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Responses of calcareous grassland plant communities to changed seasonal grazing management: results of a 31 year study

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Author contributions

L.E.R, R.F.P and J.M.B conceived the research idea and designed the study; C.B and K.W supplied the data; L.E.R performed statistical analyses with contributions from R.F.P, J.M.B and K.W; L.E.R wrote the paper; all authors discussed the results and commented on the manuscript.

Declaration of competing interest

The authors declare they have no conflict of interest.

Abstract

Calcareous grasslands are of high conservation importance and have been maintained by livestock grazing over many centuries. Following the reduction in traditional livestock grazing (cattle and sheep) of semi-natural grassland during the twentieth century, conservation-based grazing management was introduced in order to conserve remaining grasslands. In UK semi-natural grasslands, grazing pressure has fluctuated over time due to changes in conservation funding and stock availability, whilst the time of year at which stock graze has also shifted. There is little quantitative data available to demonstrate the details of changed grazing patterns, or their long-term effects on the vegetation, thus the full impacts of these changes are not well understood. This study examines the response of a diverse calcareous grassland community to changes in grazing management between 1979 and 2010 at Martin Down National Nature Reserve, southern England, using historical vegetation surveys and grazing records collected and recorded by reserve staff. Historical data showed a shift in grazing regime, whereby grazing occurred across all seasons in the early period, but switched to predominately the autumn and winter in the present century. Despite this significant shift in management over time, the vegetation community did not change dramatically over this period, although small increases in species richness and diversity were detected. The richness of calcareous grassland indicator species remained largely consistent, suggesting the conservation value of the grassland persisted, and the community types also stayed fairly constant over the 31 years. Furthermore, weak evidence was found for impacts of grazing in particular seasons on vegetation community measures; species richness, species diversity, indicator richness, indicator abundance, grass abundance and forb abundance. This study suggests that these vegetation communities are robust to changes in grazing seasonality providing that sufficient grazing pressure is provided within the year. The compartmentalised grazing employed at Martin Down may be a useful method for ensuring this outcome. However more research is required, preferably using controlled field experiments before more reliable recommendations can be prescribed.

Keywords

Conservation; grazing management; long-term; seasonal grazing; species richness; vegetation change

Introduction

Calcareous grasslands are among the most species-rich habitats across Western Europe (Wilson et al. 2012). They support a range of flora and fauna, many of which are rare or threatened (Webb et al. 2010, Habel et al. 2013). They also contribute to multiple ecosystem services including pollination, cultural value and carbon storage (Hopkins and Holz 2006, Lindborg et al. 2008, Bengtsson et al. 2019). Calcareous grasslands are considered in general to be semi-natural habitats, because without human management through grazing, cutting or burning, they would eventually turn into scrub and woodland through natural succession (Poschlod and Wallis de Vries 2002, Dengler et al. 2014). Traditionally, calcareous grasslands were used as pastures for livestock grazing over many centuries. However, during the early twentieth century traditional forms of livestock grazing decreased throughout Europe, which led to the abandonment of large expanses of calcareous grasslands. Large areas were also lost to agricultural intensification, which led to a dramatic decline in the extent of calcareous grassland across Europe during the twentieth century (Fuller 1987, Polus et al. 2007, Ridding et al. 2015). Many of the remaining areas of calcareous grassland are isolated fragments found within matrices of intensively managed agriculture, forests and roads (Poschlod and Wallis de Vries 2002).

The decline in the extent of calcareous grassland prompted the introduction of conservation management practices, whereby traditional grazing was re-established in order to maintain and conserve their characteristic flora and fauna. This type of extensive livestock grazing of small fragments of isolated grassland is generally uneconomic and impractical within modern farming systems, and therefore requires the support of agri-environment payments or other conservation funding. To overcome this problem many conservation organisations manage their own livestock flocks and herds, which are moved among grasslands. Conservation funding for such practices has fluctuated over time, whilst the availability of stock has also been a problem (Crofts and Jefferson 1999). The objectives of the grazier and conservation manager also differ, with the grazier concerned about livestock welfare, food availability and economic return, whilst the conservation manager's objective is maintaining the wildlife value of the grassland (Green 1972). Thus conservation grazing is often a compromise between these objectives, meaning that the grazing regime is not always as desired by conservation managers. Because of these issues surrounding funding, stock availability and grazing duration, reduced grazing pressure is a key concern for the conservation of many calcareous grasslands (English Nature 2005). Despite this, there is little quantitative data which documents the detail of changes in grazing regimes over time.

In Great Britain a number of calcareous grasslands are protected through designation as Sites of Special Scientific Interest (SSSI) due to their 'special interest by reason of any of its flora, fauna, or geological or physiographical features' (JNCC 2015). However of these only 39% were reported to be in "favourable" condition in 2019, where condition is assessed against targets developed for the special features for which a site was designated for, such as a specific vegetation community type (DEFRA 2019). During 1999-2005, 30% of sites were classed as "unfavourable", with the main cause attributed to under-grazing (Williams 2006). Although this information is useful, assessments represent a static point in time and do not enable the long-term relationship between grazing management and vegetation change to be examined in detail. Instead, drivers of change, such as under-grazing are represented by the presence of undesirable species, for example. Of the long-term studies that have been

undertaken on vegetation change in calcareous grassland, a range of community changes have been reported, including declines in species richness or diversity, and shifts in composition (Bennie et al. 2006, Newton et al. 2012, Ridding et al. 2020). Stroh et al. (2017) resurveyed calcareous grassland sites originally surveyed in the 1960s across lowland England and found a clear shift in composition. Despite only one of the twenty-two sites studied having quantitative grazing records, using general qualitative information on past management, the authors concluded that under-grazing and a reduction in spring and summer grazing was likely to be a driver of vegetation change. Similarly, Walker and Pinches (2011) reported a decline in the distribution of *Pulsatilla vulgaris* in calcareous grasslands in lowland England between 1968 and 2006. Again, although quantitative grazing data was not available, using information on the time of year that grazing had occurred and the management history, the vegetation change was attributed to reduced grazing. Other studies have also associated vegetation change on calcareous grassland in the UK with a shift in grazing management (Hawes 2015, Stevens et al. 2016, Hawes et al. 2018, Ridding et al. 2020).

Although vegetation change in calcareous grassland has been attributed to changes to the grazing regime across the UK in a number of studies (Walker and Pinches 2011, Stevens et al. 2016), none have investigated this using comprehensive long-term grazing records. It is extremely difficult to source reliable grazing records and where this has been possible, it is often in the form of local knowledge or anecdotal evidence from land managers (Stroh et al. 2017, Ridding et al. 2020) rather than actual stocking numbers and exact timings (e.g. Benthien et al., 2018). The other problem is acquiring concurrent long-term vegetation data collected at multiple times. The majority of studies examining long-term vegetation change evaluate two snapshots in time (van den Berg et al. 2011, Diekmann et al. 2014), however year to year fluctuations in grassland communities can be large (Morecroft et al. 2016, Bullock et al., 2001) due to factors such as summer droughts and wet winters (Pfeifer et al. 2006, Grant et al. 2014). Detailed grazing records and vegetation data over long continuous time periods are both required in order to understand how changing grazing regimes affect the vegetation. This information is important for land managers and policy makers in order to determine which grazing regimes provide suitable management for this important conservation habitat.

In this study we explore the response of a diverse calcareous grassland community to changes in grazing management over a 31 year period at Martin Down National Nature Reserve (NNR) in southern England. The specific questions were;

1. Has there been a change in grazing management over time?
2. Has the vegetation community changed over time?
3. How has the vegetation community responded to changes in grazing management?

Material and methods

Study site

The study was undertaken at Martin Down which is located on the borders of Hampshire, Wiltshire and Dorset in southern England (50.975 N, 1.937 W) (Fig 1). The majority of the 336 ha site consists of calcareous grassland, though other important habitats such as

broadleaved woodland, chalk heath and mosaics of scrub are also present. There are several types of calcareous grassland, but the site is largely dominated by British National Vegetation Classification (NVC) (Rodwell 1992) community CG3 (*Bromopsis erecta* grassland) with some smaller areas of CG2 (*Festuca-Avenula* grassland) (both phytosociological alliances - *Bromion erecti* (Rodwell et al. 2007)) (Gibbons 1989). The site has been managed jointly by the Nature Conservancy Council (now Natural England) and Hampshire County Council since it was acquired in 1978. Before this there was a lack of grazing after rabbits severely declined due to myxomatosis in the 1950s (Toynton 1994). Since 1978, the calcareous grassland at Martin Down has been managed by sheep grazing within compartments controlled by temporary electric fences, since no permanent fences exist on the site. An average of 28 sheep per ha graze for nearly four weeks (Toynton 1994), whilst at more traditionally managed reserves 2.5 sheep per ha typically graze across 52 weeks (Crofts and Jefferson 1999). Martin Down was designated as a SSSI in 1987 and is also protected through designation as an NNR.

Vegetation and grazing data

Fifty-five 1m x 1m permanent plots were established across Martin Down between 1979 and 1981, with the aim of monitoring change in vegetation communities in the different compartments (1-2 plots per compartment, see Appendix A). All vascular plant species were recorded in these plots using the Domin scale of Dahl and Hadač (1941), a system based on 10-cover/abundance categories devised for recording cover of species in a community. These fixed plots were re-located and re-surveyed somewhat idiosyncratically between 1981 and 1994, with different plots being recorded in different years, and some plots surveyed more often than others (Appendix A). There was then a hiatus in recording until 2002, after which recording continued to 2010, when P.J Wilson resurveyed thirty of the original fifty-five plots using the same methodology. We collated grazing data from the detailed records made by reserve managers for compartments which contained permanent plots between 1979 and 2010 (Fig 1). From these, we determined the number of sheep and days they spent in each compartment for each year. We calculated the sheep days per hectare by dividing by the compartment size, to ensure a fair comparison across compartments. Where grazing data were not available for a particular compartment in a given year (see Appendix A), we replaced the missing value with the median across all compartments in that year, as recommended by Legendre and Legendre (1998). We used the vegetation data from the fifty-five plots only if grazing data were available for the associated compartment. This gave us a total of 19 vegetation plots for analysis (Fig 1), where on average these plots had been surveyed 5 times between 1979 and 2010 (Appendix A).

Data analysis

To investigate whether the grazing regime had changed over time at Martin Down we used hierarchical clustering on the average sheep days per hectare within autumn (September, October, November), spring (March, April, May), summer (June, July, August) and winter (December, January, February) in each of the years between 1979 and 2010 for compartments where grazing data was collected. We performed the hierarchical clustering analysis in R v3.6.1 (R Core Team 2019) using the *vegan* package (Oksanen et al. 2007) with the complete linkage method applied. To determine the number of clusters, we looked for natural breaks using a dendrogram, with the aim of producing two clusters since we expected

a shift in grazing over time. We visualised dissimilarities between years using a Principal Coordinates Analysis (PCoA). To understand which seasons were associated with the cluster groups, we used the *labdsv* package (Roberts and Roberts 2016) which identified indicator seasons, based on the frequency and abundance. The probability of finding a higher indicator value in random permutations is calculated, where a low probability suggests the season is a significant indicator.

To determine if the vegetation community had changed over time we used the programme TABLEFIT (Hill 1996) to assign each of the compartments at Martin Down to one of the British NVC communities (Rodwell 1992) in each year when plots were surveyed. TABLEFIT assigns species composition information to habitat types by assessing the goodness-of-fit in terms of composition. To further examine changes in the vegetation communities over time, we explored four community measures; species richness, indicator richness, species diversity and species composition. Species diversity was calculated as the inverse Simpson's diversity index using the *vegan* package. Indicator richness was defined as the number of Common Standards Monitoring (CSM) positive indicator species for CG2 and CG3 grasslands extracted from JNCC (2004) (Appendix B). These species, as chosen by statutory nature conservation bodies in the UK, help define higher conservation value habitat. Monitoring the full species diversity of such grasslands can be impractical and costly, hence this sub-set of component species can be used to assess condition. In addition to the richness of indicators, we also explored the abundance of these species within the plots. The abundances of grasses and forbs were also examined, since previous studies have identified relative changes between these groups caused by different grazing seasons (Bullock et al., 2001). Domin scores were converted to percentage cover values prior to analysis using the method of Currall (1987). The cover values for indicators, grasses and forbs were weighted by the total cover within each plot.

To test for changes in species richness, indicator richness, diversity and abundance variables (indicator, grass and forb) we used generalised linear mixed models, with year as a fixed effect and plot nested in compartment as a random effect, using the *lme4* package (Bates et al. 2014). A Poisson error structure was used for species richness and indicator richness, whilst a Gaussian structure was used for diversity and the abundance variables (Zuur et al. 2009). The significance of the year term was tested by creating a model with only the plot position nested in compartment, and performing a likelihood ratio test of change in likelihood between models.

To examine whether there was a change in the species composition over time we used Principle Components Analysis (PCA) using the *vegan* package. The significance of the year term was analysed using a Permutational multivariate analysis of variance (PERMANOVA) using the *Adonis* function in the *vegan* package, which tests for a shift in the centroid location between years. Compartments were used to restrict permutations, allowing the effect of year to be considered while controlling for compartment. The PERMANOVA test assumes homogeneous dispersion; this assumption was tested beforehand using the *betadispers* and *permutest* functions in *vegan*. In cases where the assumption was violated, we also used the *manylm* function within the *mvabund* package (Wang et al. 2012) which uses generalized linear models (GLMs) to investigate the potential effect of year on the multivariate community. The residual versus fit plots suggested that the data fitted a Poisson distribution.

To investigate the influence of seasonal grazing management on the plant communities, we used generalised linear mixed models, with total average sheep days within spring, summer, autumn and winter in the previous three years as a fixed effect. We used the previous three years as we assumed that vegetation change will be caused by cumulative grazing effects over time (e.g. Ma et al., 2017), but also that influences will diminish over time. Furthermore, we aimed to retain as much as the vegetation data as possible, and having a longer period would have diminished the data set greatly. Given the complexity of changes in grazing over years, we also ran two variations of the model: 1) including year as an explanatory variable within the original model; and 2) using total average sheep days within spring, summer, autumn and winter from the previous year only (Appendix C and D). Year was included as a variable in the first model variation, as this could also influence the vegetation. For the second model variation, running the model with grazing data only from the previous year, could be important for identifying if this time period is dominating in our original model or whether the effect on the vegetation is different. Plot, nested in compartment, was included as a random effect. All predictor variables were z-standardised prior to analysis to facilitate comparison of model coefficients. We constructed models with species richness, species diversity, indicator richness, indicator abundance, grass abundance and forb abundance as the dependent variables. As before, a Poisson error structure was used for all richness variables, whilst a Gaussian structure was used for species diversity and the abundance variables. The null hypothesis in these models was that past grazing in spring, summer, autumn and winter have no effect. However the main focus of this analysis was to understand the direction and effect size of each of the grazing seasons on the vegetation community measures, rather than on their precise statistical significance (Amrhein et al. 2019, Wasserstein et al. 2019).

Results

Grazing changes over time

Grazing data were available for the years 1979-1994 (excluding 1992) and 2002-2010. The total average sheep days per hectare per year at Martin Down varied throughout these periods, but showed no directional change overall throughout the study period (Fig 2). There were, however some patterns occurring over shorter periods, such as the decline in total average sheep days per hectare between 1991 and 1994. The hierarchical clustering analysis resulted in two clusters, with cluster 1 containing the years 1979-1994 (excluding 1992), whilst cluster 2 represented the years 2002 to 2010 (Fig 3). Cluster 1 was characterised by years where sheep grazing occurred relatively evenly across all four seasons (Fig 2), whilst the years within cluster 2 tended to be dominated by grazing in the autumn and winter. This result was confirmed by the indicator analysis, which revealed that spring (indicator value: 0.89, $P = 0.001$) and summer (0.81, $P = 0.001$) grazing were significant indicators for cluster 1, as were autumn (0.72, $P = 0.003$) and winter (0.64, $P = 0.038$) for cluster 2.

Vegetation community over time

A total of 147 vascular plant species were recorded across the surveys undertaken between 1979 and 2010, of which 25 species were classified as indicators (Supplementary Material 2). The NVC community for each compartment remained fairly similar over time, with the majority of compartments assigned to a CG3 (*Bromopsis erecta* grassland) community at the

start and end of the survey period (Table 1). Species richness ($P < 0.001$, $X^2(1) = 14.136$) (Fig. 4a) and species diversity ($P < 0.001$, $X^2(1) = 21.529$) (Fig. 4b) increased overall between 1979 and 2010, though no survey data were available between 1995 and 2010. This increase was particularly pronounced between 1979 and 1983, after the compartmentalised grazing was introduced. Indicator richness fluctuated over time with a little change overall ($P = 0.577$, $X^2(1) = 0.311$) (Fig. 4c). The abundance of indicators ($P = 0.962$, $X^2(1) = 0.002$), grasses ($P = 0.2394$, $X^2(1) = 1.384$) and forbs ($P = 0.273$, $X^2(1) = 1.201$) remained fairly consistent between 1979 and 2010 (Fig 5).

The species composition appeared to have shifted over time in the PCA (Fig 6). To ease interpretation, ellipses for the years with the greatest number of plots (≥ 12) recorded were drawn (1981, 1987 and 2010). The ellipse which encloses plots recorded in 2010 is much smaller and is contained within the ellipses of 1981 and 1987, which suggests that plots were more similar to each other in 2010. The majority of species were located towards the centre of the PCA plot. The only exceptions were *Bromopsis erecta* and *Festuca ovina* which were located further towards the edge of the 1981 ellipse. The PerMANOVA test indicated a small change between years ($F = 3.78$, $P = 0.002$), but also significant heterogeneity in multivariate dispersion ($P = 0.015$). The mvabund analyses revealed that year had an overall effect on the species community ($LRT = 3675$, $P = 0.002$).

Grazing influence on the vegetation community

Spring, summer, autumn and winter grazing each had a range of effects on the plant community and abundance variables, albeit with very weak evidence and high levels of uncertainty as evident by the large variation within the 2.5 and 97.5 quantiles (Table 2). The key focus for this analysis was the direction and effect size of the different seasons of grazing on the community variables, which enables the magnitude in the differences to be explored. The effect size was greater for autumn grazing compared with the other seasons in both the species richness and indicator richness models. A median value of 1.02 implied that a 2% gain of species richness per average sheep days per ha of summer grazing in the previous three years was highly compatible with the data, however, the 2.5% quantile value of 0.97 for this model also suggested that losses up to 3% were also plausible. The indicator richness model estimated an increase of up to 7% in indicator species richness with autumn grazing. Only autumn grazing appeared to have a positive effect on species diversity, though the evidence for this was very low. The two model variations, including year and only using the previous year of grazing data, suggested that summer grazing may also have a positive influence on species diversity, though similarly with weak evidence (Appendix 3 and 4). Winter grazing within the grass abundance model was the only variable considered to be significant if $P \leq 0.05$ was employed, suggesting that winter grazing led to an increase in the abundance of grasses at Martin Down. The effect of winter grazing on grass abundance was greater compared with summer and spring grazing (Table 2). In the remaining models winter grazing had a negative effect on the community measures including species richness, species diversity, indicator richness and abundance and forb abundance, albeit with less information against the test hypothesis, suggesting there was little effect on the vegetation. Some differences in the direction of the effects were detected when comparing the original model with the second variation (including grazing in the previous year only) (Appendix 3 and 4). This was largely evident for indicator abundance where the season effects were the opposite to that identified in the original model – a decrease with spring grazing, but an increase with

all other grazing seasons when only the previous year was considered. However, again the evidence for this was very weak, suggesting little vegetation change.

Discussion

Grazing changes over time

To our knowledge, this is the first study to examine detailed grazing regimes and their impact on long-term vegetation change in calcareous grassland. The majority of studies which evaluate long-term change in such habitats have been undertaken in the UK (Diekmann et al. 2019). Where grazing has been considered this is often in the form of qualitative data, describing broad grazing trends over large time periods (Hawes et al. 2018, Ridding et al. 2020) rather than stocking densities for individual years as in this study. The analysis conducted revealed a dramatic shift in grazing regime at Martin Down between 1979 and 2010. Between 1979 and 1995 sheep grazing occurred across all four seasons on the reserve, however from 2002 grazing largely took place in the autumn and winter. Caution needs to be taken however, due to the missing data on grazing patterns between 1995 and 2002. Furthermore, it is also possible that other drivers such as nitrogen deposition were important factors during these time periods, which could have experienced changes over time.

Shifts in grazing patterns have been reported in UK grasslands (Veen et al. 2009, Stroh et al. 2017), though very few studies provide quantitative data to support this. Walker and Pinches (2011) found that a number of their *Pulsatilla vulgaris* study sites across England had winter grazing, where sites were grazed from late autumn and then were removed in spring. This was reported to have occurred since the 1980s, suggesting that the management before this time was different. This is consistent with our analysis, though the shift in regime occurred much later. This is likely to have coincided with the publication of The Lowland Grassland Management Handbook which provided advice for management of grasslands in England (Crofts and Jefferson 1999). The handbook promoted grazing in the autumn/winter rather than all year round due to concerns with grazing in the summer, which then became a standard across calcareous grasslands in England.

Vegetation community over time

Our study revealed an increase in plant species richness and diversity between 1979 and 2010 at Martin Down. This is inconsistent with other studies on calcareous grassland in the UK, which have reported a general decline in richness and/or diversity across multiple sites over similar time scales (Bennie et al. 2006, Stevens et al. 2016). The increase between 1979 and 1983 was especially pronounced, which suggests that the introduction of compartmentalised sheep grazing in 1978 was beneficial for the improving the botanical diversity of the grassland, following the lack of grazing before the reserve was taken over by Hampshire County Council and Natural England (Gibbons 1989). The indicator richness was variable throughout the study period, partly because the possible number of total indicators present was lower compared with total species richness and also fewer plots were surveyed in 1985, 1988 and 1990. This means that specific communities within certain compartments were only represented in these years. The fact that indicator richness has remained largely consistent over time excluding these years, suggests that the conservation value of the habitat has been retained over time at Martin Down, since the presence of these indicator species are used to

define the condition of such habitats by statutory nature conservation bodies in the UK. It is predicted that these indicator species will decline, with unfavourable changes such as eutrophication or excessive grazing (JNCC, 2004), thus the consistency of indicator species at Martin Down suggests the site has remained of high conservation value, continuing to support important flora and fauna. This contrasts with findings from calcareous grasslands nearby (Ridding et al. 2020) and across Europe, where the number of specialist species in dry grasslands have declined (Diekmann et al. 2019). Diekmann et al. (2019) suggest this is due to low mowing or grazing intensities compared to traditional management or an altered timing of management.

The analysis conducted in this study also showed a shift in species composition between 1979 and 2010. Plots recorded in 2010 were more similar to each other compared with those recorded earlier in the study. These were the only plots recorded after the shift in grazing, which may suggest that grazing predominately in the autumn and winter rather than across all seasons has led to less variation in the community. This could indicate a trend towards homogenization, where previously distinct plant communities become progressively more similar, though evidence for this phenomenon in calcareous grassland is lacking (Newton et al. 2012, Diekmann et al. 2019). *Festuca ovina* and *Bromopsis erecta* were both located closer to the 1979 ellipse, suggesting these species were more dominant during this early time period. This coincides with the time period when species diversity was also lower, which is to be expected if such grasses dominate the community and outcompete smaller forbs. Other long-term studies on calcareous grassland have also reported shifts in species composition (Newton et al. 2012, Diekmann et al. 2014, Bauer and Albrecht 2020). Bennie et al. (2006) assessed vegetation change in British calcareous grasslands between the 1950s and 2000s and identified a shift from species-rich CG2-type communities towards those dominated by more competitive species typical of mesotrophic grasslands (MG1, MG6, MG7). An increase in mesotrophic species has also been reported for dry grasslands across Europe (Diekmann et al. 2019). Although our analysis found a shift in species composition, this was not associated with a shift in grassland community with the majority of compartments defined as a CG3 community across the time periods (Table 1). Compartments 11a and 21 were identified as mesotrophic communities in some time periods, however this was not consistent throughout the study period. These results suggest that although there have been shifts in species composition, including species richness and diversity changes, the overall grassland community has remained largely consistent between 1979 and 2010 despite the dramatic shift in grazing regime.

Grazing influence on the vegetation community

The effect sizes identified from modelling the influence of grazing within each season on the vegetation community were variable with low support against the test hypothesis. A certain level of variability is expected as vegetation dynamics are complex and influenced by a number of factors. This highlights the difficulty of analysing vegetation data from multiple compartments recorded inconsistently through time, rather than from field experiments where certain factors can be controlled (e.g. Bullock et al., 2001, Pakeman et al., 2019). The influence of winter grazing on grass abundance was one of the few variables to provide more support against the test hypothesis. The analysis suggested that winter grazing over the previous three years led to an increase in grass abundance, which is inconsistent with Bullock et al. (2001) who identified a decrease in the number of grasses with winter grazing.

However, Wells (1972) stated that grazing during the period of rapid growth is an effective means of controlling the competitive ability of grasses. For many grass species this occurs in early spring, followed by a second growth in July. This could explain why winter grazing led to an increase in abundance in this study. Although there was less evidence, summer grazing had a negative effect on grass abundance, again supporting this notion. Winter grazing often provided greater evidence compared to grazing in other seasons across each of the vegetation community measures. Winter grazing appeared to affect the community negatively in all cases, including a decrease in species richness, species diversity and indicator richness. The direction of the effect sizes suggest that winter grazing alone is not an effective management strategy for maintaining a species-rich community. This was also suggested in *The Lowland Grassland Management Handbook* (Crofts and Jefferson 1999).

The advantages and disadvantages of grazing within particular seasons are well established (Duffey 1974, Crofts and Jefferson 1999, Blakesley and Buckley 2016). Much of the evidence to date suggests that an alteration to the timing of management may impact the vegetation community (Stroh et al. 2017, Diekmann et al. 2019). However, this study has revealed limited evidence of the influence of seasonal grazing on the vegetation community. There are a number of potential reasons for this; 1. The studied grassland communities are resilient to change. Dry grasslands are reported to be more resistant to change across Europe (Diekmann et al. 2019). For example, calcareous grassland has been shown to be relatively resistant to other drivers such as climate change (Duckworth et al. 2000, Grime et al. 2008). 2. Grazing is still occurring on a regular annual basis, where grazing is “forced” into a particular area, i.e. the compartments at Martin Down. This may be considered similar to “mob-grazing” or “cell-grazing”, where high densities of sheep/cattle graze a restricted area for a short time period (Gardiner and Haines 2008). The compartmental set up at Martin Down is unusual compared to many other nature reserves across the UK where large blocks or the whole reserve are often grazed together traditionally using set stocking (Dixon 1972, Hawes 2015). This allows the cattle/sheep to be more selective and thus particular areas may be left under-grazed even with grazing in the autumn and winter. In addition, some traditionally managed sites have had more significant shifts in grazing, including periods of no grazing for many years, (e.g. Hawes et al., 2018, Walker and Pinches, 2011) whereas grazing has been maintained throughout at Martin Down. The difference in grazing management (compartmentalised vs traditionally grazed) may explain why other reserves have reported more severe changes in the vegetation community due to a shift in grazing regime (Hawes et al. 2018, Ridding et al. 2020). This is evident in Fig 7 which compares the species richness within Compartment 11a at Martin Down alongside other calcareous grassland sites located across Wiltshire which have been traditionally managed. Although the species richness from 2010 for Martin Down was not recorded from the same location as the 1960 Nature Conservation Review quadrat (Ratcliffe 1977) (only the same compartment), as in Hawes et al. (2018), it still suggests an increase over time; something that was only evident in one of the other nearby calcareous grassland sites. 3. Although grazing in the spring and summer is recommended for maintaining floristic richness by controlling the growth and development of dominant grasses (Duffey 1974), grazing in the autumn may still be beneficial for preserving the richness. This is because by this period most flowering species will have finished flowering and set seed, and so grazing during this time can help seeds disperse through trampling (Crofts and Jefferson 1999). This is supported by our study, where although the modelled results had little evidence against the test hypothesis, the effect

size suggested that autumn grazing may increase species richness and diversity, and indicator richness. 4. Other drivers are also likely to have impacted the vegetation between 1979 and 2010 at Martin Down. Although climate change has been suggested as an important driver, Grime et al. (2008) suggests that changes to management and nutrient enrichment are currently a greater threat. Nutrient enrichment through nitrogen deposition has received considerable attention in the literature with some reporting no effect on calcareous grassland (Maskell et al. 2010), while others have found declines in species diversity and shifts in composition (van den Berg et al. 2011, Diekmann et al. 2014). Although it is extremely difficult to disentangle the effects of nitrogen deposition and changes in management (Diekmann et al. 2019), a recent study reported a decline in species diversity associated with nitrogen deposition between 1970 and 1990 in a nearby grassland, whilst declines in richness and diversity were associated with a reduction in grazing pressure between 1990 and 2016 (Ridding et al. 2020). However, in this current study at Martin Down the compartmentalised management ensured grazing occurred across the reserve between 1979 and 2010, which may have helped to mitigate against nitrogen deposition (Wilson et al. 1995, Jacquemyn et al. 2003).

Conclusions

This study highlights the importance of both long-term vegetation monitoring and maintaining comprehensive grazing records for assessing plant community dynamics over time. Our results provide quantitative evidence for a shift in grazing regime at an important calcareous grassland in southern England, whereby grazing previously occurred across all seasons but now predominately takes place in the autumn and winter. Despite this significant shift in management over time, the vegetation community showed no detrimental changes during this time. Although variable, the indicator richness remained largely consistent overall, suggesting the conservation value was retained, whilst the classified British NVC communities also stayed fairly constant throughout 1979 and 2010, with few community measures strongly associated with grazing in particular seasons. This suggests that the vegetation communities are fairly robust to such changes providing that sufficient grazing pressure is provided within the year, where compartmentalised grazing (similar to mob/cell grazing) may be a useful method for ensuring this. However, more research is required comparing this type of grazing with traditional set stocking through a controlled field experiment before more reliable recommendations can be prescribed.

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Table 1 British National Vegetation Communities (NVC) (Rodwell 1992) determined using Tablefit (Hill 1996) for each compartment surveyed at Martin Down between 1979 and 2010. Three NVC classifications with the highest goodness-of-fit are presented for each compartment and year. No entries indicate no data collected in that compartment in that year.

	4a	4b	5b	6a	6b	7b	11a	20a	21
1979	CG3a		CG3d	CG3	CG3		CG3c	CG2d	
	CG3		CG3c	CG3a	CG3c		CG3a	CG3	
	CG3c		CG3	CG3c	CG3a		CG3	CG3a	
1980	CG3a		CG3d	CG3	CG3d		CG3d	CG3a	
	CG3		CG3c	CG3a	CG3c		CG3c	CG3	
	CG3c		CG3	CG3c	CG3a		CG3	CG2d	
1981	CG3		CG3d	CG3	CG3a		MG10a	CG2d	CG2d
	CG3a		CG3c	CG3a	CG3		W24	CG3	U4b
	CG3c		CG3	CG3c	CG3c		W24a	CG3a	CG2c
1982	CG3a	CG3	CG3				CG3d		U4b
	CG3	CG3c	CG3c				CG3c		U4
	CG3c	CG3a	CG3d				CG3		U4c
1983				CG3	U4b			CG8	
				CG3a	CG3a			CG8a	
				CG3c	CG3c			CG3c	
1984						CG3a			
						CG3			
						CG3d			
1985							CG3d		
							CG3		
							CG3c		
1986	CG3c	CG3a	CG3			CG3a			CG2d
	CG3	CG3	CG3d			CG3			CG3a
	CG3a	CG3c	CG3a			CG3c			CG3
1987				CG3	U4b	CG3a	MG1d	CG3a	
				CG3a	CG3a	CG3	MG1	CG3c	
				CG3c	CG3c	CG3c	U4b	CG3	
1988									CG4c
									MG6
									MC9
1989	CG3c								U4b
	CG3								CG2d
	CG3d								U4
1990					CG3				U4b
					CG3d				MC9e
					CG3c				MC9c
1991				CG3					
				CG3a					
				CG3c					
1992	CG3c	CG3a							U4b
	CG8a	CG3							CG2d
	CG3	CG3b							U4
1994			CG3	CG3a	CG3c		CG3d		
			CG3d	CG3	CG3a		CG3c		
			CG3a	CG2d	CG3		CG3		
2010	CG2c	CG6a	CG3	CG3a	CG3a	CG3a	CG3d	CG3a	CG6a
	CG3a	CG3	CG3a	CG3	CG3	CG3	CG3	CG3	CG6
	CG3	CG3a	CG6a	CG6a	CG3c	CG3c	CG3a	CG3b	CG2c

Table 2. Model coefficients, 2.5 and 97.5% quantiles for species richness, species diversity, indicator richness, indicator abundance, grass abundance and forb abundance, with total average sheep days within spring, summer, autumn and winter in the previous three years as explanatory variables. Coefficients for species richness and indicator richness have been exponentiated.

Model	Explanatory variable	Median	2.5% quantile	97.5% quantile	<i>P</i> -value	AIC
Species richness	Spring grazing	0.967	0.910	1.029	0.289	430.445
	Summer grazing	1.002	0.944	1.058	0.944	
	Autumn grazing	1.023	0.973	1.075	0.368	
	Winter grazing	0.986	0.935	1.041	0.600	
Species diversity	Spring grazing	-0.432	-1.280	0.417	0.292	377.784
	Summer grazing	-0.011	-0.909	0.887	0.996	
	Autumn grazing	0.549	-0.201	1.299	0.154	
	Winter grazing	-0.462	-1.274	0.351	0.255	
Indicator richness	Spring grazing	1.019	0.917	1.126	0.710	354.391
	Summer grazing	1.018	0.914	1.127	0.740	
	Autumn grazing	1.065	0.972	1.162	0.163	
	Winter grazing	0.953	0.858	1.054	0.354	
Indicator abundance	Spring grazing	0.009	-0.021	0.039	0.535	-60.870
	Summer grazing	-0.010	-0.043	0.024	0.553	
	Autumn grazing	-0.002	-0.029	0.024	0.884	
	Winter grazing	-0.020	-0.049	0.010	0.175	
Grass abundance	Spring grazing	0.013	-0.018	0.043	0.418	-62.399
	Summer grazing	-0.003	-0.035	0.030	0.934	
	Autumn grazing	0.016	-0.012	0.043	0.244	
	Winter grazing	0.029	0.000	0.058	0.046	
Forb abundance	Spring grazing	-0.010	-0.036	0.017	0.445	-80.453
	Summer grazing	0.009	-0.018	0.035	0.481	
	Autumn grazing	-0.004	-0.028	0.021	0.771	
	Winter grazing	-0.022	-0.047	0.003	0.105	

Fig 1 Compartments (2.9 – 11.9 ha) containing plots (dark-grey dots) which were surveyed at Martin Down National Nature Reserve (black dot), southern England, between 1979 and 2010 (EPSG:27700). Compartments which were surveyed are labelled with their compartment number (see Appendix A).



Fig 2 Average sheep days per hectare in autumn (brown; September, October, November), spring (yellow; March, April, May), summer (green; June, July, August) and winter (grey; December, January, February) using available data between 1979 and 2010 at Martin Down.

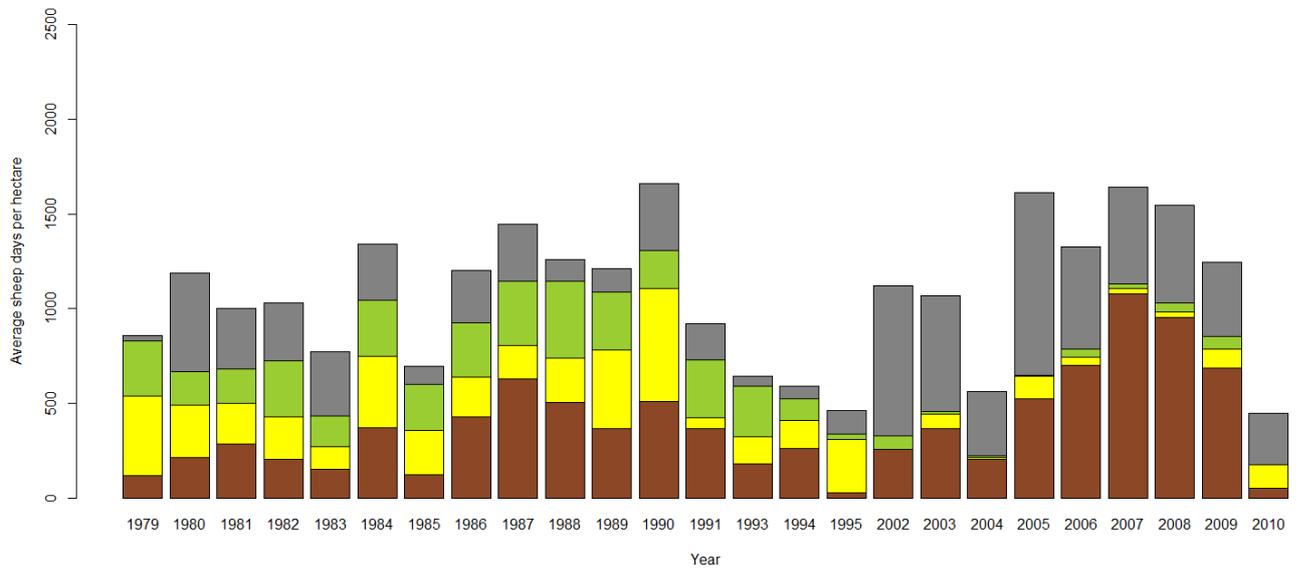


Fig 3 Plot of the principal coordinates analysis (PCoA) of the change in average sheep days per hectare within autumn, spring, summer, winter in the years 1979-2010 (where grazing data for the year is available) at Martin Down. Years are grouped into two clusters using hierarchical clustering.

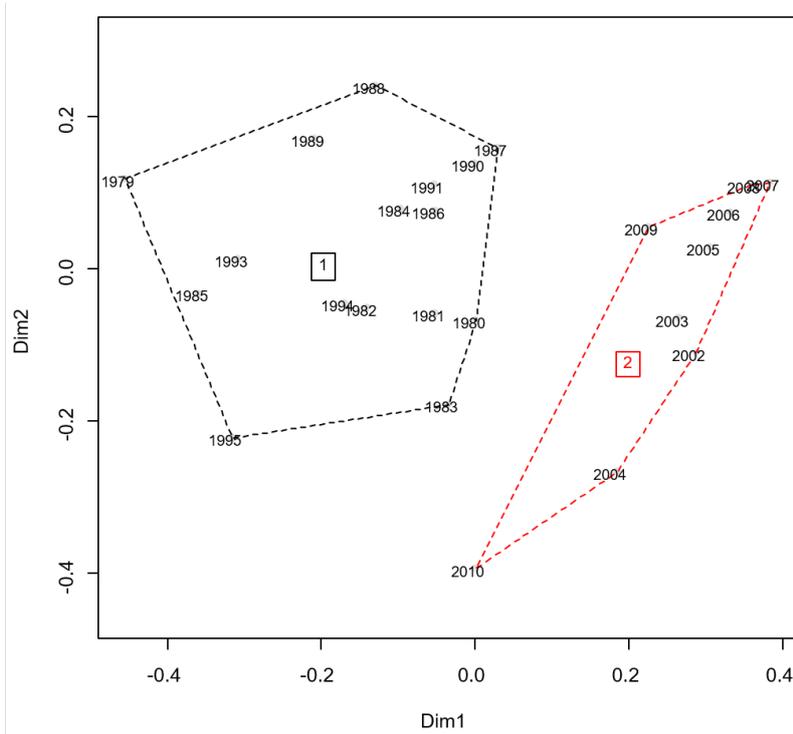


Fig 4 Species richness (a), species diversity, using Simpson's index (b) and indicator richness (c) for 104 plots (1m x 1m) between 1979 and 2010 at Martin Down. The dashed lines joining points are to allow visual clarity.

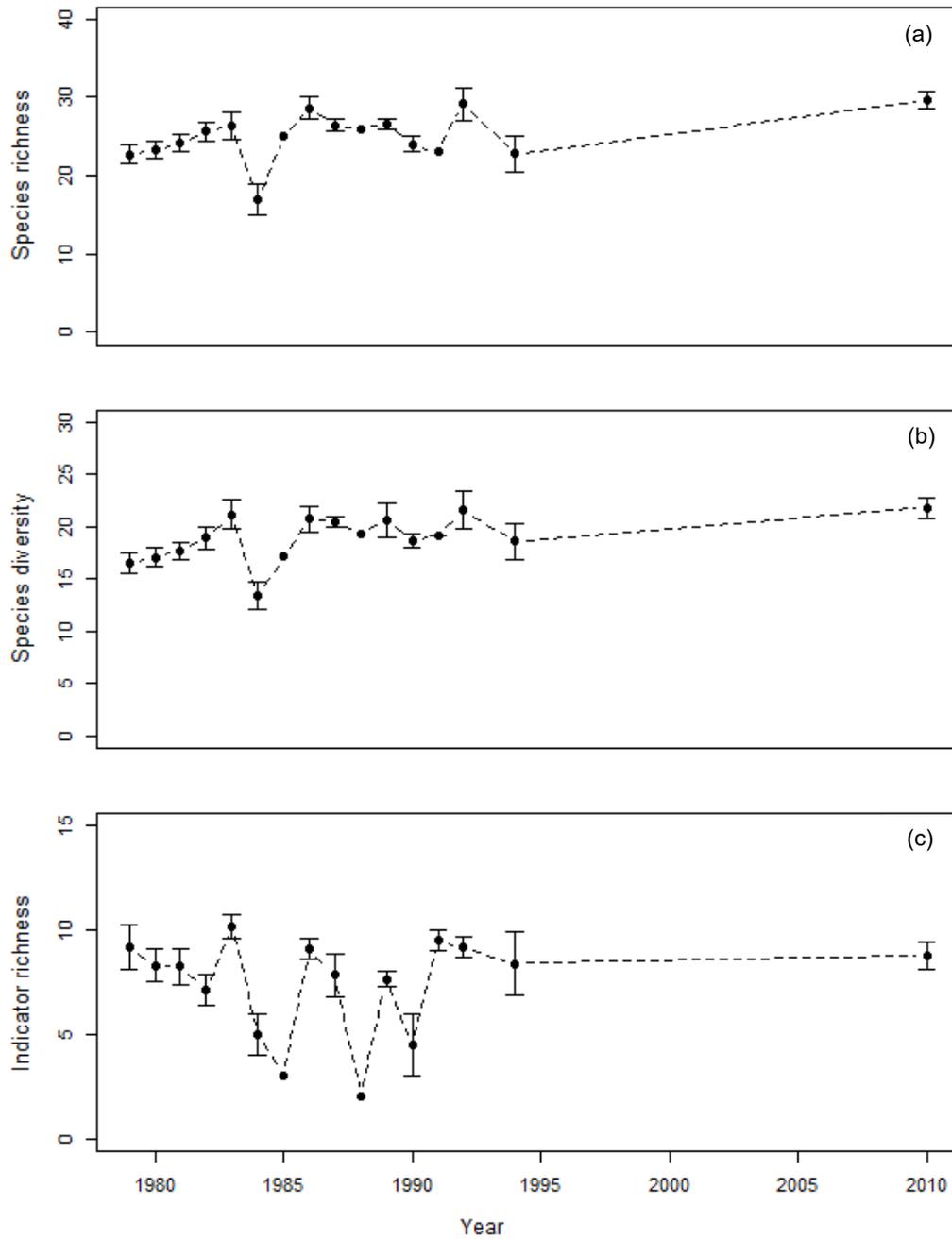


Fig 5 Average abundance of indicators (a), grass species (b) and forb species (c) weighted by the total abundance for each of the 104 plots (1m x 1m) recorded between 1979 and 2010 at Martin Down. The dashed lines joining points are to allow visual clarity.

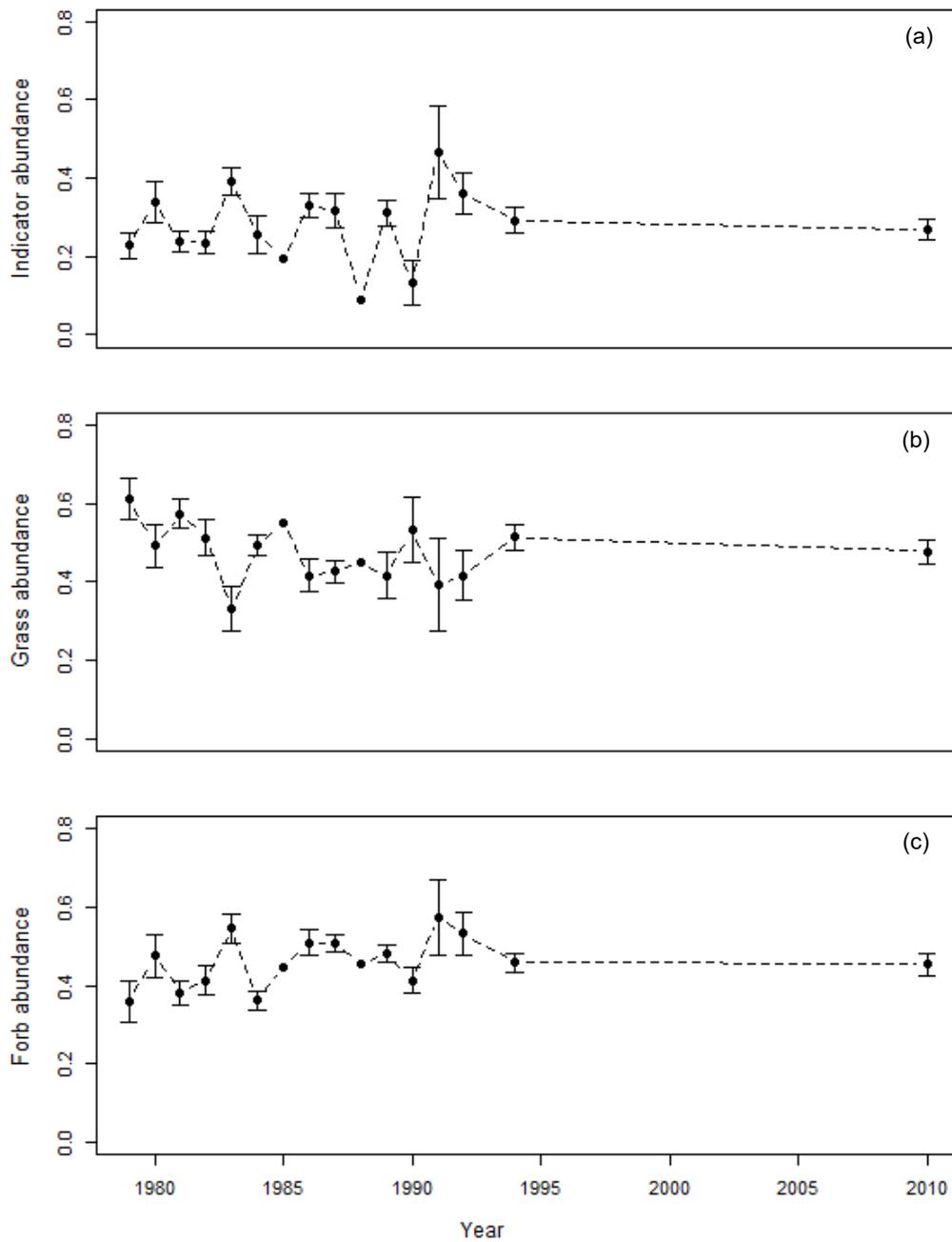


Fig 6 Principal Components Analysis (PCA) plot based on plant species cover (%) from 105 plots surveyed at Martin Down between 1979 and 2010. PCA1 and PCA2 have constrained Eigenvalues 27.23 and 17.29 respectively and explained 32.0% and 20.0% of the variation. Polygons enclose plots by three of the main survey years, where the majority of plots were recorded, 1981 (white), 1987 (yellow) and 2010 (green) on standard deviation of point scores. Only the most abundant species (*Bromopsis erecta* (Brom.erc), *Festuca ovina* (Fest.ovn), *Carex flacca* (Care.flc), *Carex humilis* (Care.hum), *Holcus lanatus* (Holc.lan), *Leontodon hispidus* (Leon.hsp)) are labelled, in order of relative diversity (using the inverse Simpson index). Small crosses indicate species whose names have been suppressed to declutter the ordination.

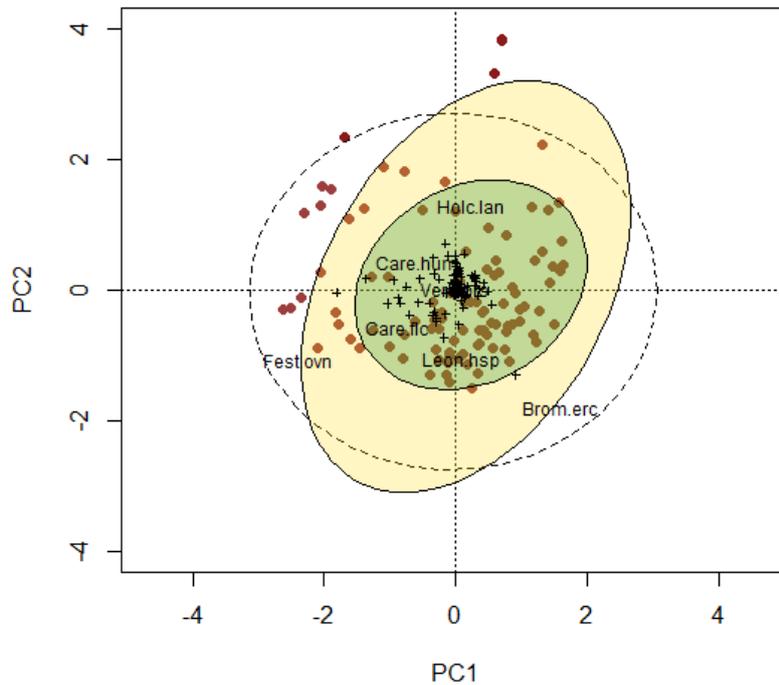
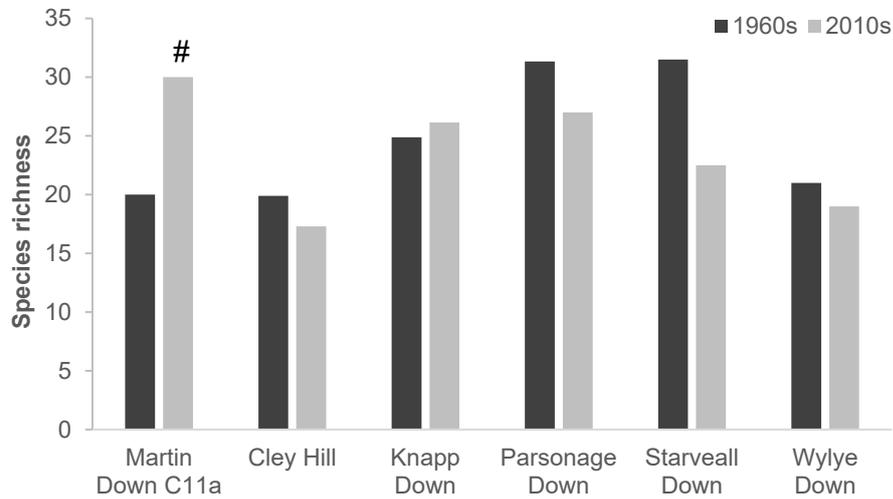


Fig 7 Average plant species richness within 1m x 1m quadrats recorded across calcareous grasslands in Wiltshire in the 1960s as part of the Nature Conservation Review (Ratcliffe 1977). The same quadrats at Cley Hill, Knapp Down, Parsonage Down, Starveall Down and Wyle Down were resurveyed by Hawes et al. (2018). # The species richness for Martin Down in 2010 is represented by the relevant plot within the same compartment in this study which is not co-located with the 1960 quadrat.



Appendix A Availability of vegetation and grazing data between 1979-1994 (excluding 1992) and 2002-2010 at Martin Down, where V and G indicate vegetation and grazing data respectively.

Plot	Compartment	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	2002	2003	2004	2005	2006	2007	2008	2009	2010
1	5b	VG	VG	VG	VG	G	G	G	VG	G	G	G	G	G		G	VG	G	G	G	G	G	G	G	G	G	VG
2	6b	VG	VG	VG	G	VG	G	G	G	VG	G	G	G	G		G	G	G	G	G	G	G	G	G	G	G	VG
3	6b	VG	VG	VG	G	VG	G	G	G	VG	G	G	G	G		G	VG	G	G	G	G	G	G	G	G	G	VG
5	6a	VG	VG	VG	G	VG	G	G	G	VG	G	G	G	VG		G	VG	G	G	G	G	G	G	G	G	G	VG
6	6a	VG	VG	VG	G	VG	G	G	G	VG	G	G	G	VG		G	VG	G	G	G	G	G	G	G	G	G	VG
13	11a	VG	VG	VG	VG	G	G	G	G	VG	G	G	G	G		G	VG	G	G	G	G	G	G	G	G	G	VG
15	20a	V	V	V		V		G	G	VG	G	G	G	G		G	G	G	G	G	G	G	G	G	G	G	VG
16	20a	V	V	V				G	G	VG	G	G	G	G	V	G	G	G	G	G	G	G	G	G	G	G	VG
19	4a	VG	VG	VG	VG	G	G	G	VG	G	G	G	G	G		G	G	G	G	G	G	G	G	G	G	G	VG
20	4a	VG	VG	VG	VG	G	G	G	VG	G	G	VG	G	G	V	G	G	G	G	G	G	G	G	G	G	G	VG
24	21			V	V		G	G	VG	G	G	VG	G			G	G	G	G	G	G	G	G	G	G	G	VG
25	21			V	V		G	G	VG	G	G	VG	G		V	G	G	G	G	G	G	G	G	G	G	G	VG
26	4b	G	G	G	VG	G	G	G	VG	G	G	G	G	G	V	G	G	G	G	G	G	G	G	G	G	G	VG
27	4b	G	G	G	VG	G	G	G	VG	G	G	G	G	G	V	G	G	G	G	G	G	G	G	G	G	G	VG
30	7b	G	G	G	G	G	VG	G	VG	VG	G	G	G	G			G		G	G	G	G	G	G	G	G	VG
31	7b	G	G	G	G	G	VG	G	VG	VG	G	G	G	G			G		G	G	G	G	G	G	G	G	VG
42	11a	G	G	G	G	G	G	VG	G	VG	G	G	G	G		G	G	G	G	G	G	G	G	G	G	G	G
53	6b	G	G	G	G	G	G	G	G	VG	G	G	V	G		G	G	G	G	G	G	G	G	G	G	G	G
54	21						G	G	G	VG	VG	G	V	G		G	G	G	G	G	G	G	G	G	G	G	G

Appendix B Positive indicators for CG3 and CG2 grasslands extracted from the Common Standards Monitoring for lowland grasslands (JNCC 2004), which have been recorded at Martin Down between 1979-2010.

Species	CG3	CG2
<i>Anthyllis vulneraria</i>	Y	Y
<i>Asperula cynanchica</i>	Y	Y
<i>Brachypodium pinnatum</i>	Y	
<i>Bromopsis erecta</i>	Y	
<i>Cirsium acaule</i>	Y	Y
<i>Filipendula vulgaris</i>	Y	Y
<i>Galium verum</i>	Y	Y
<i>Gentianella amarella</i>	Y	Y
<i>Gentianella anglica</i>	Y	Y
<i>Helianthemum nummularium</i>	Y	Y
<i>Pilosella officinarum</i>	Y	Y
<i>Hippocrepis comosa</i>	Y	Y
<i>Leontodon hispidus</i>	Y	Y
<i>Leontodon saxatilis</i>	Y	Y
<i>Leucanthemum vulgare</i>	Y	Y
<i>Linum catharticum</i>	Y	Y
<i>Lotus corniculatus</i>	Y	Y
<i>Plantago media</i>	Y	Y
<i>Polygala calcarea</i>	Y	Y
<i>Polygala vulgaris</i>	Y	Y
<i>Primula veris</i>	Y	Y
<i>Sanguisorba minor</i>	Y	Y
<i>Scabiosa columbaria</i>	Y	Y
<i>Succisa pratensis</i>	Y	Y
<i>Thymus polytrichus</i>	Y	Y

Appendix C. Model coefficients, 2.5 and 97.5% quantiles for species richness, species diversity, indicator richness, indicator abundance, grass abundance and forb abundance with year and total average sheep days within spring, summer, autumn and winter in the previous three years as explanatory variables. Coefficients for species richness and indicator richness have been exponentiated.

Model	Explanatory variable	Median	2.5% quantile	97.5% quantile	P-value	AIC
Species richness	Year	1.058	1.000	1.120	0.049	428.616
	Spring grazing	0.977	0.919	1.040	0.463	
	Summer grazing	1.016	0.958	1.073	0.576	
	Autumn grazing	0.996	0.942	1.053	0.875	
	Winter grazing	0.971	0.920	1.027	0.300	
Species diversity	Year	0.884	0.050	1.719	0.034	375.441
	Spring grazing	-0.242	-1.084	0.601	0.536	
	Summer grazing	0.244	-0.669	1.156	0.579	
	Autumn grazing	0.103	-0.741	0.948	0.814	
	Winter grazing	-0.684	-1.502	0.134	0.092	
Indicator richness	Year	1.035	0.929	1.152	0.528	355.996
	Spring grazing	1.026	0.922	1.133	0.623	
	Summer grazing	1.027	0.919	1.141	0.626	
	Autumn grazing	1.048	0.942	1.160	0.379	
	Winter grazing	0.945	0.850	1.048	0.294	
Indicator abundance	Year	-0.005	-0.036	0.025	0.701	-52.503
	Spring grazing	0.008	-0.023	0.039	0.588	
	Summer grazing	-0.012	-0.046	0.023	0.496	
	Autumn grazing	0.001	-0.031	0.032	0.940	
	Winter grazing	-0.018	-0.049	0.012	0.224	
Grass abundance	Year	0.012	-0.020	0.044	0.431	-54.548
	Spring grazing	0.015	-0.016	0.046	0.341	
	Summer grazing	0.000	-0.033	0.034	0.916	
	Autumn grazing	0.010	-0.022	0.041	0.528	
	Winter grazing	0.026	-0.004	0.056	0.082	
Forb abundance	Year	-0.006	-0.035	0.024	0.690	-72.026
	Spring grazing	-0.011	-0.038	0.017	0.410	
	Summer grazing	0.008	-0.019	0.035	0.539	
	Autumn grazing	-0.001	-0.029	0.027	0.943	
	Winter grazing	-0.021	-0.047	0.006	0.146	

Appendix D. Model coefficients, 2.5 and 97.5% quantiles for species richness, species diversity, indicator richness, indicator abundance, grass abundance and forb abundance with total average sheep days within spring, summer, autumn and winter in the previous year as explanatory variables. Coefficients for species richness and indicator richness have been exponentiated.

Model	Explanatory variable	Median	2.5% quantile	97.5% quantile	<i>P</i> -value	AIC
Species richness	Spring grazing	0.979	0.934	1.027	0.372	559.450
	Summer grazing	0.997	0.951	1.045	0.903	
	Autumn grazing	1.019	0.974	1.064	0.411	
	Winter grazing	0.988	0.944	1.034	0.603	
Species diversity	Spring grazing	-0.300	-1.088	0.489	0.430	505.503
	Summer grazing	0.245	-0.565	1.054	0.556	
	Autumn grazing	0.647	-0.087	1.381	0.092	
	Winter grazing	-0.110	-0.822	0.602	0.736	
Indicator richness	Spring grazing	0.995	0.904	1.091	0.909	452.629
	Summer grazing	1.040	0.945	1.140	0.408	
	Autumn grazing	1.060	0.978	1.145	0.149	
	Winter grazing	1.017	0.940	1.099	0.663	
Indicator abundance	Spring grazing	-0.003	-0.030	0.024	0.844	-88.055
	Summer grazing	0.003	-0.026	0.032	0.827	
	Autumn grazing	0.010	-0.014	0.034	0.402	
	Winter grazing	0.002	-0.021	0.025	0.846	
Grass abundance	Spring grazing	0.007	-0.023	0.038	0.632	-71.637
	Summer grazing	-0.012	-0.043	0.019	0.477	
	Autumn grazing	-0.004	-0.032	0.025	0.810	
	Winter grazing	0.013	-0.015	0.040	0.374	
Forb abundance	Spring grazing	-0.002	-0.028	0.024	0.888	-94.065
	Summer grazing	0.014	-0.012	0.040	0.287	
	Autumn grazing	0.007	-0.018	0.032	0.581	
	Winter grazing	-0.013	-0.038	0.011	0.332	