Monteith et al., 2016).

Lastly, the monitoring methods were designed to assess species occurrence at a standardized detection level. Species that are “new” or “disappear” may still be present at low occurrence. So for example, *Sphagnum subnitens*, a species of relatively nutrient-rich conditions (Ellenberg value = 2 compared to *S. capillifolium* = 1, Hill et al., 2007) has appeared recently and this might result from recent elevated nitrogen loads increasing (a) its colonization, (b) abundance from an existing low population, or (3) both. We do not have the information to determine which with these data. Site-based change must be also viewed against national trends; for example our measured reduction in *P. nutans* is consistent with recent national trends (Atherton et al., 2010).

In spite of these issues, this experiment is unique in comparing multiple, long-term, burning rotations on moorland vegetation over relatively long time-scales.

CONCLUSIONS AND IMPLICATIONS FOR CONSERVATION

The results from this long-term experiment provide important information to guide conservation. Importantly, the presumption that rotational prescribed burning of moorland communities dominated by *C. vulgaris* will lead to an increase in its abundance and a reduction in “peat-forming” species (*Eriophorum* spp. and *Sphagnum* spp.) is not supported. Indeed, *C. vulgaris* was lowest and *Eriophorum* spp. and *Sphagnum* spp. in greatest abundance in the most frequently-burned treatment. The low *C. vulgaris* abundance is almost certainly because of a relatively slow post-fire recovery; observations on these plots suggest that *C. vulgaris* takes between seven and ten years after burning to re-assert its dominance (Hobbs, 1984). As *C. vulgaris* is a fire-adapted shrub (Måren et al., 2010; Santana et al., 2016), its dominance in the unburned plots is potentially worrying from a wildfire perspective. *C. vulgaris* biomass increases during the post-fire succession (Santana et al., 2016), so hot summer wildfires could be very intense and cause severe damage. Nature conservation authorities, therefore, have a dilemma, either to burn on rotation to provide vegetation patches of reduced biomass and hence reduced wildfire risk, or to stop burning and risk potentially very serious damage in terms of increasing smouldering fires (Davies et al., 2013), that cause substantive damage to peat and its regeneration potential (Maltby et al., 2013; Lee et al. 2013b). The no-burn option is favoured by some conservation groups to minimize C losses and to assist in water management (RSPB, 2014; Thompson et al., 2016; Harper et al., 2018). Irrespective, to minimize fuels loads and maintain a

vegetation composition similar to the unburned plots, a 20-year burning cycle could be optimal. Given that this site is probably one of the most extreme climatically in England, rotation lengths on other sites with less extreme climates and on different soils might need to be shorter (Santana et al., 2016).

It is also important to consider the associated bryophyte and lichen communities. The pleurocarpous mosses (mainly *H. jutlandicum*) were more abundant in the long-rotation burns (L and especially N) and *Sphagnum* spp., acrocarpous mosses, lichens and liverworts being more abundant in the short-rotation burns (S). The analyses of functional groups and vegetation structure suggest that the light getting through the canopy after burning may be one reason why these latter groups are more abundant in the short-rotation (S) treatment. The very high probability of occurrence of *Sphagnum* spp. in the ungrazed (S) treatment after two burns supports this conclusion. However, this hypothesis remains to be verified by further experiment.

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SUPPORTING INFORMATION

Methods S1. Detailed methodology including Table S1.

Tables S2-S6. Full statistical results of the analyses presented in Figures 3-8.

Accepted Article

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Accepted Article

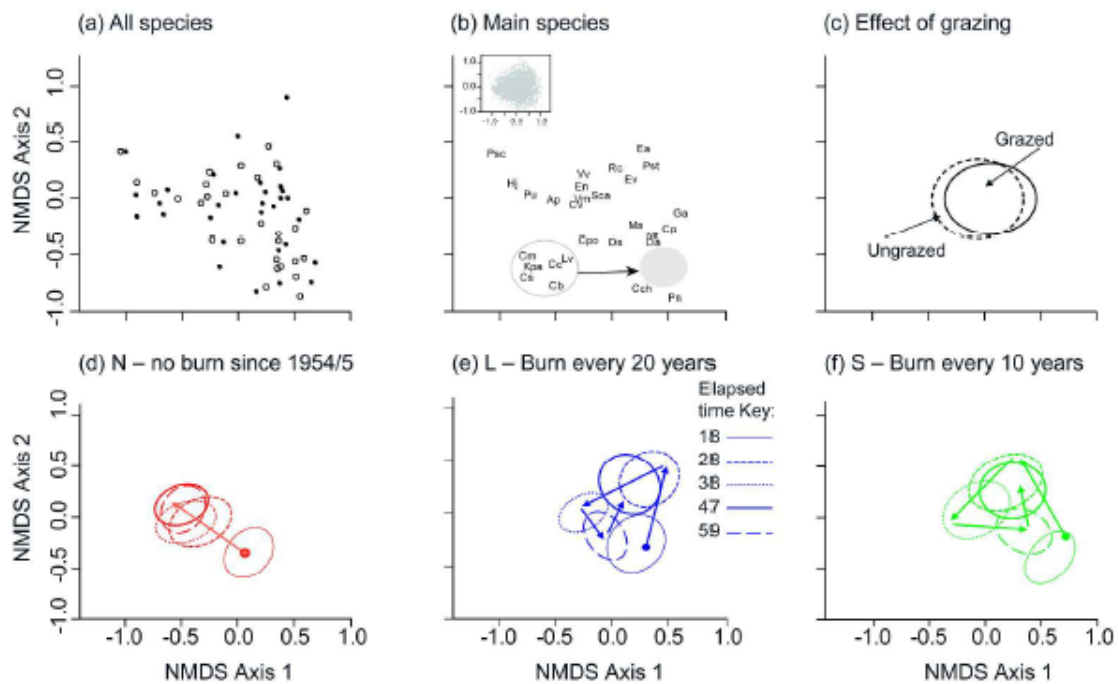


Figure 1. Plots for the Non-Metric Multi-Dimensional scaling analysis of community composition within the Hard Hill grazing and burning experiment at Moor House: (a) all species distribution with the major species identified with the larger symbols, (b) the most abundant species with the quadrat plot as an inset, (c) differences between the two grazing treatments (Grazed= solid line, Ungrazed = dotted line), and (d-f) the three burning rotations through time: (d) N-treatment , no burning since 1954, (e) L- treatment burning every 20 years and (f) S- burning every 10 years. Treatment distributions are illustrated with 2-D standard deviational ellipses; the approximate trajectories of changes through time are arrowed. Species codes: Ap=Aulacomnium palustre, Bf=Barbilophozia floerkei, Ca=Calyptogea azurea, Cb=Cephalozia bicuspidata, Cc=Cephalozia connivens, Cch=Cladonia chlorophaea, Cd=Cephalozia divaricata, Cdi=Cladonia diversa, Cf=Calyptogea fissa, Cfi=Cladonia fimbriata, Cfu=Cladonia furcata, Ci=Campylopus introflexus, Cm=Calyptogea muelleriana, Cp=Campylopus paradoxus, Cpo=Cladonia portentosa, Cs=Cladonia squamosa, Csq=Cladonia squamules/sp, Cv=Calluna vulgaris, Da=Diplophyllum albicans, Dd=Dryopteris dilatata, Df=Deschampsia flexuosa, Ds=Dicranum scoparium, Ea=Eriophorum angustifolium, En=Empetrum nigrum, Ev=Eriophorum vaginatum, Ga=Green algae, Hj=Hypnum jutlandicum, Hp=Hypogymnia physodes, Hs=Hylocomium splendens, Kp=Kindbergia praelonga, Kpa=Kurzia pauciflora, Lb=Lophocolea bidentata, Lh=Lichenomphalia hudsoniana, Lr=Lepidozia reptans, Lv=Lophozia ventricosa, Ma=Mylia anomala, Mh=Mnium hornum, Mt=Mylia taylorii, Os=Odontoschisma sphagni, Pc=Polytrichum commune, Pci=Ptilidium ciliare, Pf=Polytrichum formosum, Pn=Pohlia nutans, Pp=Pseudoscleropodium purum, Psc=Pleurozium schreberi, Pst=Polytrichum strictum, Pu=Plagiothecium undulatum, Rc=Rubus chamaemorus, Rl=Rhytidiadelphus loreus, Rs=Rhytidiadelphus squarrosus, Sc=Scirpus cespitosus, Sca=Sphagnum capillifolium, Sf=Sphagnum fallax, Spa=Sphagnum papillosum, Ss=Sphagnum subnitens, St=Sphagnum tenellum, Tp=Tetraxis pellucida, Vm=Vaccinium myrtillus, Vv=Vaccinium vitis-idaea.

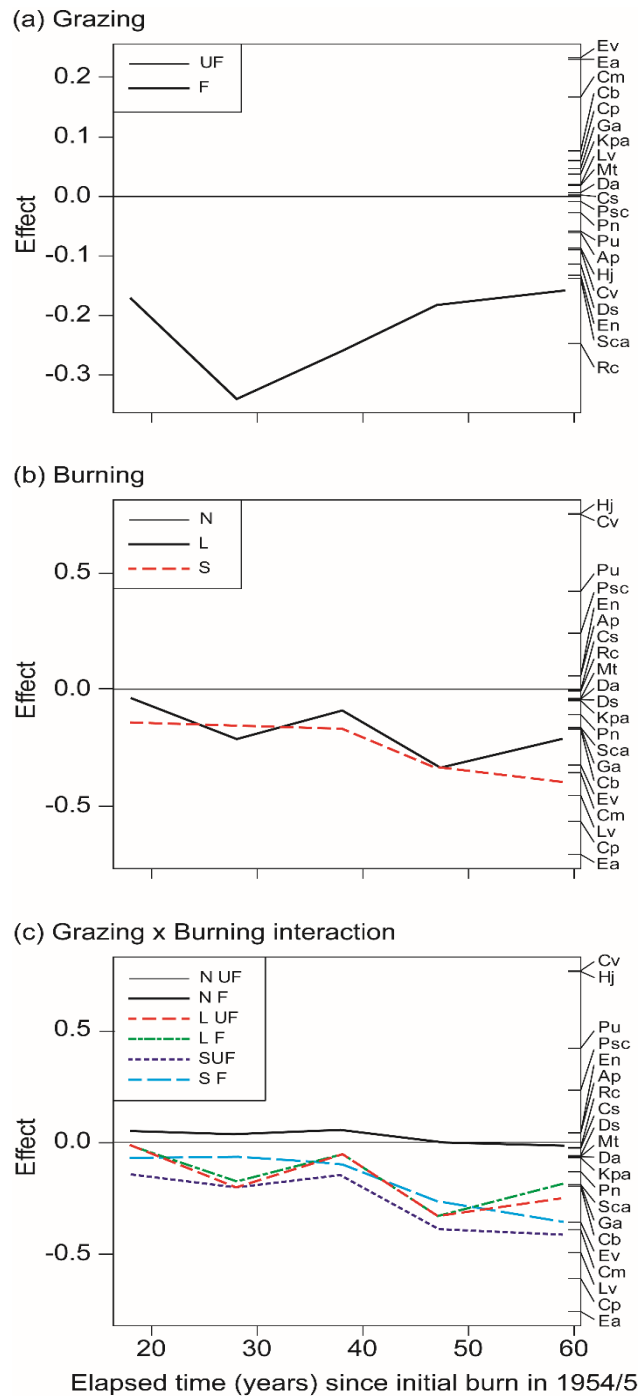
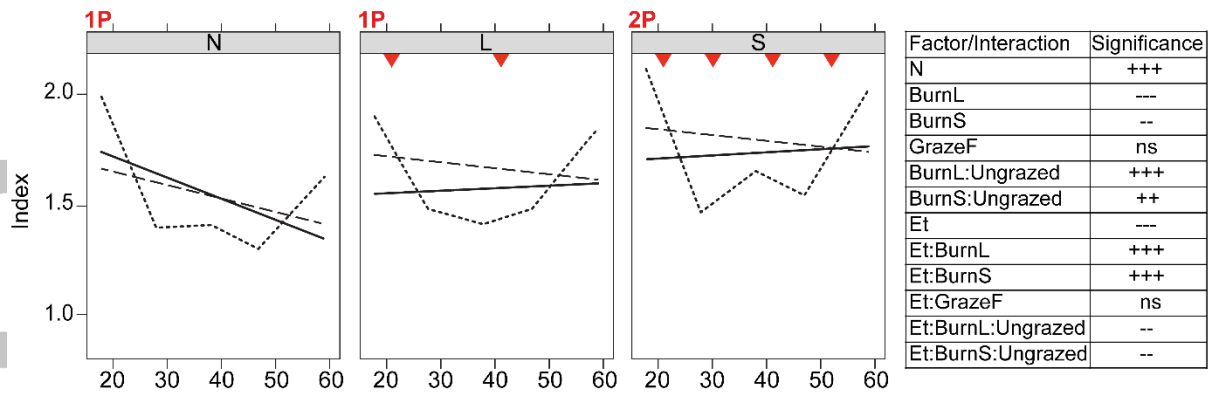
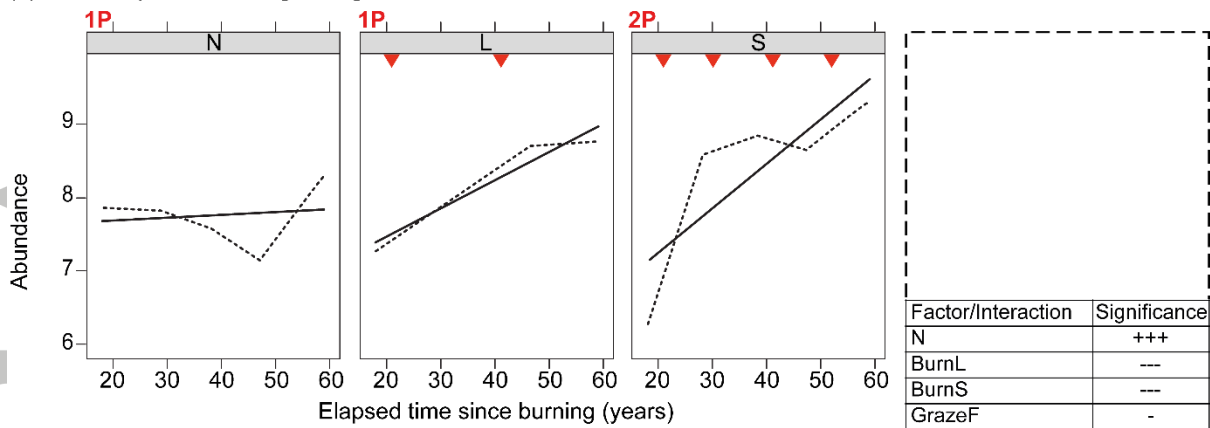


Figure 2. Principal Response Curve analysis of species of community response through time to moorland at Moor House, testing effects of (a) no sheep grazing (F) versus sheep grazed (UF), (b) burning rotations (short (S) and long (L) rotations versus no burn since 1954/5 (N)), and (c) the grazing x burning interaction tested against the UF N treatment). The change in species composition is relative to the first axis of a RDA and the species position on this axis is represented on the vertical axis; only the most abundant species are illustrated; Species codes: Ap=Aulacomnium palustre, Cm=Calypogeia muelleriana, Cp=Campylopus paradoxus, Cs=Cladonia squamosa, Cv=Calluna vulgaris, Ds=Dicranum scoparium, Da=Diplophyllum albicans, Ea=Eriophorum angustifolium, En=Empetrum nigrum, Ev=Eriophorum vaginatum, Ga=Green algae, Hj=Hypnum jutlandicum, Kpa=Kurzia pauciflora, Lv=Lophozia ventricosa, Mt=Mylia taylorii, Pn=Pohlia nutans, Psc=Pleurozium schreberi, Pu=Plagiothecium undulatum, Rc=Rubus chamaemorus, Sca=Sphagnum capillifolium, Vm=Vaccinium myrtillus.

(a) Shannon-Wiener Diversity Index: Burning through time



(b) Vascular plants: Burning through time



(c) Vascular plants: burning x grazing interaction

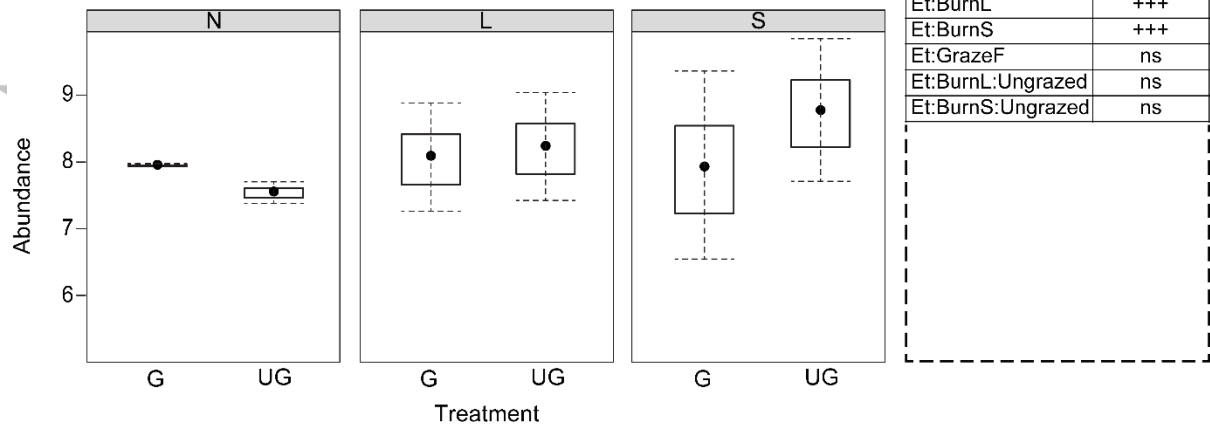


Figure 3. Modelled responses of the interactions between three burning and two grazing treatments applied on moorland at Moor House on community properties: (a) species diversity (Shannon-Wiener index), and (b,c) total abundance of vascular plants. Burning treatments coded: 1P and 2P indicate the number of burns before the modelled period and ▾ indicates burning occasions within modelled period. The modelled grazed and ungrazed responses are denoted with the dark and dashed straight lines respectively; the dotted line indicates the overall mean values for both treatments though time. The side-table provides a summary of the statistical significance (full data in Supplementary Tables): + or - indicates the direction of the response and the number of symbols indicates significance level; one symbol = $P < 0.05$, two = $P < 0.01$, three = $P < 0.001$, ns = $P > 0.05$.

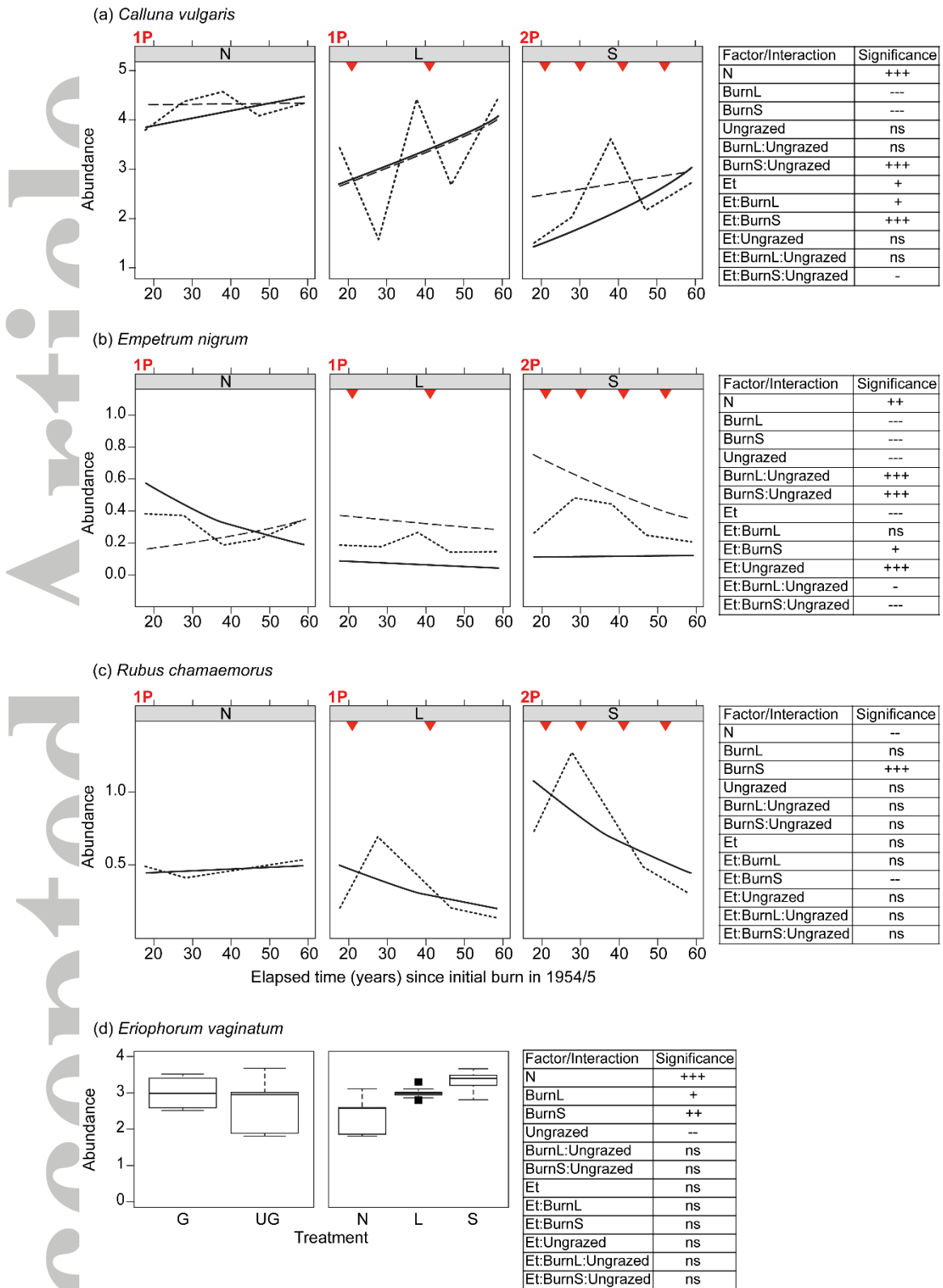


Figure 4. Modelled responses of the effects of three burning and grazing treatments applied to moorland at Moor House on vascular plants: (a) *Calluna vulgaris*, (b) *Empetrum nigrum*, (c) *Rubus chamaemorus*, and (d) *Eriophorum vaginatum*. See Figure 3 for explanation of the codings.

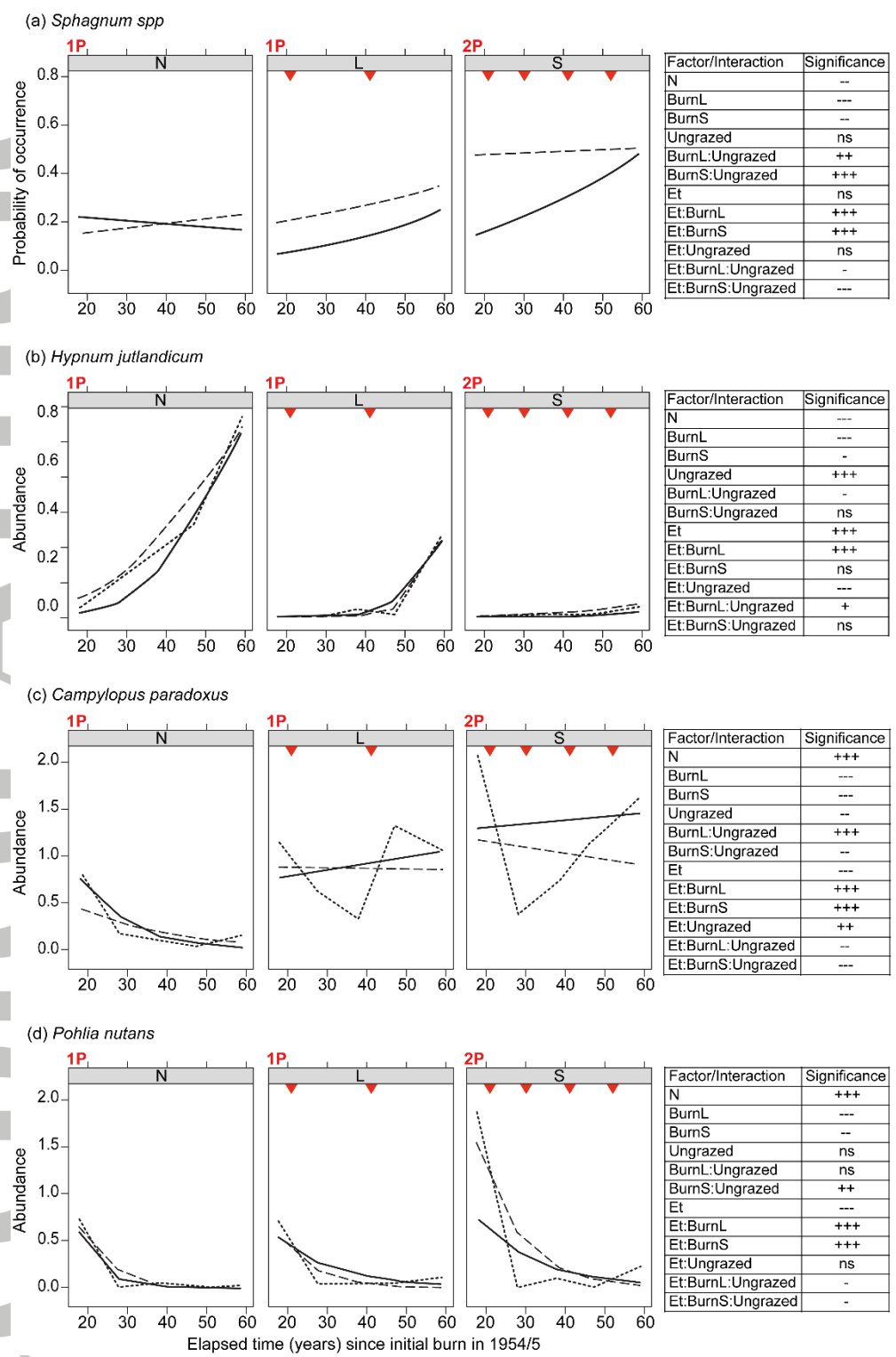


Figure 5. Modelled responses of the effects of three burning and grazing treatments applied to moorland at Moor House on bryophytes: (a) *Sphagnum* spp., (b) *Hypnum jutlandicum*, (c) *Campylopus paradoxus*, and (d) *Pohlia nutans*. See Figure3 for explanation of codings.

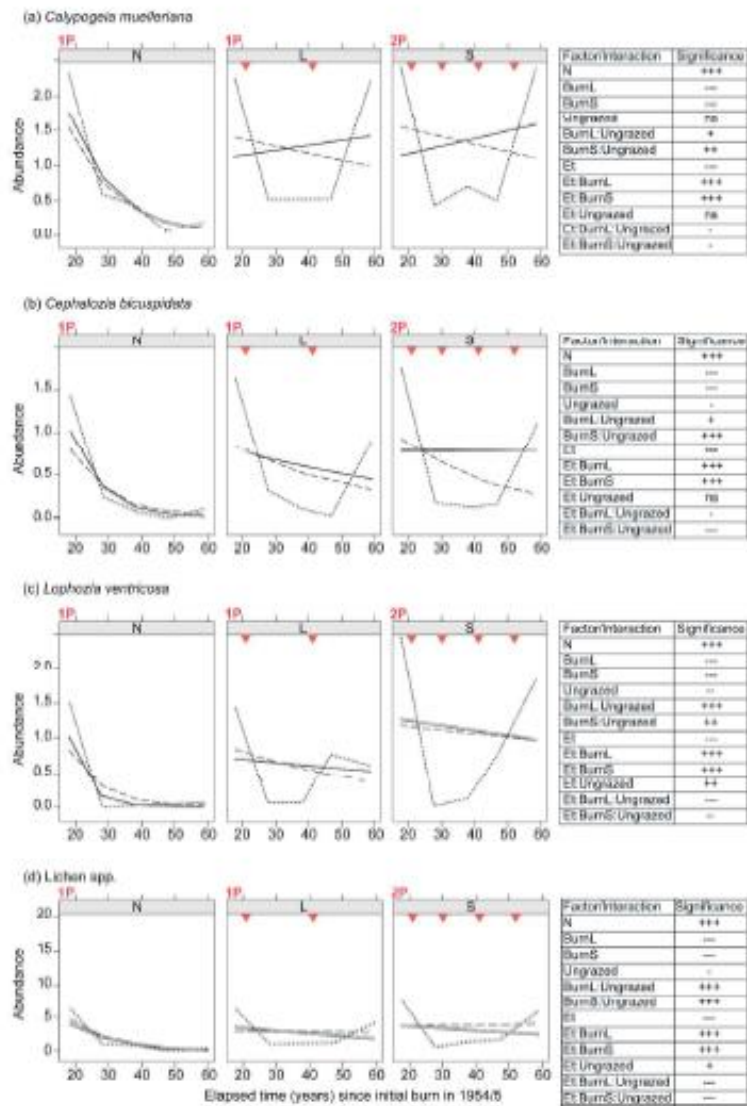


Figure 6. Modelled responses of the effects of three burning and grazing treatments applied to moorland at Moor House on liverworts and lichens: (a) *Calypogeia mulleriana*, (b) *Cephalozia bicuspidata*, (c) *Lophozia ventricosa*, and (d) total lichens, and total lichen abundance. See Figure 3 for explanation of codings.

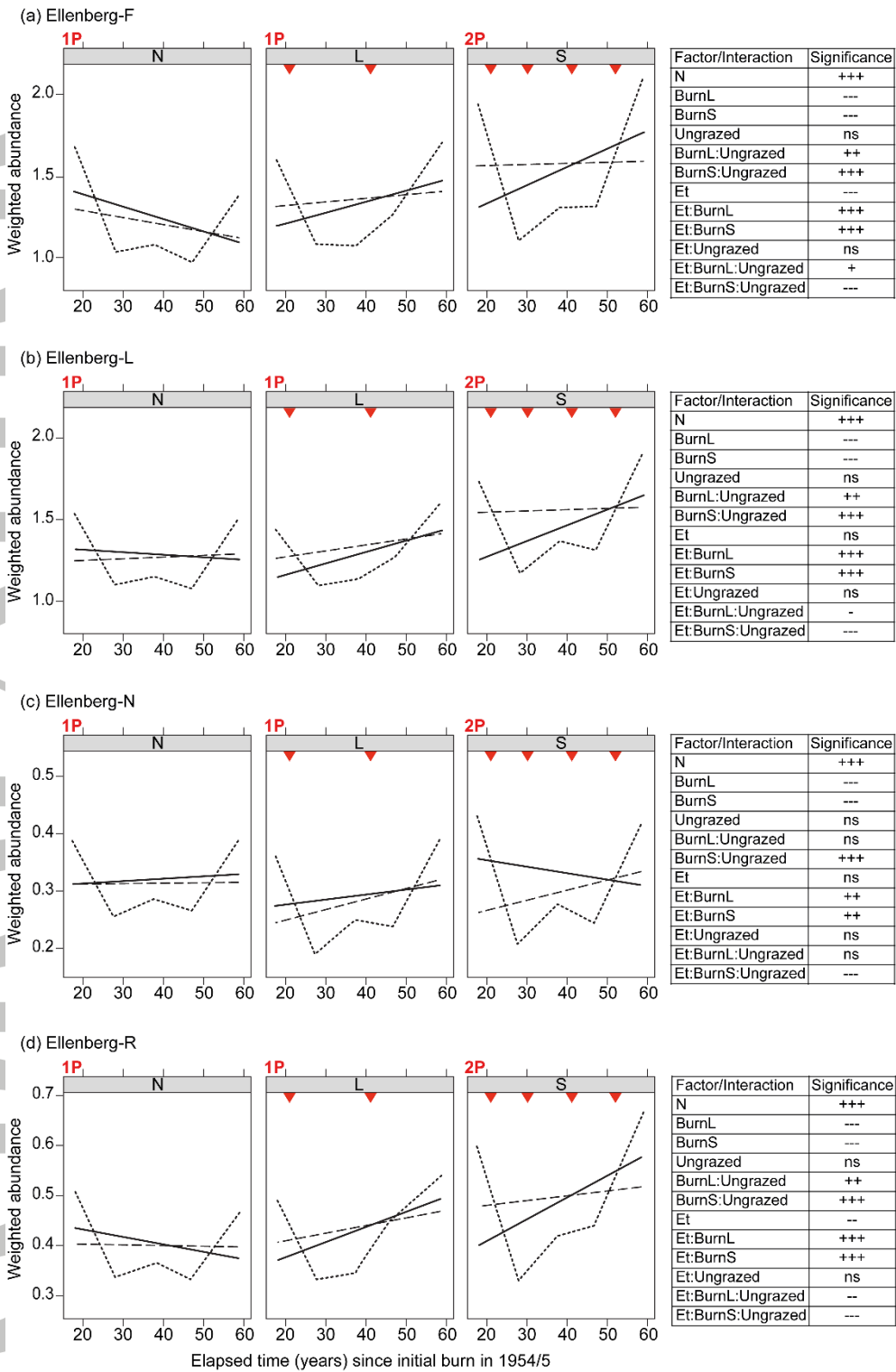


Figure 7. Modelled responses of the effects of three burning and grazing treatments applied to moorland at Moor House on four functional plant groups based on weighted Ellenberg values (a) F = moisture, (b) L = Light, (c) N=soil fertility, and (d) R = acidity. See Figure 3 for explanation of codings.

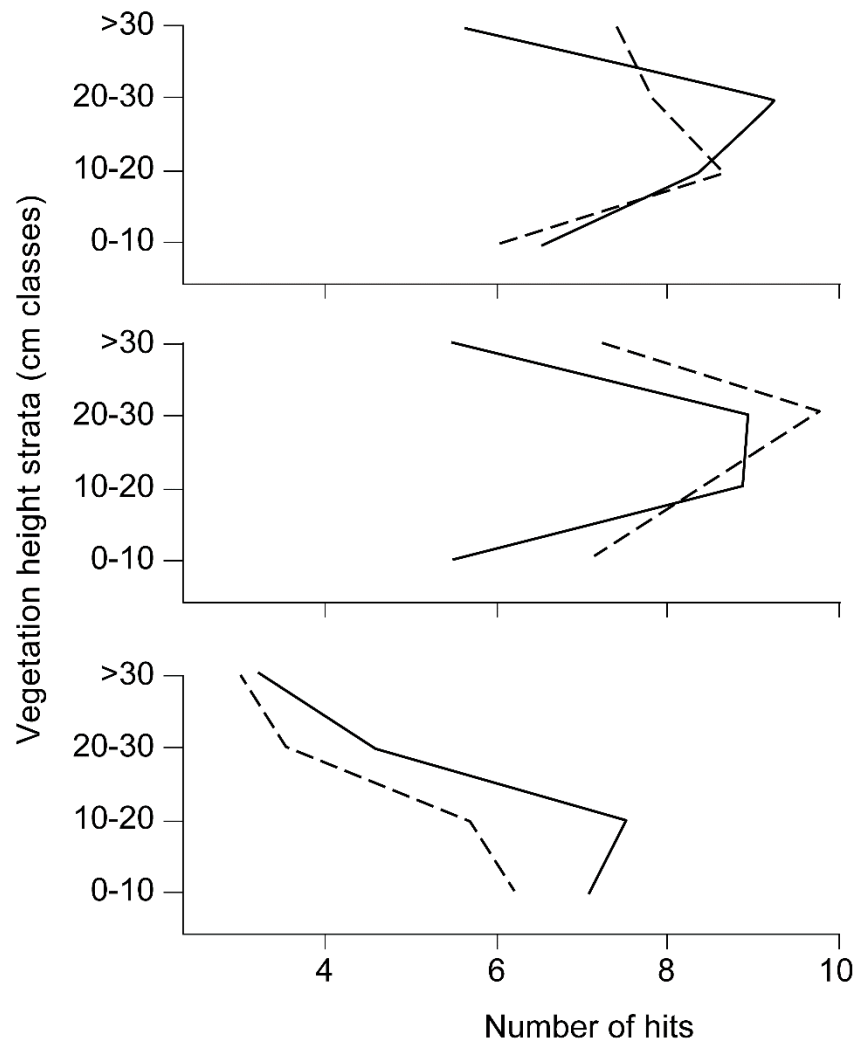


Figure 8. Modelled responses of the effects of three burning and grazing treatments applied moorland at Moor House on vegetation structure (a) N – burned only in 1954/5, (b) L = burned in 1954/5 and on a 20-year cycle, and (c) S = burned in 1954/5 and on a 10-year cycle. Solid line = grazed treatment, dashed line = ungrazed treatment.