



Long-term change in calcareous grassland vegetation and drivers over three time periods between 1970 and 2016

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Abstract Analysis of long-term vegetation change is limited. Furthermore most studies evaluating change only examine two snapshots in time, which makes it difficult to define rates of change and accurately assess potential drivers. To assess long-term change in calcareous grassland over multiple time periods, we re-surveyed a transect study undertaken at Parsonage Down National Nature Reserve, Wiltshire, southern England in 1970 and 1990 by T. Wells. We examined differences in soil properties and

species traits in each of the survey years to understand potential drivers of vegetation change, including nitrogen deposition and grazing management. There was a clear shift in species composition, combined with significant declines in species richness and diversity between 1970 and 2016, with the greater rate of change occurring between 1990 and 2016. A significant increase in soil total nitrogen was found, which was significantly associated with the decline in species diversity between 1970 and 1990. Significant changes in community-weighted mean traits were identified for plant height (increasing), specific leaf area (decreasing), grazing tolerance (decreasing) and Ellenberg N (decreasing) between 1970 and 2016. By using survey data from multiple time periods, we suggest that N deposition may have contributed

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towards community changes between 1970 and 1990, as indicated by the change in soil properties and the associated decline in species diversity. Vegetation change between 1990 and 2016 is likely to be largely attributable to a decline in grazing pressure, indicated by the increase in taller species and a decrease in grazing tolerance.

Keywords Calcareous grassland · Grazing · Long-term · Nitrogen deposition · Soil properties · Species traits

Introduction

Habitat degradation is one of the main drivers of biodiversity loss worldwide (Newbold et al. 2015). Unlike habitat destruction, degradation involves a gradual decline in habitat quality, and can be difficult to detect. Furthermore, most studies examining habitat degradation or change over time only use a single or two snapshots in time (e.g. Diaz et al. 2013; Keith et al. 2009). This static approach makes it difficult to understand trajectories of change (Renard et al. 2015) or to assess potential drivers accurately. Understanding these drivers is essential for predicting future changes and consequently adapting management to mitigate these impacts in order to conserve habitats and their species.

Calcareous grassland is a classic example of a habitat that has undergone considerable destruction and degradation across Europe. The loss was particularly severe during the twentieth century (Fuller 1987; Polus et al. 2007; Ridding et al. 2015; van Dijk 1991) due to agricultural intensification or abandonment (Poschlod and Wallis de Vries 2002). For example, Fuller (1987) estimated that 97% of semi-natural grassland had been lost between 1932 and 1984 in England and Wales. Calcareous grasslands have high conservation value, supporting a high

diversity of plant and animal species and providing multiple ecosystem services (Bullock et al. 2011).

The condition of remaining calcareous grasslands has also declined over time (Bennie et al. 2006; Diekmann et al. 2014; Stevens et al. 2016), with very few studies finding increases in species richness over time (Mitchell et al. 2017). Contemporary surveys, which assess the condition of vegetation at a single point in time, show that only 29% of lowland calcareous grasslands designated as Sites of Special Scientific Interest (SSSI) (or “Areas of Special Scientific Interest” in Northern Ireland (ASSI)) were in “favourable condition” in the UK (Williams 2006). A/SSSIs are the basic unit of statutory protection in the UK for areas of land selected for ‘special interest by reason of any of its flora, fauna, or geological or physiographical features’, with their condition assessed against a standardised ideal (JNCC 2015). These studies are useful for assessing current status, however, they provide limited insight into detailed community changes, the rate of change over time and potential drivers of this.

Ecologists use three main approaches to examine drivers of vegetation change: controlled experiments, long-term monitoring or temporal re-surveys and space-for-time substitutions (Elmendorf et al. 2015). For example, Maskell et al. (2010) used “space-for-time” substitution to understand temporal changes in grassland status using spatial differences in nitrogen (N) deposition. However, this method is often criticised and has been found to be less effective compared with time-based “before-after-control-impact” approaches (França et al. 2016). Other studies using long-term vegetation data from two snapshots in time have shown significant decreases in species richness (Bennie et al. 2006; Stevens et al. 2016) and shifts in species composition (Diekmann et al. 2014; Newton et al. 2012) in calcareous grasslands. These impacts have been attributed to possible management changes, climate and/or N deposition. Although perennial vascular plant assemblages are generally more stable than annual ones, caution should be taken when evaluating two time points, since this may reflect normal inter-annual variation or abnormal variation caused by unusual weather, for example. Useful indicators of drivers such as management, climate and N deposition can be derived from the traits of species present in the community (Keith et al. 2009; Smart et al. 2006). For example, specific leaf area

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(SLA) and plant height are relevant traits for understanding the effects of grazing pressure and N deposition, since more competitive plants typical of nutrient rich conditions are more likely to have a higher SLA and canopy height (Stevens et al. 2016, 2011b). Weighted Ellenberg values of a vegetation community (Hill et al. 2004), particularly soil fertility (N), and soil acidity (R), have been shown to be sensitive to N deposition in other studies (Emmett et al. 2011; Rowe et al. 2017), although some find no relationship with Ellenberg N (Stevens et al. 2010). Despite this, Ellenberg N and R are often used to suggest the influence of N deposition on vegetation change (Diekmann et al. 2014; Newton et al. 2012).

However, using traits to attribute environmental change to particular drivers can be problematic, as they can vary in their sensitivity across spatial scales and may respond to multiple drivers (Ames et al. 2016; Shipley et al. 2016), thus contemporaneous direct measures of drivers are often preferable. Despite the number of long-term vegetation studies, few have examined detailed vegetation data across multiple time periods for calcareous grassland with measures of drivers at each interval. This would provide more reliable insights into factors influencing change over time, especially as this is likely to be driven by policy, biophysical, and socioeconomic characteristics, all of which will vary (Renard et al. 2015). Furthermore, if the levels of different drivers have changed over time, as has been reported for N deposition (Du 2016; Tipping et al. 2017), having multiple surveys may allow these shifting effects to be disentangled.

N deposition has been well documented as a driver of change in acidic grasslands using space-for-time approaches (Diekmann et al. 2014; Duprè et al. 2010; Maskell et al. 2010). However, fewer clear findings have been reported for calcareous grasslands. For Britain, a space-for-time study examining the effects of atmospheric N deposition in heathland, acid, calcareous and mesotrophic grassland, found a significant reduction in species richness in acid grassland, however, this was not identified for calcareous grassland (Maskell et al. 2010). A similar study by Diekmann et al. (2014) also reported no effect on species richness, but they did identify a shift in species composition in calcareous grassland in North-west Germany. N deposition is known to affect the status of grassland soils, where increases in soil N, decreases in the total C/N ratio and declines in base cations have

been reported (Phoenix et al. 2012; Rowe et al. 2017; Stevens et al. 2011a). Because of this, soil properties are often used as indicators of N deposition.

Changes to the management of grasslands in recent decades, particularly grazing, are also suggested as one of the drivers of degradation in calcareous grassland (Williams 2006). Under-grazing can lead to scrub encroachment and the loss of indicator grassland species, whilst over-grazing can cause unpalatable species to dominate (Bullock et al. 2011). Other potential management influences include indirect nutrient enrichment through grazing improved and unimproved pastures together, or supplementary feeding, which can lead to a loss of plant diversity (Kirkham 2006).

Utilising records of past vegetation, therefore, provides an opportunity to quantify and understand the mechanisms behind long-term environmental change. In this study, we repeat a detailed transect survey, originally recorded in the 1970s, to examine vegetation change over time and identify potential drivers. The original survey was led by Terry Wells in 1970 to investigate the floristic composition of calcareous grassland overlying a Celtic field system at Parsonage Down National Nature Reserve (NNR) in southern England. Celtic field systems are prehistoric agricultural systems, and where boundaries are still evident, as at Parsonage Down, this suggests that a field has never been ploughed (Rhodes 1950). In 1990, Wells and colleagues repeated the survey to examine if N deposition and its effects were apparent, although none were identified (Wells 1993). This study thus offers a rare assessment of long-term vegetation changes in calcareous grassland across three time points with complete supporting data for the close examination of drivers. Based on the evidence reviewed above, we hypothesise that:

- i) Vegetation change between 1970 and 2016 is non-linear, reflecting changes in drivers over time.
- ii) Changes in soil properties over time are a consequence of N deposition and will be evident through increases in soil N and declines in base cations.
- iii) Changes in vegetation will reflect the soil status over time.

- iv) Changes in N deposition and grazing are evident through changes in the trait profile of the vegetation.

Methods

Study area

The survey was undertaken at Parsonage Down NNR, Wiltshire (51°10' 17" N, 1°55' 25" W). Parsonage Down was designated as an NNR and SSSI in 1973 and 1986, respectively, and consists of 188 ha of chalk grassland. Until 1979, the owner had farmed the land using traditional methods for 53 years, grazing it with both cattle and sheep, with stocking levels carefully controlled (Table 1). Under the subsequent ownership of Natural England, the statutory nature conservation body for England, the grassland has continued to be grazed with sheep and cattle, with no mineral fertiliser usage, however, the timings and numbers of cattle and sheep grazing have been more variable compared with earlier time periods (Table 1, Online Resource 1). Modelled N deposition data show a steady increase in total N deposited at Parsonage Down between 1800 and 1990, with a decline since the 1990s (Tipping et al. 2017) (Fig. 1). The decline in N deposition across the UK since the 1990s is largely attributed to the reduction in industrial and vehicle emissions of nitrogen compounds, after new policy measures were introduced (RoTAP 2012), though reduced N has declined much less than oxidised N.

Survey method

Four transects were set up in 1970; transects three and four measured 18.3 m, whilst transects one and two were 33.8 m and 31.1 m in length, respectively, to encompass the Celtic field boundaries. Vascular plant

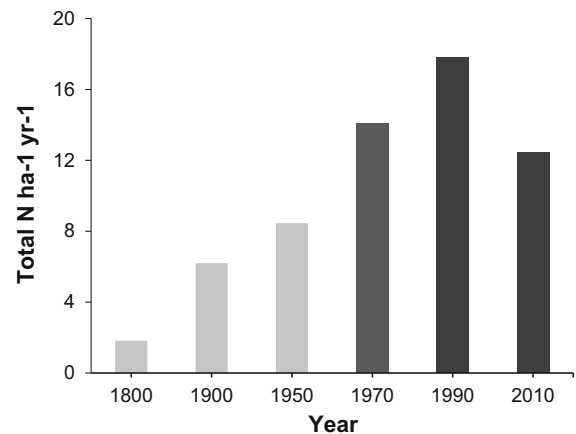


Fig. 1 Total nitrogen deposition for the 5 km by 5 km grid square which includes Parsonage Down National Nature Reserve for six snapshot years between 1800 and 2010 (method described in Tipping et al. 2017). The years which correspond exactly (1970 and 1990) or closely (2016) to the survey periods are shown in black

species were recorded 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, in 20 cm × 20 cm quadrats every 0.9 m on each of the four transects, giving a total of 115 quadrats. Vascular plants were identified to species level, with the exception of *Taraxacum* microspecies. The sward height was determined using the direct measurement method (Stewart et al. 2001). Twenty two soil samples were taken at 11 positions along each of the four transects (Online Resource 2), at two depths, 0–5 cm and 5–10 cm, using a corer of 3.5 cm diameter. The following soil properties were determined for each sample; pH, loss on ignition (LOI), exchangeable potassium (K), magnesium (Mg) and calcium (Ca), phosphate (PO₄-P) and total nitrogen (N). For further details on chemical analysis see Online Resource 3. Wells and colleagues re-surveyed the same quadrats in August 1990 and collected soil samples which were analysed in 1990 using the same methodology and locations as used in 1970 (Wells 1993).

In 2016, transects were accurately relocated by geo-referencing Wells' original survey maps with a 1:125 scale map (held at the UK Centre for Ecology & Hydrology (UKCEH), Wallingford) showing the Celtic field systems, using archaeological GIS layers provided by the Defence Infrastructure Organisation,

Table 1 The upper and lower estimates of the total number of cattle and sheep grazing at Parsonage Down between 1970 and 2016 using qualitative data from reserve managers (see Online Resource 1)

| Time period | Cattle | Sheep |
|-------------|---------|---------|
| 1970–1990 | 330–350 | 430 |
| 1990–2016 | 75–90 | 250–380 |

which also highlighted the same Celtic field boundaries. Reliably re-locating transects are essential when evaluating change over time, since imprecise locations can increase the likelihood of pseudo-turnover, where species may be incorrectly recorded as extinct or colonising due to misplacement (Fischer and Stöcklin 1997). The geo-referencing procedure was completed using ESRI ArcGIS v10.4 (© ESRI, Redlands, CA). Vegetation data and soil samples were collected in the same locations as the original survey during a similar time of year (June and August for the vegetation and soil sampling, respectively) and were analysed using the methodology outlined above. Grid references were recorded for the start and end of the four transects, accurate to ± 2 m (Online Resource 4).

Potential drivers of change

Measurements of soil properties (pH, LOI, exchangeable K, Mg and Ca, $\text{PO}_4\text{-P}$ and total N) were evaluated for each survey year. These are important metrics for N deposition and may be considered a more direct method or a midpoint indicator (“links in the cause-effect chain”) for evaluating the influence of N deposition, where a midpoint indicator indicates progress towards changes in biodiversity (the endpoint) (Rowe et al. 2017). We used community-weighted mean Ellenberg indicator values (Hill et al. 2004) for soil N, and soil R to examine the potential influence of N deposition on vegetation change (Emmett et al. 2011; Newton et al. 2012; Rowe et al. 2017). We also used database-derived values for a species’ height (Hill et al. 2004), SLA (Kleyer et al. 2008) and grazing tolerance (Briemle et al. 2002) to assess the potential impact of grazing pressure (Bullock et al. 2001; Grant et al. 1985).

Data analysis

Vegetation data from the first two surveys (Wells 1993) were digitised from record cards archived at UKCEH. Nomenclature from the earlier surveys was adjusted to follow Stace (2010). To assess changes in individual species, we used two separate Chi-squared tests to test for changes in frequency between (1) 1970 and 1990, and (2) 1990 and 2016. Due to the large number of comparisons, P values were adjusted in order to control the false discovery rate using the method of Benjamini and Hochberg (1995).

Species richness and diversity in each quadrat were calculated for each of the three survey years. Species diversity was calculated as the inverse Simpson’s diversity index (Hill number 3) in the “vegan” package (Oksanen et al. 2007) in R v3.0.2 (R Core Team 2017), since this is mostly commonly used and easier to interpret than the Simpson’s index (Morris et al. 2014). Species which are designated as positive indicator species for CG2 grasslands in the UK are of particular relevance for assessing stand quality at our site (Online Resource 5) and were thus assessed for their richness and diversity [Common Standards Monitoring (JNCC 2004)].

To test for non-linear changes in species richness and diversity of all species and CG2 positive indicator species, we used generalised additive mixed models (GAMMs), a technique which is often used to detect non-linear patterns (Devictor et al. 2008; Polansky and Robbins 2013). Species richness of all species and CG2 indicator species were modelled using a Poisson error structure, whilst a Gaussian error structure was used for the diversity variables (Zuur et al. 2009). We included year as a smoother term and transect as a random effect using the “mgcv” package (Wood 2017) in R. To further examine whether vegetation change between 1970 and 2016 was non-linear, we also calculated the rates of change in species richness and diversity for 1970–1990 and 1990–2016. We compared the difference in time periods by pairing the change in species richness and diversity in 1970–1990 with the change in species richness and diversity in 1990–2016 using a Wilcoxon signed-rank test in R.

To examine whether soil properties over time were a consequence of N deposition, we assessed differences in the soil properties (LOI, pH, K, Mg, Ca, $\text{PO}_4\text{-P}$ and N) over the three survey periods. We used general linear mixed models, with year as a fixed effect and transect as a random effect, using the “lme4” package (Bates et al. 2014) in R. The significance of the year term was tested by creating a model with only transect, and performing a likelihood ratio test of change in likelihood between models. The inclusion of a compound symmetry structure, which is often useful for the analysis of short time series (Zuur et al. 2009), had little effect on Akaike’s Information Criterion (AIC), suggesting temporal autocorrelation was not an issue in our dataset; this error structure was not included in the final models.

To reveal if changes in vegetation reflected the soil status over time, we examined the correlation between the change in each of the soil properties with both the change in species richness and diversity. This was carried out for both time period comparisons (1970–1990 and 1990–2016) using Spearman's rank correlation, since the data were not normally distributed. In addition to examining species richness and diversity, we also assessed whether the soil properties combined to have a significant effect on the variation in species composition in 1970, 1990 and 2016, using a Redundancy Analysis (RDA). RDA was deemed the most appropriate technique, since a Detrended Correspondence Analysis revealed the gradient lengths were too short for a Canonical Correspondence Analysis (Ramette 2007). A subset of quadrats was used for this analysis, since not all quadrats had soil data associated with them. The significance of the constraining factors were analysed using ANOVA-like permutation tests (Oksanen et al. 2007).

To assess if signals of N deposition and grazing changes were evident through changes in the trait profile of the vegetation, we calculated community-weighted mean (CWM) traits (i.e. plot-level trait values weighted by species abundance) per quadrat for each survey year (Garnier et al. 2004) for plant height, SLA, grazing tolerance and the two Ellenberg indicators (N and R) to assess the potential impact of grazing pressure. We examined whether the CWM values of these traits differed between quadrats surveyed in 1970, 1990 and 2016, using general linear mixed models, with year as a fixed effect and transect as a random effect. The significance of the year term was tested as described above. The same methodology was used to determine changes in sward height in 1970, 1990 and 2016, modelled with a Gaussian distribution, since this is likely to be related to grazing pressure. We also assessed whether soil properties were associated with CWM Ellenberg N values using Spearman's rank correlation, since CWM Ellenberg N has been used to detect N deposition as a driver of vegetation change (Diekmann et al. 2014; Emmett et al. 2011; Stevens et al. 2010).

Results

Vegetation change between 1970 and 2016

In total, 83 vascular plant species were recorded during the three surveys (Online Resource 5). During

the survey period, 22 of the 83 species showed an increasing trend in cover (27%), whilst 61 species had a decreasing trend (73%) between 1970 and 2016. Only three of the CG2 positive indicator species, *Helianthemum nummularium*, *Serratula tinctoria* and *Succisa pratensis* increased overall during between 1970 and 2016, whilst the other 12 species decreased (Online Resource 5). Species richness in 20 cm × 20 cm quadrats decreased from a mean ± 1 S.E. of 23.44 ± 0.36 in the 1970s to 20.97 ± 0.31 in 1990, to 14.43 ± 0.28 in 2016. Year as a smoother term was significant, suggesting a non-linear decline in species richness between the survey period ($p < 0.001$, $F = 115.6$, estimated degrees of freedom (edf) = 1.93) (Fig. 2a). This was also evident when evaluating only CG2 positive indicator species ($p < 0.001$, $F = 28.4$, edf = 1.92) (Fig. 2c). There were also significant non-linear declines in diversity in terms of all species ($p < 0.001$, $F = 165.2$, edf = 1.88) and CG2 indicators ($p < 0.001$, $F = 59.93$, edf = 1.97) between 1970 and 2016 (Fig. 2b and d). The rate of species richness, diversity, indicator richness and indicator diversity change was significantly higher between 1990 and 2016, compared with between 1970 and 1990 (Table 2), which supports the GAMM results suggesting the rate of vegetation change between 1970 and 2016 was not linear. The species composition for the subset of quadrats in 1970 and 1990 in the RDA were more similar compared to that in 2016 (Fig. 3), suggesting a larger shift in species composition in the final survey period.

Soil properties

Chemical analysis of the soil revealed a statistically significant increase in total N across the three survey years ($p = 0.04$, $X^2(1) = 4.22$) (Fig. 4, Online Resource 2). Extractable Mg, on the other hand showed a significant decrease over the same period ($p = 0.003$, $X^2(1) = 8.85$). Many of the other soil properties show more complex patterns of change (Fig. 4), where an increase was evident between 1970 and 1990, followed by a decrease during 1990 and 2016. This was the case for pH ($p = 0.10$, $X^2(1) = 2.64$), LOI ($p = 0.12$, $X^2(1) = 2.47$), $\text{PO}_4\text{-P}$ ($p < 0.001$, $X^2(1) = 30.32$) and extractable K ($p = 0.002$, $X^2(1) = 9.99$). Extractable Ca decreased between 1970 and 1990, but increased during 1990 and 2016 ($p = 0.002$, $X^2(1) = 9.87$).

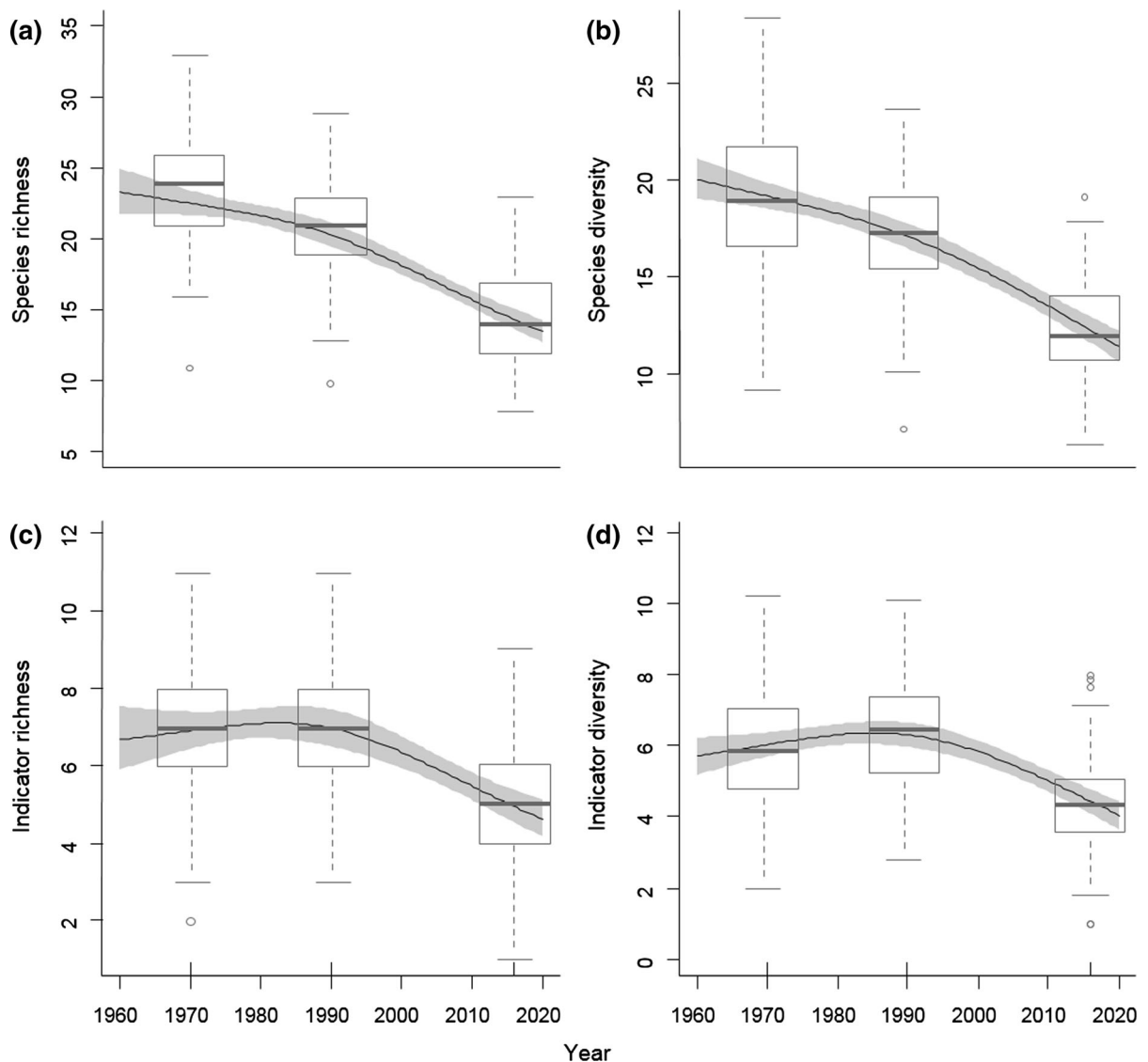


Fig. 2 Boxplots of **a** species richness, **b** species diversity, **c** indicator richness and **d** indicator diversity, for 115 quadrats (20 cm \times 20 cm) in 1970, 1990 and 2016 at Parsonage Down.

Trend lines represent the fitted generalised additive mixed model, with \pm SE indicated in grey

Changes in vegetation and soil status

Between 1970 and 1990, a significant negative correlation was found between changes in soil total N and species diversity (Table 3). In the later time period, soil K change was significantly negatively correlated with changes in both species richness and diversity, whereby small losses in Soil K were associated with a decrease in richness and diversity,

however, large losses led to an increase. The shift in composition from 1970 and 1990 to 2016 appears to be associated with a negative relationship with soil $\text{PO}_4\text{-P}$, Mg, K and LOI, though the ANOVA-like permutation test suggested that only soil phosphate had a significant influence (Fig. 3a, Online Resource 6). *Carex flacca* was the only species to be located in the bottom right-hand quadrant associated with a lower soil $\text{PO}_4\text{-P}$, Mg, K and LOI (Fig. 3b).

Table 2 Average rate of change of species per year (± 1 S.E.) and Wilcoxon signed-rank test summary for species richness, indicator richness, diversity and indicator diversity between 1970–1990 and 1990–2016 at Parsonage Down

| | Average rate of change 1970–1990 | ± 1 S.E | Average rate of change 1990–2016 | ± 1 S.E | V | p |
|---------------------|-------------------------------------|----------------|-------------------------------------|----------------|------|----------|
| Species richness | – 0.105 | 0.024 | – 0.232 | 0.017 | 4689 | < 0.0001 |
| Indicator richness | 0.007 | 0.012 | – 0.081 | 0.008 | 4754 | < 0.0001 |
| Diversity | – 0.098 | 0.024 | – 0.191 | 0.016 | 4366 | 0.004 |
| Indicator diversity | 0.015 | 0.011 | – 0.074 | 0.007 | 5108 | < 0.0001 |

Trait profile

Several significant trends in community-weighted mean traits were identified between 1970 and 2016 (Fig. 5). There was an increasing trend towards taller plant species between 1970 and 2016 ($p < 0.001$, X^2 (1) = 58.37), whilst the weighted average SLA decreased during the same period ($p < 0.001$, X^2 (1) = 40.19). Grazing tolerance was greater in 1970 compared with 1990 and 2016 ($p < 0.001$, X^2 (1) = 13.98). Ellenberg N declined significantly ($p < 0.001$, X^2 (1) = 32.60), whilst Ellenberg R values remained consistent across the years, with a slight decrease in 2016, which was not significant ($p = 0.13$, X^2 (1) = 2.26). Ellenberg N was significantly correlated with soil pH ($r_s = -0.38$, $p = 0.028$) and Ca ($r_s = 0.37$, $p = 0.035$). No association was detected with Ellenberg N and soil N ($r_s = 0.02$, $p = 0.931$), $\text{PO}_4\text{-P}$ ($r_s = -0.05$, $p = 0.776$), K ($r_s = -0.05$, $p = 0.772$), Mg ($r_s = -0.05$, $p = 0.779$) or LOI ($r_s = 0.11$, $p = 0.546$).

The sward height in 2016 (12.94 ± 0.47 cm) had increased considerably from 3.63 ± 0.09 cm in the 1970s and 1.99 ± 0.05 cm in 1990 ($p < 0.001$, X^2 (1) = 239.92), which appears to be consistent with the qualitative records obtained for grazing management at Parsonage Down between 1930 and 2011 (Table 1). The records show a decline in the number of cattle and sheep, suggesting a reduction in grazing pressure.

Discussion

Vegetation change between 1970 and 2016

Analysis of long-term changes in vegetation is limited, with very few studies evaluating multiple time points

over nearly 50 years, with driver information (Diekmann et al. 2014; Newton et al. 2012; Stroh et al. 2017). This study has provided a rare opportunity to re-examine detailed transects, with driver data from multiple time periods. Although the analysis of re-survey data is commonly associated with some uncertainty, we have followed recommendations suggested by Verheyen et al. (2018) to increase the precision and strength of the inferences drawn from our study. This includes re-surveying a large number of plots, ensuring that transects were accurately relocated, having a team of well-trained surveyors (including one that was involved with the original survey) and by having a hypothesis-driven trait-based approach.

The analysis conducted in this study revealed a shift in species composition over the last 46 years. The shift was also associated with a non-linear loss in species richness and diversity, as hypothesised. This trend was also evident when examining just positive indicator species, which suggests that the quality of the vegetation at Parsonage Down is less favourable compared to that in the 1970s. Shifts in species composition in calcareous grasslands across the UK (Bennie et al. 2006; Newton et al. 2012) and Europe (Diekmann et al. 2014) have also been identified, whilst Stevens et al. (2016) also highlighted significant decreases in species richness and diversity in calcareous grasslands in the Sheffield region. Our study, for the first time was able to contrast the rate of change between two time periods. This rate was significantly higher between 1990 and 2016, compared with 1970 and 1990, suggesting change during the whole period was non-linear. This was further supported by the fitted GAMMs, which show a rapid decline in the species richness and diversity of indicator species in the latter time period. The trend line appears more

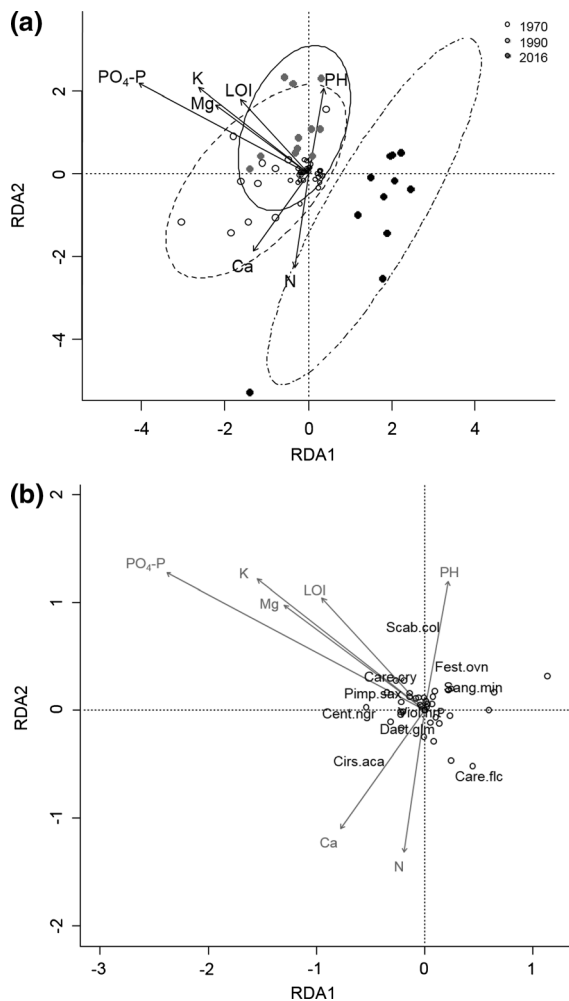


Fig. 3 Redundancy analysis (RDA) plot based on 33 quadrats surveyed at Parsonage Down in 1970, 1990 and 2016. RDA1 and RDA2 have constrained Eigenvalues 8.48 and 4.56, respectively, and explained 23.28% of the variation. Only soil phosphate (PO₄-P) was found to have a significant influence ($p = 0.001$). **a** Site scores. Quadrats surveyed in 1970 filled in white, while 1990 are represented in light-grey and dark-grey for 2016. Polygons enclose quadrats by date of survey, based on standard deviation of point scores. **b** Species scores. Only the most abundant species are labelled, in order of relative diversity (using the inverse Simpson index). Open circles indicate species whose names have been suppressed to declutter the ordination

linear for the species richness and diversity of all species, however, the decline is more rapid in the 1990–2016 period and the significance of year as a smoother term also suggests the trend is non-linear, though caution must be taken when evaluating the P values alone (Zuur and Ieno 2016).

The increased rate of species richness and diversity loss between 1990 and 2016 coincides with a decline in grazing pressure at Parsonage Down. A sufficient grazing pressure is required to prevent the dominance of coarse grasses, allowing smaller forbs to flourish, thus a reduction in grazing may lead to the decline of these smaller species, and hence a loss of species richness and diversity. The grazing information provided in Table 1 suggests that the numbers of cattle and sheep grazing at Parsonage Down had decreased during the study period and there was a significant change from cattle over-wintering on the site during earlier years to being taken off the site during winter (Online Resource 1). The patterns of grazing routines are also important; for instance at Parsonage Down, cattle favour the area where supplementary feeding was provided in the past, then they use the grassland close to trees when shelter is required (S. Hope 2017, Reserve Manager, pers. comm.). Thus, the location where the transects were recorded is currently grazed much later on in the season, once other areas have already been grazed down, allowing the sward to grow higher in this area. The height of the sward can also be used to represent grazing pressure (van den Berg et al. 2011). At Parsonage Down, the sward height increased significantly over our time series, suggesting a reduction in grazing pressure, particularly during the latter time period, although it is important to consider that the wet spring and summer experienced in 2016 would have also contributed to this. Weather fluctuations are an important consideration when assessing vegetation change. The average temperature and total precipitation remained largely consistent between 1961 and 2015 at Parsonage Down (Online Resource 7) and where larger fluctuations did occur (e.g. 1976, 1983 for rainfall), these did not correspond with our survey periods (1970 and 1990).

Soil properties

Significant changes in soil properties were identified over the survey period at Parsonage Down. Our findings show a significant increase in soil total N content between 1970 and 2016, which is a signal often associated with N deposition (Zhang and Han 2012). The results also revealed significant declines in two of the base cations, Mg and K, which are released to buffer against N-induced soil acidification, providing further evidence for N deposition as a potential

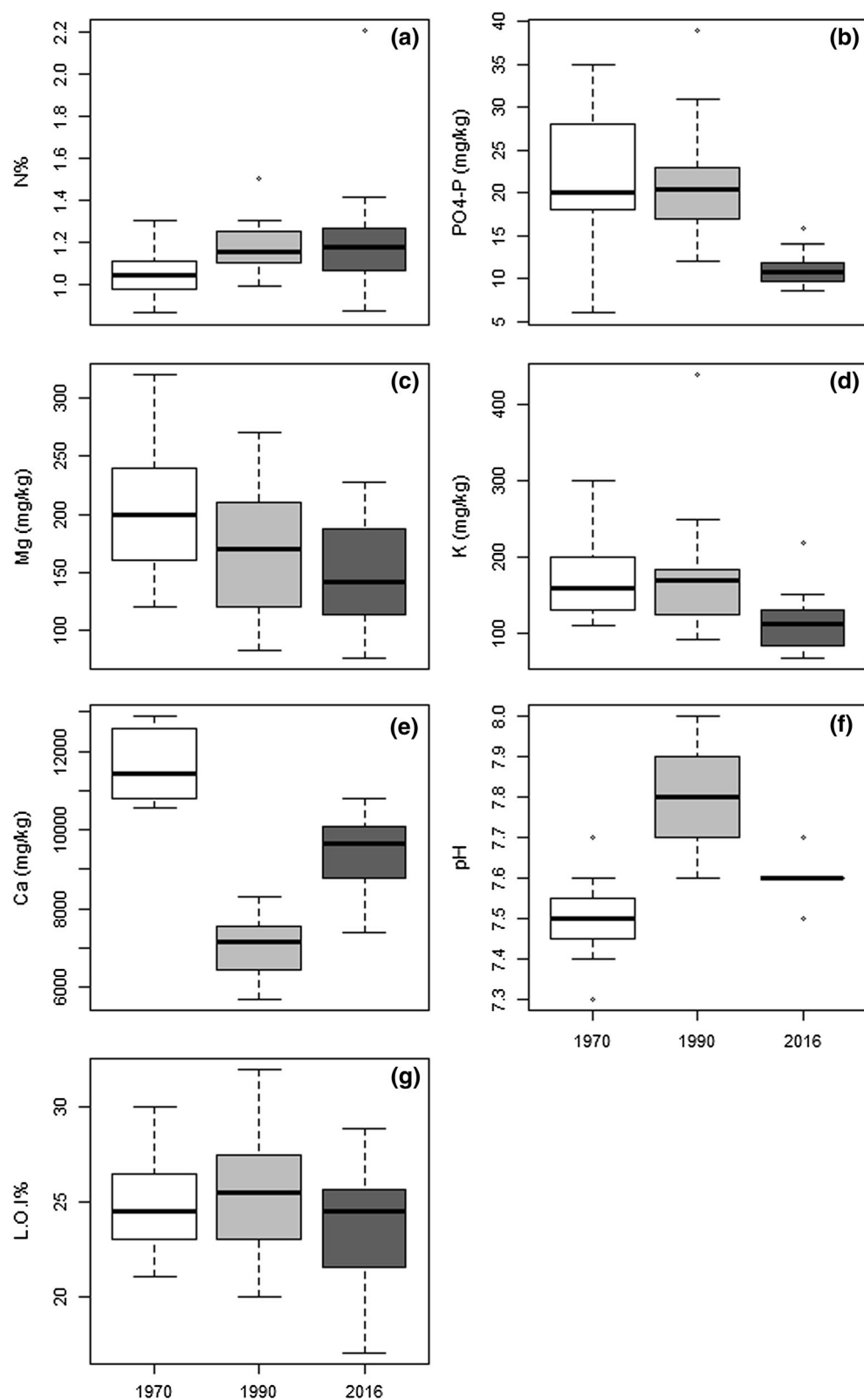


Fig. 4 Boxplots of soil **a** total nitrogen, **b** PO₄-P, **c** Extractable Mg, **d** Extractable K, **e** Extractable Ca, **f** pH and **g** LOI from soil samples collected at Parsonage Down in 1970 (white), 1990 (light-grey) and 2016 (dark-grey)

Table 3 Spearman rank correlations between changes in each soil property (pH, PO₄-P, N, K, Ca, Mg, LOI) with changes species richness and species diversity between 1970–1990 and 1990–2016 ($n = 33$)

| Soil property | Species richness | | Species diversity | |
|--------------------|------------------|--------------|-------------------|--------------|
| | r_s | p | r_s | p |
| 1970–1990 | | | | |
| pH | – 0.107 | 0.754 | 0.032 | 0.926 |
| PO ₄ -P | – 0.251 | 0.457 | – 0.118 | 0.734 |
| N | – 0.474 | 0.141 | – 0.716 | 0.013 |
| K | – 0.105 | 0.759 | – 0.264 | 0.435 |
| Ca | – 0.337 | 0.311 | – 0.481 | 0.137 |
| Mg | 0.214 | 0.527 | 0.282 | 0.402 |
| LOI | – 0.424 | 0.194 | – 0.609 | 0.052 |
| 1990–2016 | | | | |
| pH | – 0.14 | 0.682 | – 0.121 | 0.723 |
| PO ₄ -P | 0.1 | 0.776 | 0.036 | 0.924 |
| N | 0.209 | 0.539 | 0.055 | 0.882 |
| K | – 0.764 | 0.009 | – 0.836 | 0.002 |
| Ca | 0.218 | 0.521 | – 0.055 | 0.882 |
| Mg | – 0.181 | 0.595 | – 0.163 | 0.634 |
| LOI | 0.518 | 0.107 | 0.491 | 0.129 |

P values < 0.05 are indicated in bold

driver (Bowman et al. 2008; Horswill et al. 2008). This supports our second hypothesis where increases in soil N and declines in base cations have occurred as a consequence of N deposition. Large declines in base cations were also detected in an experimental N deposition study in both acid and calcareous grassland in England (Phoenix et al. 2012), whilst Clark et al. (2007) used structural equation modelling to find species loss was higher with a lower soil cation exchange capacity (greater potential for acidification and loss of nutrient cations) using results from 23 N addition experiments across North America. The inconsistent trend demonstrated by pH over our study period has been observed in other research (Phoenix et al. 2012). Rowe et al. (2017) suggest that pH as a metric of N pollution and recovery is weakened by the

impacts of historical sulphur deposition, which caused widespread and persistent acidification. Soil pH has increased in some areas due to the decline in sulphur deposition after the 1970s, however, this is believed to have affected the N cycle. Soil phosphate remained consistent in 1970 and 1990, but declined significantly in 2016. Insufficient phosphate can lessen the effects of N deposition, which may explain why the impact of N deposition on the vegetation in this study was detected between 1970 and 1990 (see below). It is possible that grazing may have also contributed towards changes in the soil, however, contrasting results are often reported in the literature. For instance, Bullock et al. (2001) found NO₃-N increased with winter grazing and heavier summer grazing, whilst Epelde et al. (2017) reported no effect of grazing on soil nutrient chemical parameters. Since grazing was kept largely consistent between 1970 and 1990 at Parsonage Down (Table 1), grazing is unlikely to have affected the soil during this period.

Changes in vegetation and soil status

To examine whether the soil changes evident in this study affected the vegetation, we assessed correlations between changes in each soil property and species richness and diversity between 1970–1990 and 1990–2016. Soil total N was significantly associated with a decline in species diversity in 1970 and 1990, suggesting that N deposition may have been a significant driver of vegetation change during this period, thus supporting our hypotheses. This coincides with the increasing period for total N in Fig. 1. Declines in species diversity associated with increasing deposition of atmospheric nitrogen were also reported by van den Berg et al. (2011). They analysed 106 plots in nature reserves on calcareous grassland sites in the UK and identified a decrease in species diversity with high rates of N deposition. Our results also suggest that even with consistent grazing management (Table 1), which occurred through 1970 and 1990, adverse effects of N deposition may still occur, as suggested by van den Berg et al. (2011). In the later survey period, a small decline in soil K was associated with a decrease in both species richness and diversity, whilst large declines were associated with an increase. Moderately high levels of potassium have been found to be associated with high levels of species diversity (Janssens et al. 1998), which may explain why a small

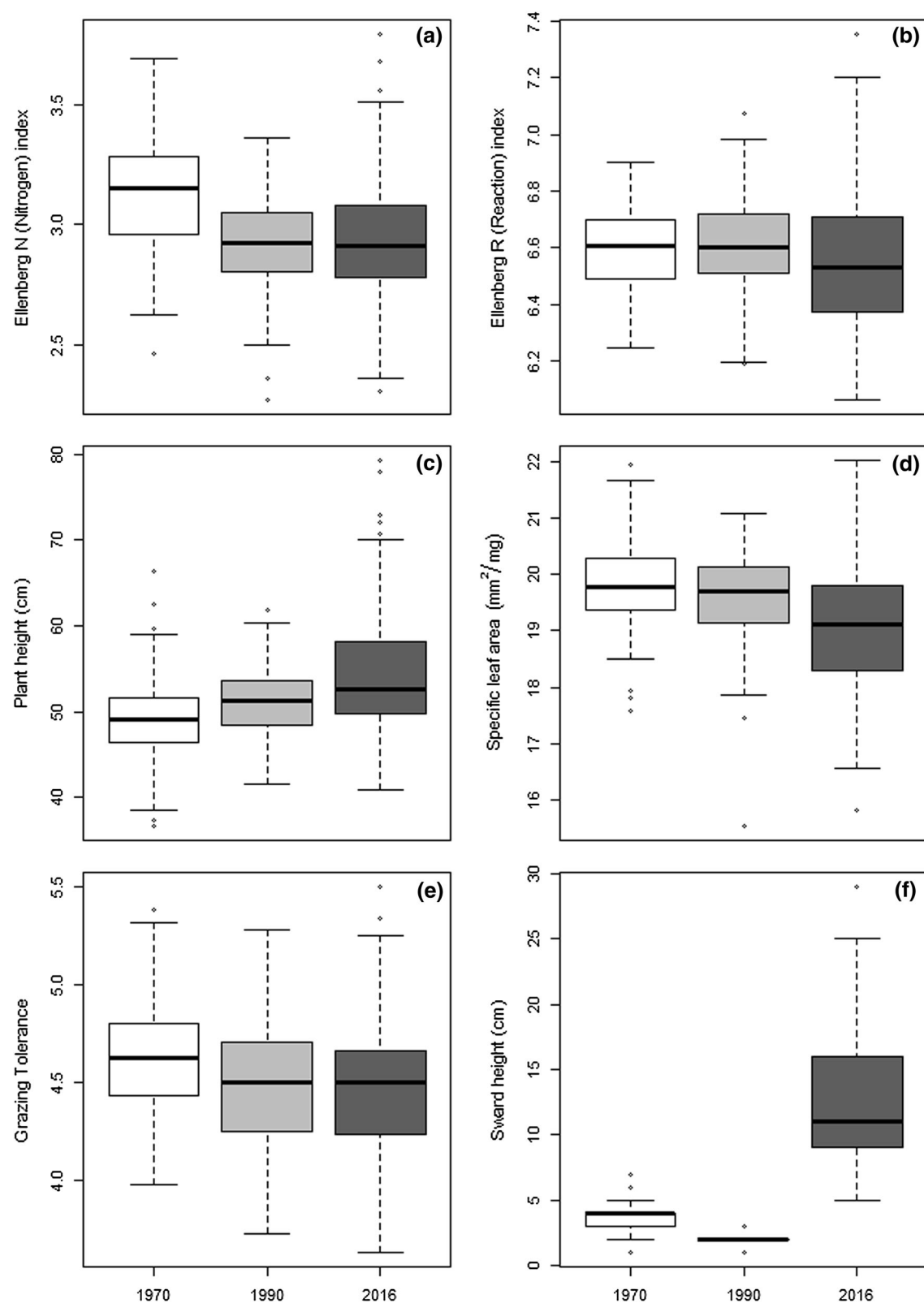


Fig. 5 Boxplots of community-weighted traits in 1970 (white), 1990 (light-grey) and 2016 (dark-grey) at Parsonage Down; **a** Ellenberg Nitrogen (N) and **b** Ellenberg Reaction (R), **c** plant height, **d** specific leaf area, **e** grazing tolerance and **f** field-measured sward height

loss in soil K led to a decline in species diversity at Parsonage Down, however, this does not explain the increase in species diversity associated with a large decline in soil K in this study. Janssens et al. (1998) observed that the maximum species number is observed when the potassium content is 20 mg/100 g, which corresponds closer to the average potassium content recorded in our study in 1970 (17 mg/100 g) and 1990 (17 mg/100 g) compared with 2016 (11 mg/100 g), where species diversity was the lowest. Other studies, however, have found no impact of soil nutrients such as P and K on species richness and diversity (Bullock et al. 2001; Huber et al. 2017). A report by Wilson and Wheeler (2016) revealed higher potassium levels for sheep-grazed vegetation compared with mown, pony-grazed or unmanaged vegetation. During 1990 and 2016, the number of sheep grazing at Parsonage Down decreased (Table 1), which may, therefore, be related to the decline in potassium.

Although soil total N was associated with species diversity, we found no significant influence on species composition, in contrast to Diekmann et al. (2014). Phosphate was the only soil parameter to significantly influence species composition at Parsonage Down, with the greatest shift apparent in 2016 associated with a decline in phosphate. *Carex flacca* was also related with this shift, which may be because *Carex flacca* has the potential to grow dauciform roots in areas of low phosphate (Davies et al. 1973; Shane et al. 2005), thus is able to perform well where phosphate is limited. The location of *Carex flacca* on the RDA plot (Fig. 3.) could also be linked to the lower grazing pressure experienced in 2016, since *Carex flacca* is fairly persistent in ungrazed areas and is also predicted to be less palatable (Grime et al. 2007).

Trait profiles as indicators of drivers of change

The increased fertility indicated by elevated Ellenberg N is often used to represent the effects of atmospheric N deposition on plant communities. Our findings show

a significant decline in community-weighted mean Ellenberg N values over time, which would suggest eutrophication is not one of the main factors responsible for the vegetation change evident at Parsonage Down. This is inconsistent with other studies reporting increases in Ellenberg N which have been attributed to increasing N deposition (Bennie et al. 2006; Keith et al. 2009; Newton et al. 2012). Others argue that Ellenberg N is unlikely to be an accurate predictor of the response to increasing N deposition. Wilson et al. (1995) found certain forb species, including *Thymus polytrichus*, *Scabiosa columbaria* and *Filipendula vulgaris* (all low Ellenberg N values) responded positively to N supply, suggesting Ellenberg N is not a reliable measure of a species' ability to compete under conditions of high N inputs. This supports our findings, where evidence of N deposition through soil status changes, associated with species diversity declines between 1970 and 1990, is not reflected through the Ellenberg N CWM indicator. Stevens et al. (2010) also found no change in Ellenberg N. Furthermore, no association between Ellenberg N and soil N was revealed, instead Ellenberg N was found to increase significantly with a lower pH and a greater Ca content. Diekmann (2003) reported similar results, supporting the idea that nitrogen values would be better referred to as "productivity values". No significant changes in Ellenberg R were detected overtime in this study, which suggests that eutrophication, rather than soil acidification contributed towards the vegetation change associated with nitrogen deposition. This contrasts with Stevens et al. (2010) who identified soil acidification as the contributing factor for calcifuge grasslands across the UK.

Grazing management is known to have a significant effect on grassland species composition (Wallis de Vries et al. 2002). Our analysis revealed a significant shift over time towards a community with a greater share of taller species (Fig. 5a). Taller species can outcompete low growing species through competition for light, which can lead to a decline in species richness (Jacquemyn et al. 2003; Walker et al. 2009), as found in this study. Walker and Pinches (2011) found that negative population trends in *Pulsatilla vulgaris*, increased sward height and increased cover of *Bromopsis erectus* were related to a decrease in grazing pressure. *Bromopsis erectus* had established in around 17% of the Parsonage Down quadrats in 2016, where in 1970 and 1990 there was no record of the

species (Online Resource 5). *Bromopsis erectus* is known to be a dominant species, with greater shoot thrust (Campbell et al. 1992), which can restrict the growth of surrounding species. This coincides with our finding of more taller species in the community and may explain why smaller species such as *Euphrasia nemorosa*, *Campanula glomerata* and *Prunella vulgaris* decreased significantly between 1990 and 2016 (Online Resource 5). Species with smaller SLA values increasingly dominated the sward between 1970 and 2016. This maybe partly driven by the large increase in *B. erectus* in 2016, as previously mentioned which has a low SLA. *Lolium perenne* was another grass which had established in 35% of plots in 2016, despite being absent in the 1970s (Online Resource 5). This was most likely introduced from the supplementary feeding which occurred on the Down, which was stopped in 2003. Our results also show a decreasing trend in grazing tolerance within the vegetation community, which provides further support for reduced grazing pressure, although unexpectedly the greatest difference in grazing tolerance occurred between 1970 and 1990, rather than 1990 and 2016 as suggested by the sward height and management information.

Many of the traits used to indicate grazing pressure as a driver are also used to detect N deposition. For instance, dominance by taller species is typical of competitive species in nutrient rich situations (Emmett et al. 2011). However, since signs of N deposition detected in the soil and its influence on species diversity was only evident for 1970–1990, this may suggest that the changes evident in the vegetation between 1990 and 2016 are largely attributable to grazing management. Although, Parsonage Down is only a single nature reserve, similar conclusions have been reported in other recent long-term re-survey studies which are within close proximity to Parsonage Down over similar time periods (Hawes et al. 2018; Stroh et al. 2017) and across the rest of the UK and Europe (Diekmann et al. 2019). Stroh et al. (2017) concluded that changes in lowland calcareous grassland were probably due to adjustments to grazing regimes, particularly regarding the fluctuations in timing and duration of livestock grazing. Similar conclusions were made by Hawes (2015) who reported no significant increase in total nitrogen, and concluded that vegetation changes were largely due to grazing. Furthermore, many argue that grazing management

has a greater impact on species composition compared with N deposition (Jacquemyn et al. 2003; Wilson et al. 1995). This may mean that N deposition was still contributing to vegetation change in the later period since it accumulates in the soil, but the majority of change was caused by differences in grazing management. This is further supported by that fact that the rate of vegetation change was apparently greater in 1990–2016 compared with 1970–1990. Alternatively, the more intensive grazing management in the earlier time period may have helped mitigate the full impacts of N deposition.

Conclusions

This study has revealed a shift in species composition, combined with declines in species richness and diversity between 1970 and 2016 at Parsonage Down, with the greatest rates of change occurring between 1990 and 2016. There is some evidence that N deposition contributed towards these community changes between 1970 and 1990, as indicated by an increase in soil %N and the associated decline in species diversity. However, the evidence also suggests that vegetation change during 1990 and 2016 was largely attributable to a decline in grazing pressure, as indicated by an increase in taller species, decrease in grazing tolerance and reported grazing management changes. It is often difficult to disentangle grazing pressure and N deposition as drivers of change (Clark et al. 2007; Wilson et al. 1995), since vegetation often responds similarly to both drivers (Stevens et al. 2016; Stroh et al. 2017). However, as this study benefits from assessing multiple time periods, and a time series of soil analyses, it provides the first evidence of differential influences of N deposition and grazing pressure impacting on vegetation change during different time periods.

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Author contributions LER, RFP and PH conceived the research idea; LER, JMB, OLP and RFP designed the analysis; LER, PH and RW collected the data; MGP, SAT and POK. conducted the soil analyses; LER performed statistical analyses with contributions from JMB, OLP, and UD; LER wrote the paper; all authors discussed the results and commented on the manuscript.

Data availability The vegetation and soil data are freely available from The Environmental Information Data Centre (EIDC) and can be accessed at: <https://doi.org/10.5285/ffc06839-e64c-4844-aae7-db3b0a012e2e>

Compliance with ethical standards

Conflict of interest We have no conflict of interest to declare.

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