



Drivers of vegetation change in grasslands of the Sheffield region, northern England, between 1965 and 2012/13

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Acidic grassland; Atmospheric N deposition; Calcareous grassland; Grazing; Land-use change; *Pteridium aquilinum*

Nomenclature

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Introduction

Over the past 50 yr, humans have changed ecosystems more rapidly and extensively than in any comparable period of human history (Mace et al. 2005). In the UK these changes have been particularly apparent; during the second half of the twentieth century the population of the UK grew by roughly a quarter and food production from agriculture increased dramatically (UKNEA 2011), with impacts on the natural environment.

Abstract

Questions: How has vegetation species diversity and species composition changed between 1965 and 2012/13 in acidic and calcareous grasslands? What has driven this change in vegetation?

Location: A 2400-km² area around Sheffield, northern England.

Methods: In 1965 a survey was conducted to describe grassland vegetation of the Sheffield region. We repeated this survey in 2012/13, revisiting acidic and calcareous grassland sites (455 quadrats). Climate, N and sulphur deposition, cattle and sheep stocking rates, soil pH, altitude, aspect and slope were considered to be potential drivers of variation in vegetation. We analysed temporal changes in vegetation and examined relationships with spatial and temporal variation in driver variables.

Results: Both acidic and calcareous grasslands showed clear changes in species composition between the two time periods. In acidic grasslands there was no significant change in richness but there were declines in diversity. There were significant increases in Ellenberg N. Nitrogen deposition and grazing were identified as potential drivers of spatial and temporal patterns but it was not possible to discriminate the respective impacts of potential drivers. In calcareous grasslands there were declines in species richness, diversity and appropriate diversity indices. Climate and soil pH were identified as potential drivers of spatial and temporal patterns.

Conclusions: Despite only small site losses compared to other surveys in the UK, especially within the national park, both calcareous and acidic grasslands showed very clear changes in species composition. In acidic grasslands, high abundance of *Pteridium aquilinum* was a particular problem and had increased considerably between the two survey periods. Atmospheric N deposition and grazing were identified as drivers of species diversity. A number of calcareous grasslands showed signs of reduced management intensity leading to scrub invasion.

Semi-natural grasslands make up 37% of UK land area (Carey et al. 2008) but have declined considerably in their extent during the last century. Enclosed semi-natural grasslands declined by 97% in England and Wales between 1930 and 1984 (Fuller 1987). More recently, the UK Countryside Survey (CS) identified a significant decrease in the area of calcareous and acidic grasslands between 1990 and 1998, although no change was observed between 1998 and 2007 (Carey et al. 2008). The UK National Ecosystem Assessment (NEA) (2011) identifies

major drivers of change. For semi-natural grasslands major drivers of habitat loss since the 1940s are agricultural grassland improvement and conversion to arable and forestry, whereas other conversion (e.g. roads, building quarries) and inadequate management are moderate threats.

The quality of the remaining semi-natural grasslands is also likely to have declined, with several authors reporting declines in typical species or the species richness of these habitats over time (Preston et al. 2002; Bennie et al. 2006; Duprè et al. 2010). Major drivers are agricultural improvement, N deposition and overgrazing, as well as the positive driver of protection through designation for conservation (UKNEA 2011). Agricultural improvement is likely to lead to domination by productive grasses and other competitive species, whereas N deposition is likely to lead to similar changes but with less severe impacts. Overgrazing is likely to result in the loss of grazing-intolerant species and an increase in unpalatable species. An additional threat is inadequate management (including absence of management), and in particular insufficient grazing resulting in succession and loss of characteristic grassland species (Rothschild & Marren 1997; Hodgson et al. 2014).

There remain knowledge gaps about the changes in vegetation species diversity and composition that have occurred in many regions of the UK over the last 50 yr, together with what the most important drivers of change have been at a regional scale (UKNEA 2011). In this study we utilize historical and current data from grasslands in the Pennines, northern England, to quantify vegetation change in acidic and calcareous grasslands. By repeating a survey originally conducted in 1965 we examine how vegetation has changed in terms of species composition and the potential drivers of vegetation change. The original survey was conducted in 1965 by a team from the Unit of Comparative Plant Ecology, University of Sheffield, led by P.S. Lloyd and J.P. Grime. The survey was conducted to describe grassland vegetation of the Sheffield region using random site selection and consistent methodology (Lloyd et al. 1971; Lloyd 1972; Grime & Lloyd 1973). However, the data were also used to provide invaluable standardized information on individual species (Grime & Lloyd 1973) and, combined with other surveys in the region and growth trials, provide the basis for 'Comparative Plant Ecology: a functional approach to common British species', the most recent edition of which was published in 2007 (Grime et al. 2007). We hypothesized that, in line with much of the UK, we would see the complete loss of some sites due to agricultural conversion, and a reduction in habitat quality and species richness in areas that remain. Based on previous studies we hypothesized that major drivers of change would be atmospheric N deposition, agricultural improvement and change in number of grazing animals.

Methods

1965/68 survey

The survey focussed on a 2400 km² area around Sheffield encompassing a large part of the Peak District National Park. Within the survey region the geology is variable, with Carboniferous limestone in the southwest, then millstone grit, coal measures, Magnesian limestone and Triassic sandstone to the east. Areas were selected to ensure reasonable geographic coverage. Within these selected areas, quadrats were positioned using random coordinates at a density of one per 200 m² (number of quadrats per site ranged from two to 40 quadrats). Sites with reseeding, fertilization or heavy trampling were excluded but are discussed below. A total of 630 quadrats were recorded. We were able to resurvey over 70% of these grasslands for this analysis: 196 quadrats spread across 18 sites located in acidic pasture grasslands (grazed grasslands of moderately to strongly acid soils; Lloyd 1972) and 259 quadrats spread across 27 sites located in calcareous grassland (grazed grasslands on Carboniferous and Magnesian limestone; Lloyd 1972; Fig. 1).

Vascular plant species data were collected in 1-m² quadrats, with frequency of individual species recorded using 10 cm × 10 cm divisions. Plants were identified to species level, with the exception of several taxonomically difficult genera treated as aggregate species (e.g. *Taraxacum officinale*) and a few other exceptions (see Lloyd et al. 1971).

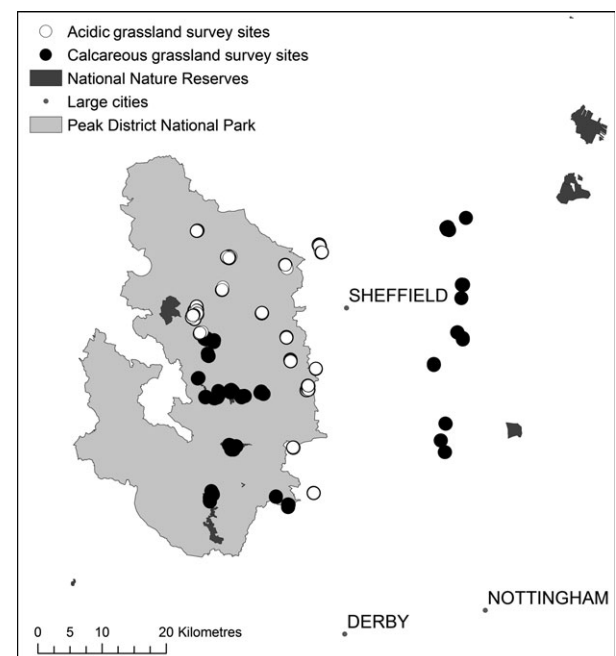


Fig. 1. Map showing location of acidic and calcareous grassland sites surveyed in 1965 and in 2012/13.

Environmental records were also collected, providing information on slope, aspect, altitude, geology and management. Grid references (UK national coordinate system) were recorded for all sites.

Soil samples were taken from each quadrat at a depth of 0–3 cm. Fresh soils were saturated with distilled water, and pH determined using a glass electrode.

2012/13 survey

The 2012/13 survey focused on acidic and calcareous grasslands. The 18 acidic pasture sites (196 quadrats overlaying millstone grit and coal measures) were revisited between the start of May and the end of Aug 2012. The 27 calcareous pasture sites (259 quadrats overlaying Carboniferous and Magnesian limestone) were revisited between the start of May and the end of Sept 2013. To ensure that a full complement of species was recorded, sites that had contained vernal or winter-annual species in the 1963 survey were sampled during May and June. Original sampling procedures were followed. Sites were relocated using original grid references and detailed paper records, and one of the recorders in the original survey (JGH) was on site during much of the recording. Quadrat locations had not been recorded in the original survey, so we could only relocate sites. Not being able to relocate quadrats exactly may have limited the accuracy of analysis of change in heterogeneous habitats (Chytrý et al. 2014). However, the majority of sites were large enough to contain multiple quadrats, minimizing the likely impact of this source of error. Vegetation frequency was estimated in bands of ten by counting frequency in two opposing quarters of the quadrat and adjusting the value obtained according to species occurrence in the remainder of the quadrat. Although less accurate than the previous method, this technique permitted considerably faster survey.

Sites that had changed from grassland to arable fields or sown meadow as a result of changes in land use were removed from the main analysis to avoid confounding more subtle changes observed in sites that have been less dramatically altered. These changes are discussed separately.

Soil samples were collected and analysed following the same procedures as in 1965. A Metler Toledo Seven Compact pH meter was used to determine pH. In all analysis, acidic and calcareous grassland plots are considered separately, as it is likely that different relationships between drivers and services are observed in the two grassland types.

Driver variables

Climate, N and sulphur deposition, cattle and sheep stocking rates, soil pH, altitude, aspect and slope were

considered to be potential drivers of variation in vegetation. Maximum July temperature, minimum January temperature and annual precipitation data for 1965 and 2011 (the most recent data set available) were obtained from the UK Met Office. (<http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/download/>, accessed 07/04/2014). Data on total N and sulphur deposition to upland grasslands were derived from the C-BED model (Smith et al. 2000) for the period 2010–2012. It was not possible to obtain estimates from the same model for 1965 because the model is based on interpolated data, and so plots from both years were given the same deposition values, with the assumption that, while absolute deposition values have changed, the spatial pattern in deposition has remained relatively constant (Fowler et al. 2004). This is considered to be a reasonable assumption, given that the main local sources of N and sulphur pollution are likely to occur in similar places. Both climate and deposition data are resolved at the 5 km × 5 km scale.

Data on cattle and sheep stocking rates at a 2 km × 2 km resolution were obtained from the Agricultural Census for 1969 and 2010, the closest years available to the survey dates (data obtained from <http://edina.ac.uk/agcensus/>, accessed 09/04/14). Soil pH was measured by taking samples from each survey plot and measuring pH after mixing to a paste with water. It was not possible to be certain that the pH measurement precision was exactly the same between the two survey periods, so pH measurements were centred and standardized for each survey period. This allowed investigation of spatial differences in soil pH between plots while removing any absolute differences between years potentially due to differences in sampling methodology. At two sites some soil pH measurements are missing in the resurvey, so that there are fewer replicates for these sites in the resurvey year.

Altitude, aspect and slope were calculated for each survey plot. In 1965 these measurements were taken using field measurements. For resurvey plots the exact location of each plot was defined by GPS and altitude, aspect and slope calculated from the NextMap digital terrain model (Intermap Technologies, Englewood, CO, US) using ArcGIS 10.2 (ESRI, Redlands, CA, US).

Data analysis

Species richness, Simpson's diversity index and 'appropriate' plant diversity were calculated. Appropriate plant diversity is defined as the number of Common Standards Monitoring (CSM) positive indicator species grasslands per unit area (Smart et al. 2010). These species have been selected by the statutory nature conservation bodies in Britain as those that help to define higher conservation value habitat. Hence 'appropriate' reflects their expert

judgements as to which species best characterize habitat in better condition. Examples of positive CSM species for acid grasslands are: *Agrostis capillaris*, *Erica cinerea* and *Potentilla erecta*. For calcareous grasslands examples of species that count towards appropriate diversity are: *Briza media*, *Helianthemum nummularium* and *Viola hirta*. Grassland CSM species were extracted from JNCC Guidance documents (JNCC 2004, 2006), a full list is given in Appendix S1. By measuring the abundance of positive indicators for acid and calcareous grassland habitats, as defined by the statutory conservation agencies, the indicator conveys potential delivery of the cultural ecosystem service that is maximized when habitats are in 'favourable condition' and therefore where nature conservation objectives are being met.

Ellenberg N scores (Ellenberg 1974; Hill et al. 1999) were calculated without cover-weighting, whilst canopy height class (Hodgson et al. 2005) was cover-weighted. These response variables were included to aid interpretation of vegetation changes.

Analysis was conducted in R v 3.0.3 (R Foundation for Statistical Computing, Vienna, AT). To assess whether response variables had changed between 1965 and 2012/13, linear, or generalized linear, mixed models were constructed for each variable, with year as a fixed effect and site as a random effect, using the nlme and lme4 packages. The significance of the year term was tested by constructing a model with only the site random effect, and conducting a likelihood ratio test of the change in likelihood between models.

To investigate whether variation in response variables was related to driver variables, further mixed models were constructed with both year and driver variables as explanatory terms. Strong collinearity between climate variables prevented all climate variables being included in the models. Minimum January temperature was chosen as a representative climate term as it was the most highly correlated with the other climate variables and showed lowest collinearity with the non-climatic driver variables. Significance of parameter estimates in the full model was estimated using *z*- or *t*-tests. A deposition by year interaction term was included in the models when either of the deposition terms was significant, to test whether the effect of deposition was the same between years. The interaction term was kept in the model if $\Delta\text{AIC} > 2$.

Two response variables modelled with linear mixed models had to be transformed to fit a normal distribution with log (Ellenberg N) and cube (Simpson's diversity in acidic grassland) transformations used. Simpson's diversity in calcareous grassland was strongly negatively skewed so the variable was inverted then logged to approximate a normal distribution. Due to the large number of

parameters tested over all models, *P*-values were corrected for multiple comparisons using the false discovery rate (Benjamini & Hochberg 1995).

For all quadrats, species composition data were analysed with detrended correspondence analysis (DCA) in CANOCO 4.5 (Biometris, Wageningen, NL) to detect and examine change in species presence and abundance between 1965 and 2012/13. Default settings were used, with rare species down-weighted. Axis scores were correlated with driver variables using pair-wise Spearman correlations.

Results

Three calcareous grassland sites had been converted to arable crops and one had been ploughed and re-seeded as a silage crop. These 28 quadrats were excluded from the analyses below.

Vegetation composition

A full species list is given in Appendix S1. In the acidic grasslands there was no significant difference in species richness between 1965 and 2012 (Fig. 2a); however, there was a significant decline in Simpson's diversity ($P < 0.001$; Fig. 2b); appropriate plant diversity also declined ($P < 0.001$; Fig. 2c). There was a significant increase in Ellenberg N score from a mean of 2.54 (range 1.7–4.8) in 1965 to 3.64 (range 1.9–7.0) in 2012, and canopy height class also showed a significant increase ($P < 0.01$; 1965 mean 5.1, range 4.2–7.0; 2012 mean 7.7, range 4.2–8.0).

Figure 3 shows an ordination bi-plot with quadrats for 1965 and 2012. There is a similar distribution of scores on axis 1 between the two time periods, although there is an increase in the number of quadrats to the right of axis 1. Correlating the axis scores for samples for axis 1 with mean Ellenberg N values yielded a strong positive correlation ($r = 0.35$, $P < 0.001$), and the left of the axis is associated with high nutrient status. Quadrats from 1965–68 show a much more tightly clustered distribution on axis 2 than recorded in the 2012 data. There is an increase in the number of quadrats at the bottom left of the bi-plot; these quadrats are from three sites and are the same sites for which quadrats are clustered in this area of the diagram in 1965–68. There are considerably more quadrats located on the upper half of axis 2 and centre of axis 1. There is also an increase at the low end of axis 1 and upper end of axis 2. Axis 2 seems to show a successional sequence from open grassland species at its lower end to shade-tolerant species associated with the *Pteridium aquilinum* canopy at the upper end. Correlating DCA axes with potential driver variables and Ellenberg N values showed that axis 1 was most

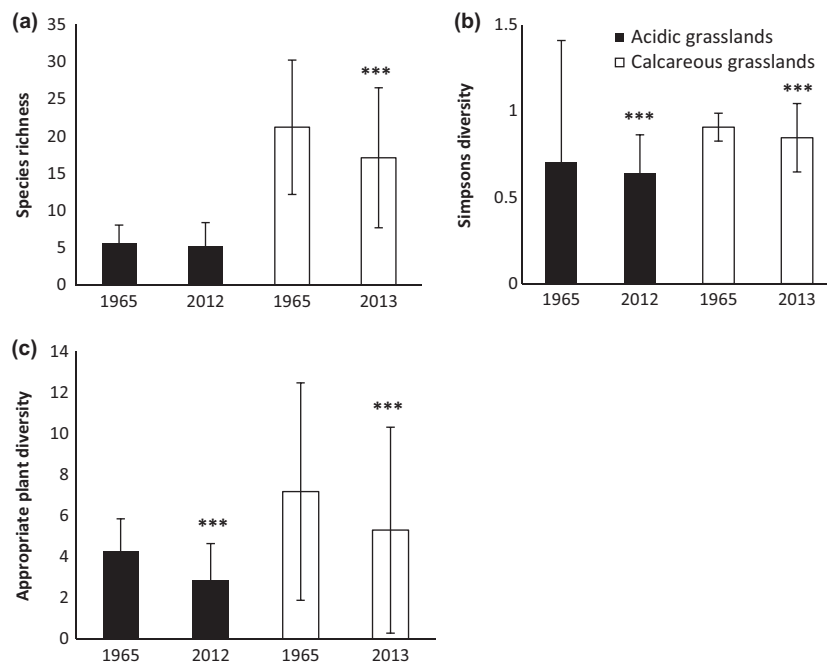


Fig. 2. Mean (\pm SD) for diversity indicators (a) species richness, (b) Simpson's diversity index, (c) appropriate diversity for 196 quadrats in 18 sites for acidic grasslands and 259 quadrats in 27 sites for calcareous grasslands in 1965 and 2012/13. Significance is indicated between the two survey periods: * $P < 0.5$; ** $P < 0.01$; *** $P < 0.001$.

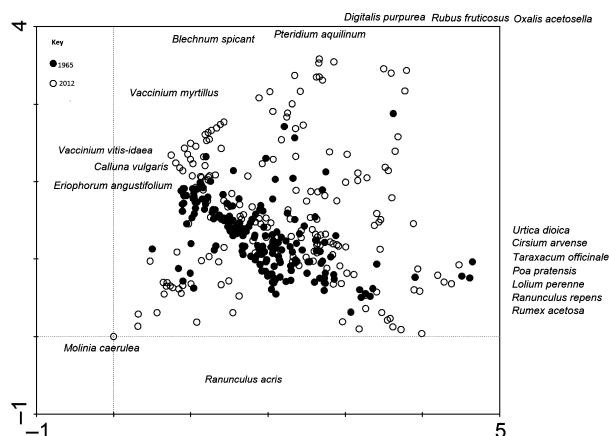


Fig. 3. DCA biplot (axes 1 and 2) of 196 quadrats at 18 acidic pasture sites in the Sheffield region for 1965 and 2012 based on species occurrence and abundance. Axes 1 and 2 have Eigenvalues of 0.52 and 0.41, respectively. Species with highest or lowest axis scores have been plotted on the diagram. Species shown to the edge of the plot have the following axis scores (axis1, axis2): *Digitalis purpurea* (2.51, 6.42), *Rubus fruticosus* (3.74, 7.51), *Oxalis acetosella* (5.21, 8.56), *Urtica dioica* (5.10, 2.73), *Cirsium arvense* (5.64, 2.27), *Taraxacum officinale* (5.95, 2.18), *Poa pratensis* (5.15, 1.29), *Lolium perenne* (5.99, 1.27), *Ranunculus repens* (6.30, 1.19), *Rumex acetosa* (4.87, 1.74).

strongly correlated with Ellenberg N value ($r = 0.49$, $P < 0.001$) and axis 2 with sulphur deposition ($r = 0.39$, $P < 0.001$).

In calcareous grasslands there was a significant decrease in species richness, Simpson's diversity and appropriate diversity (Fig. 2a–c). There was no significant difference in Ellenberg N score between 1960 (mean 5.6, range 1–15) and 2013 (mean 5.21, range 1–17), but canopy height class increased significantly ($P < 0.001$) from a mean of 5.21 in 1965 (range 4.3–6.9) to 5.4 in 2013 (range 4.3–11.0).

Similar to acidic grasslands, calcareous grasslands show a larger spread of points in 2013 than in 1965, with the most distinctive area of change being an increase in sites with scores low on axis 1 but high on axis 2 (Fig. 4). Separating sites on Magnesian limestone and Carboniferous limestone suggests a more marked change in vegetation on the Magnesian limestone. There is a similar distribution of sites along axis 1, which appears to be associated with a pH gradient characterized by the presence of calcicolous species at the lower end and more calcifuge species at the higher end. Magnesian limestone sites are restricted to the lower end of this axis. There is an increase in sites at the upper end of axis 2, which corresponds to species with a preference for moist or shaded habitats (e.g. *Chrysosplenium oppositifolium*, *Hedera helix*). An area of increase in the number of sites in an area at the centre of axis 2 and the lower end of axis 1 corresponds with the presence of shrub species. Axis scores were significantly different between years (axis 1 decreased, $P < 0.05$; axis 2 increased, $P < 0.05$). Correlating DCA axes with potential

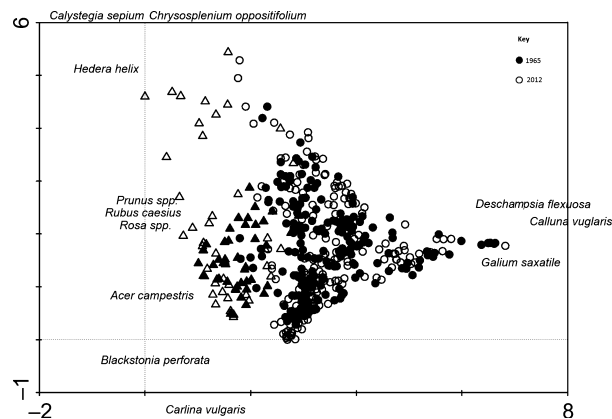


Fig. 4. DCA biplot (axes 1 and 2) of 231 quadrats at calcareous pasture sites in the Sheffield region for 1965 and 2012 based on species occurrence and abundance. Carboniferous limestone sites are shown with circles and Magnesian limestone sites with triangles. Axes 1 and 2 have Eigenvalues of 0.50 and 0.43, respectively. Species at the ends of axes have been plotted on the diagram. Species shown to the edge of the plot have the following axis scores (axis1, axis2): *Carlina vulgaris* (1.42, -1.44), *Calystegia sepium* (0.25, 6.29), *Chrysosplenium oppositifolium* (1.92, 5.59).

driver variables and Ellenberg N values showed that in calcareous grasslands axis 1 was also most strongly correlated with Ellenberg N value ($r = 0.72$, $P < 0.001$) whilst axis 2 was most strongly correlated with altitude ($r = 0.5$, $P < 0.001$).

Drivers of change

In acidic grasslands species richness showed a negative relationship with N deposition and Simpson's diversity showed a positive relationship with sheep numbers and a negative relationship with N deposition. There were no significant relationships between driver variables and appropriate diversity or Ellenberg N.

In calcareous grasslands species richness was positively related to aspect and soil pH and negatively related to minimum January temperature. Simpson's diversity and Ellenberg N did not show any relationships but appropriate diversity was positively related to aspect, total cattle numbers and soil pH.

Full results are given in Appendix S2.

Discussion

Land-use change

Between 1965 and 2013, four calcareous grassland sites (accounting for 28 out of 259 quadrats) and no acidic grassland sites (out of 196) were lost to ploughing. Further, grasslands showed differing degrees of agricultural improvement, ranging from some signs of fertilization to clear signs of liming and fertilization. Two acidic grasslands

sites (seven quadrats) and one calcareous grassland site (two quadrats) could now be described as improved pasture. Bennie et al. (2006) resurveyed 263 calcareous grasslands in East Anglia, Dorset, Kent and Yorkshire originally surveyed in 1952 and 1953. They found that 72 of 263 plots (27%) had undergone land-use change to arable or improved pasture. In Dorset, Newton et al. (2012) reported 212 calcareous grassland sites completely destroyed and 64 sites partially destroyed since original surveys conducted in 1931–36, leaving 174 sites intact (39% partially or completely destroyed). Further regional surveys reported in the UK NEA (2011) give even higher rates of loss, up to 62%. The relatively low losses to alternative land uses may be partly accounted for by many of the sites being located within the Peak District National Park. Each national park in England is overseen by a statutory planning authority, providing stricter regulations on building developments. The National Parks Authority also provides advice and guidance to farmers on the management of their land and access to agri-environment scheme funding. The Peak District National Park was designated in 1951, so was already well established at the time of the 1965 survey. A further contributor to the lack of conversion to arable or improved pasture is likely to be the landscape terrain of the Peak District. Many of the sites are steeply sloping and are unsuitable for agricultural vehicles.

Vegetation composition

Despite the lack of conversion to arable or improved pasture, the DCA showed that there have been some clear changes in the species composition of the grasslands. In acidic grasslands there was no significant change in species richness overall, but this masked considerable variation between sites, with some sites increasing and others decreasing. Appropriate diversity declined, which indicates that the species composition has become less typical of what we would hope to find in grassland in good condition.

Species richness was related to atmospheric N deposition. The analysis was only able to consider the spatial relationship, but this is consistent with earlier work in acidic grasslands showing a negative association between species richness and N deposition (e.g. Maskell et al. 2010; Stevens et al. 2010). Not only did Ellenberg N scores significantly increase between the two sampling periods but they were also correlated with axis 1 in the DCA ordination, indicating that nutrient status is a major driver of compositional change. Few sites were completely converted to intensive pasture as described above, but fertilization through the addition of inorganic and organic fertilizers, import of animal feed and atmospheric deposition of N are all likely to have contributed to increasing nutrient status. The amount

of organic or inorganic fertilizer N required to maintain productive pasture depends on stocking rates and fertilizer history, but can be between 170 and 290 kg-N·ha⁻¹·yr⁻¹ (Defra 2010). At these levels vegetation becomes dominated by productive grasses and a small number of common forbs, e.g. *Ranunculus* spp., *Trifolium repens*, and less agriculturally desirable species such as some *Cirsium* spp. and *Urtica dioica*. Although these changes were apparent in some grasslands, it is very difficult to separate low-level fertilizer additions from atmospheric N deposition. Atmospheric deposition of N at the acidic grassland sites ranged from 19.4 to 30.8 kg-N·ha⁻¹·yr⁻¹. There is a strong evidence base indicating that ambient levels of N deposition can result in changes in vegetation species composition (Maskell et al. 2010; Stevens et al. 2010). The levels currently observed in these grasslands are higher than the European average of ca. 17 kg-N·ha⁻¹·yr⁻¹ (Stevens et al. 2004). In acidic grasslands the increase in estimated above-ground production also likely reflects the combined impacts of fertilization and atmospheric N deposition. We were not able to consider any temporal relationships with N deposition due to a lack of model estimates for the earlier survey dates; however, national trends indicate that it is very likely deposition of reactive N will have increased (RoTAP 2012).

In acidic grasslands Simpson's diversity was significantly reduced, indicating that although species richness has not changed there is an increased dominance of a few species. The driver attribution models indicated relationships with atmospheric N deposition and sheep numbers. The positive association with sheep numbers shows a reduction in species richness and evenness where sheep numbers are low. Individual species respond differently to grazing intensity (Del-Val & Crawley 2005) and responses are likely to have interactions with N inputs (Pakeman 2004; Stevens & Gowing 2014). These findings are in line with the humped-back model (Grime 1974), whereby we might expect maximum species richness at intermediate levels of grazing but reduced diversity at higher or lower levels of disturbance.

The increase in shade-tolerant species observed in the DCA and the increase in vegetation height is likely to be related to a reduction in grazing pressure and a related increase in the cover of *P. aquilinum*. Average cattle numbers (data obtained from <http://edina.ac.uk/agcensus/>, accessed 09/04/14) declined from 168 livestock units (LSU) per 2 km × 2 km in 1965 to 32 LSU per 2 km × 2 km, while sheep increased slightly from 640 to 679 LSU in this time period. However, this masks considerable variation, with some sites showing large increases and others showing large decreases. The Natural England Lowland Grassland Management Handbook (Crofts & Jefferson 1999) advises guidance stocking rates of two sheep or

1 cow·ha⁻¹·yr⁻¹ for acidic grassland. If we take one LSU as a mature Friesian cow, current rates of 32 LSU are equivalent to 0.32 cows·ha⁻¹, considerably less than recommended levels. The significant increase in potential canopy height supports the importance of grazing. *P. aquilinum* is a problem species in the UK, with its increase in dominance attributed to lack of exploitation, reduced land-use intensity, reductions in cattle numbers and improved drainage (Pakeman et al. 1996). The increase in *P. aquilinum* within the data set is very clear, with three quadrats having occurrence in a frequency class of 5 or more in 1965 and 21 in 2012. Considering that *P. aquilinum* is a large plant, even low rooting frequency can result in the formation of a complete canopy, leaving a number of sites almost completely dominated by *P. aquilinum*.

In calcareous grasslands both species richness and diversity declined between 1965 and 2013. Main drivers of species richness were soil pH and climate-related variables (aspect and temperature). There is a large variation in soil pH observed in these grasslands, and the occurrence of quite low pH soils on calcareous bedrock where organic soils had developed. This is also apparent in the DCA. The importance of climate is well known to be an important driver of species composition and richness and was identified in the original survey (Grime & Lloyd 1973).

Appropriate diversity was also related to soil pH and aspect, with the further addition of cattle grazing. As with acidic grasslands, there is also a significant increase in potential canopy height, again emphasizing the importance of grazing. In the DCA, the increase in shrub species was a common change in the species composition and is likely to be due to a reduction in management intensity, particularly grazing, at some sites. As in acidic grasslands, average cattle numbers have actually fallen between 1965 and 2013 (336 to 276 LSU, respectively), but average sheep numbers increased considerably (457 to 809 LSU, respectively). However this masks a considerable variation, and a number of sites show quite large decreases in grazing pressure offset by intensification at others. This change is particularly apparent on grasslands on the Magnesian limestone, which occur to the east of the region. Bennie et al. (2006) similarly observed scrub invasion on 23.9% of their calcareous grassland sites that were originally surveyed in 1952/53; where several quadrats appear to have become more moist and shaded, possible reflecting changing local conditions (e.g. sites that have become more moist due to damaged field drains, for example) or increased shade from shrubs. The absence of a relationship with N deposition possibly reflects the high sensitivity of acidic grasslands compared to calcareous grasslands, and was also observed in a national study of N deposition impacts on habitats (Maskell et al. 2010); although there were

indications of nutrient enrichment, with axis 1 of the DCA most highly correlated with Ellenberg N value.

Implications for management

Few sites were lost entirely, indicating that the national park has afforded protection to these grasslands. The most visible and recorded change in the acidic grasslands was the increased dominance of *P. aquilinum*, with some sites becoming dominated by *P. aquilinum* with few other species present. This presents a considerable challenge for management and is likely to require a combination of cutting and spraying followed by on-going cutting (Lowday & Marrs 1992). On hill slopes that are not easily accessed by machinery this is likely to be expensive and time-consuming. Other drivers of change identified were N deposition and reduction in grazing pressure. N deposition is a national problem, and addressing it through management presents many challenges. Reductions in N emissions are likely only achieved by changes in national policy. Grazing intensity was related to a number of variables in both acidic and calcareous grasslands. Increases in grazing intensity to maintain optimal sward heights are highly likely to benefit species richness and composition in both grassland types.

Conclusions

Despite only small site losses, both calcareous and acidic grasslands showed very clear changes in species composition over time. In acidic grasslands the species composition has become less typical of those in good condition. These changes appear to be related to atmospheric N deposition and grazing intensity. High abundance of *P. aquilinum* is a particular problem and has increased considerably between the two survey periods. A number of calcareous grasslands showed signs of reduced management intensity leading to scrub invasion. Changes were particularly apparent in grasslands from outside the area of the national park.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Species lists for acid and calcareous grasslands in 1965 and 2012/13 with appropriate diversity indicators shown.

Appendix S2. Model output for drivers of spatial and temporal patterns in species composition in acid and calcareous grasslands.