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RESEARCH ARTICLE

The effect of different grazing managements on butterfly abundance, diversity and composition at a calcareous upland site

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Abstract

1. Butterfly populations have experienced substantial declines in recent decades due to land-use change, agricultural intensification and climate change. In the UK uplands, the impact of livestock grazing on butterfly populations has not been well documented.
2. In this study we used long-term monitoring from the Ingleborough National Nature Reserve in the English uplands to examine the impact of sheep grazing, cattle grazing and ungrazed management on butterfly abundance and species diversity across an upland calcareous site.
3. Lightly cattle-grazed sites were found to have 4.9 times the abundance of butterflies compared to sites lightly grazed by sheep. There were 3.6 times as many butterflies on ungrazed sites compared to sheep-grazed sites. The species richness of butterflies was also significantly higher on cattle-grazed and ungrazed sites compared to sheep-grazed sites.
4. Our study provides evidence of the conservation benefits of low-intensity cattle grazing for butterfly abundance and diversity on calcareous grasslands in the UK uplands.
5. *Practical implication*. For effective butterfly conservation, a shift from sheep grazing to light cattle grazing or stock exclusion in upland calcareous landscapes should be considered.

KEYWORDS
butterflies, calcareous grassland, cattle grazing, ecological restoration, habitat mosaic, sheep grazing, UK uplands, upland grazing management

1 | INTRODUCTION

Grassland insects, including butterflies, have declined in abundance and diversity in recent decades, as a result of agricultural intensification, land-use change and climate change (Goulson, 2019; Seibold et al., 2019; Wagner, 2020). Butterflies play important ecosystem roles as pollinators, nutrient cyclers and prey (Ghazanfar et al., 2016). They also serve as key bioindicators of ecosystem health due to their sensitivity to environmental change (Chowdhury et al., 2023) and act as charismatic focal species for habitat restoration efforts that benefit a broader range of taxonomic groups (New, 1997; Spitzer et al., 2009). Despite their ecological and conservation importance, butterfly populations are declining across Europe, with particularly severe trends in the UK (Maes et al., 2019). Within the UK, the state of butterfly populations is the worst in England, where 62% of species have decreased in abundance since the 1970s (Fox et al., 2023). Habitat specialists, characterised as species with narrow niche requirements (Botham et al., 2015), are especially at risk and contribute substantially to the overall declines across England (Fox et al., 2023).

The drivers of declining butterfly populations are not fully understood, but changing land-use practices, such as grazing, may play an important role. Grazing can indirectly influence butterflies by altering vegetation structure and plant diversity (Bussan, 2022), and while some research has examined effects on individual species (e.g. Johansson et al., 2019; van Noordwijk et al., 2012), community-level responses remain poorly understood. By contrast, the effects of grazing on vegetation are well documented (e.g. Marrs et al., 2020; Rook et al., 2004), providing insight into mechanisms that may influence butterfly populations. Both the type of grazing animal and grazing intensity alter vegetation structure, diversity and composition (Fraser et al., 2007, 2014; Lyons et al., 2017). Differences in vegetation heterogeneity arise partly from the distinctive feeding habits and anatomy of different grazing animals. Sheep, with their smaller body size and dental morphology, selectively feed on high-nutrient plants (Demment & Van Soest, 1985; Rook et al., 2004), increasing the cover of competitively dominant grasses and reducing plant species richness compared with cattle-grazed systems (Lyons et al., 2017; Porton et al., 2026). Cattle, by contrast, facilitate plant regeneration by creating microtopographical features through trampling (Thomas et al., 1986). In addition, reducing grazing intensity leads to increased vegetation height and structural diversity (Pöyry et al., 2006). Vegetation structure and composition directly influence butterfly populations by determining resource availability, with higher plant species richness providing host plants and nectar sources, and structural heterogeneity creating microhabitats for basking, thermoregulation, egg-laying and shelter (Farruggia et al., 2012; Jerrentrup et al., 2014; Milberg et al., 2016; Öckinger et al., 2006; Potts et al., 2009). This diversity supports both generalist and specialist butterfly species by meeting their varied ecological needs (Turlure et al., 2019).

These vegetation-butterfly relationships are particularly relevant in the UK uplands, where historical and ongoing grazing has strongly shaped the landscape. These landscapes contain some of the most ecologically diverse habitats across Europe, including calcareous grasslands, limestone pavements and temperate rainforests (Poschlod & Wallis de Vries, 2002; Wallis de Vries et al., 2002). However, large-scale habitat loss and degradation driven by agricultural intensification has meant these diverse habitats are now rarer, highly fragmented and often in poor condition. Sheep numbers in England rose by 144% between 1950 and 1990 (Department for Environment, Food and Rural Affairs, 2011) and, despite recent decline, currently remain 60% higher than 1950 levels (Department for Environment, Food and Rural Affairs, 2025). This intensification has shaped the upland landscapes of England, which have long been dominated by sheep farming, resulting in heavily grazed grasslands interspersed with small patches of higher ecological value (Natural England, 2009).

Despite grazing having large impacts on vegetation in the English uplands, the effects of different grazing managements on butterfly populations remain largely unstudied. Recent work has highlighted the conservation benefits of low-intensity grazing with native breed cattle (Porton et al., 2024), and a meta-analysis suggests that cattle grazing can support butterfly communities (Bussan, 2022), while livestock removal can enhance butterfly caterpillar survival (Johansson et al., 2019; van Noordwijk et al., 2012). However, these findings are based on individual species or have focused on lowland habitats, leaving community-level responses in upland areas largely unknown.

Here, we investigate the effects of sheep grazing, cattle grazing and livestock exclusion on the abundance, species richness and composition of butterfly communities at a calcareous upland site in northwest England. By exploring these relationships, this study aims to address key knowledge gaps regarding the impact of different grazing management strategies on butterfly populations, informing the development of environmentally conscious land management practices in the UK uplands.

2 | MATERIALS AND METHODS

2.1 | Study site

Data was collected from Ingleborough National Nature Reserve, surrounding Yorkshire Wildlife Trust reserves and farmland in the Yorkshire Dales National Park, England (Figure 1). Collectively, the sites cover around 1200 ha and are made up of a mix of acid, calcareous and improved grassland, along with limestone pavement, peatland and a few small fragments of trees and woodland. The included sections of the butterfly transects (Figure 1) spread across the lower sites, dominated by calcareous grassland and limestone pavement, with an elevation range of 285–355 m a.s.l.

The study site is situated within a landscape dominated by sheep grazing, as is common for UK upland landscapes. However, there is also a long history of nature restoration in the area, with a focus on changing grazing management at some sites, from sheep

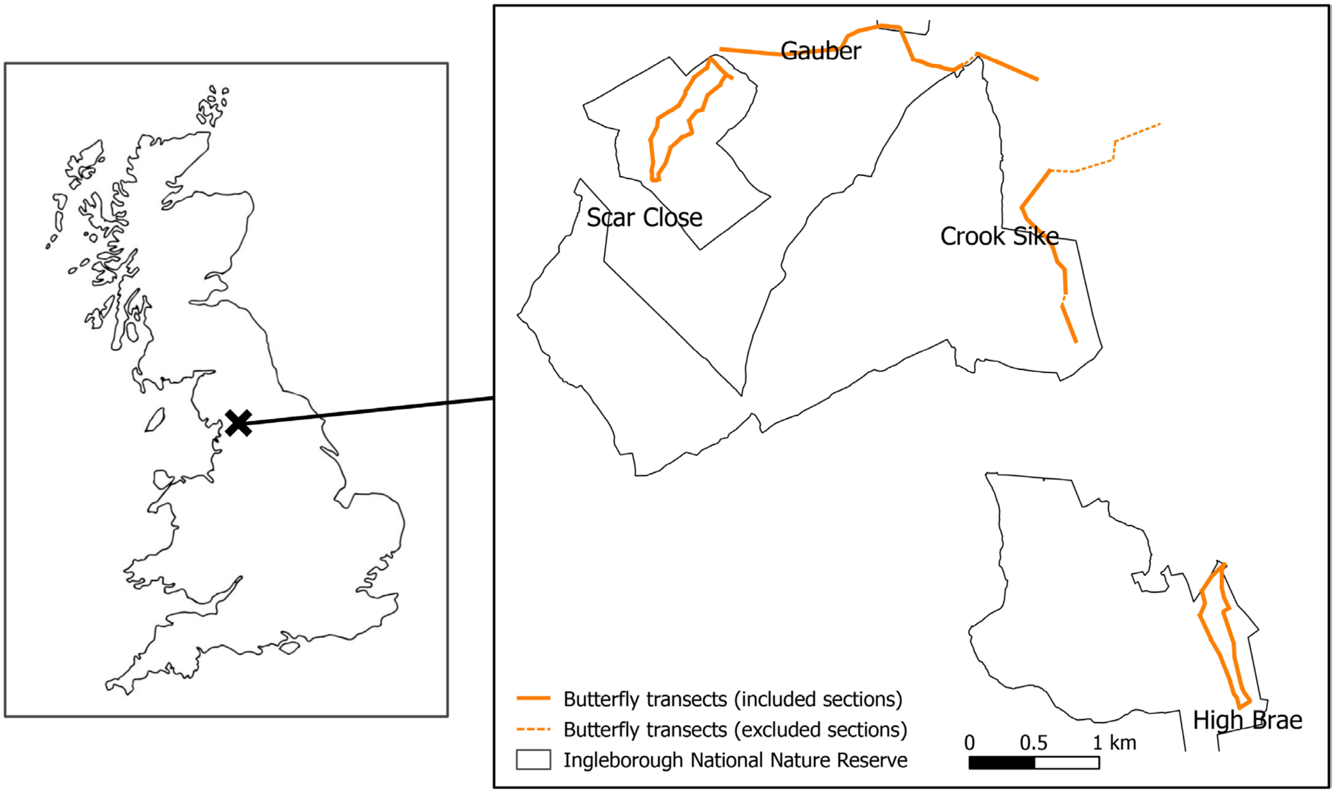

FIGURE 1 A map displaying the location of Ingleborough National Nature Reserve (NNR) within a map of the UK. The righthand box shows the locations of the butterfly transects in relation to Ingleborough NNR, with solid lines showing transect sections included in the analysis in this study and dotted lines showing sections excluded.

grazing to either cattle or complete removal of grazing. Prior to current grazing managements on sites used in this study, all were sheep-grazed. The switch to cattle grazing was made by Natural England in 2004 with the main aims being to increase vegetation diversity, improve calcareous grassland habitat quality and increase vegetation structural complexity. The transition was carried out systematically, with entire land parcels being switched from sheep to cattle grazing, rather than selecting specific sites for each livestock type. Consequently, it is likely that the sheep- and cattle-grazed sites were similar in condition before the change in grazing management. Long-term vegetation monitoring supports this, showing that the shift from sheep to cattle grazing has led to higher vegetation diversity, particularly among calcareous grassland species (Porton et al., 2026).

At the cattle-grazed site, average grazing intensity was approximately 0.2 livestock units (LU) $ha^{-1}year^{-1}$, which is characterised as light grazing and is lower than the average stocking rate of 0.7 LU $ha^{-1}year^{-1}$ in upland areas of England (Harvey & Scott, 2021). Native breed cattle were used, with a mix of Red Polls and Shorthorns. Grazing timings were not regimented, with cattle rotated across the NNR to encourage a more naturalistic grazing pattern. Between 2014 and 2024, cattle grazed the study site for an average of 8.5 months per year. No manure or fertiliser was applied at the cattle-grazed site, and no antibiotics or prophylactics were administered to the cattle in this study.

Average grazing intensity at the sheep-grazed sites was also 0.2 LU $ha^{-1}year^{-1}$ ensuring that any effects from grazing are attributable to the type of livestock rather than differences in grazing intensity. Stocking consisted of Cheviot and Swaledale sheep and was stocked for 8.5 months per year. Sheep-grazed sites comprised a mix of organic certified land, mid-tier Countryside Stewardship Agreement land and Higher-Level Environmental Stewardship Agreement land, with variation in manure and fertiliser applications. Although some cattle grazing occurred on sites predominantly grazed by sheep, it was brief; therefore, these sites were still classified as sheep-grazed for this study. Sheep were routinely administered treatments in line with standard practice for sheep farming in the UK, including anthelmintics (for worming) and ectoparasitic treatments (for dipping).

Livestock were excluded from the ungrazed site, with no grazing taking place since the 1970s. No manure or fertiliser was applied to this site, and the vegetation was largely left to succeed naturally, with only minimal management intervention.

While the potential effects of differences in chemical inputs between grazing treatments have not been analysed in this study, the chemicals associated with sheep management reflect standard UK sheep farming practices. As such, in this study, they are considered part of the overall management with sheep, and their effects are not separated from the grazing animal. Additionally, where manure or fertiliser has been applied to sheep-grazed sites, it is at relatively low levels as is required by stewardship agreements. Furthermore, wild herbivores, mainly rabbits and deer, have access to all study sites.

2.2 | Butterfly surveys

Butterflies have been surveyed annually at Ingleborough since 2004, following methods set out by the UK Butterfly Monitoring Scheme (UKBMS) (Butterfly Monitoring Scheme, n.d.). Surveys were conducted over a 26-week period from the start of April to the end of September, with the targeted surveying effort being once per week, although this could be limited by weather and surveyor availability. Abundance of butterfly species was recorded along a series of fixed transects, each split into sections of varying lengths and 5 m in width. As per the UKBMS methodology, only surveys carried out between 10:00 and 17:00 and with a minimum temperature of 11°C when there is >60% clear sky, or above 17°C when <60% clear sky, were included in the analysis. In total there were 435 surveys included in the analysis of this study.

This analysis included data only from sections of transects that had been under the same management (sheep-grazed, cattle-grazed or ungrazed) for at least 5 years. The transects ranged in length from 1409 to 2596 m and had a survey effort of 7 to 14 surveys year^{-1}, where survey effort is the average number of surveys per year (Table 1).

2.3 | Data analysis

Butterfly abundance per 100 m and species richness were compared between grazing managements. For abundance, each survey's data was summarised to per 100 m to account for the varying transect lengths. For species richness analysis, shortened transects were used to ensure similar total survey lengths. Transect lengths were shortened by selecting consecutive sections that together most closely matched the length of the shortest transect (within a 54 m margin). This adjustment was necessary as species richness is expected to follow a species accumulation curve, and so shortening the transects ensured species richness was comparable across different management types. Species richness was chosen for its simplicity and lower sensitivity to zero counts when compared with indices like Shannon's H or Simpson's (Gotelli & Colwell, 2001; Magurran, 2013).

Additionally, butterfly species composition was compared between grazing managements to assess differences in overall community structure. A management-by-species matrix of butterfly abundances per survey was used to quantify compositional dissimilarity among management types.

We also focused on abundance of rare and declining species across the different management types. Four subsets of butterflies were used to achieve this. The first subset (A) included species classified as *Vulnerable* or *Near Threatened* on the Great Britain Red List (Fox et al., 2022). The second subset (B) included habitat specialist species (Butterfly Conservation, 2025). The third subset (C) included species showing significant declines in distribution across England between 1976 and 2019 (Fox et al., 2023), while the fourth subset (D) included species that have experienced significant declines in abundance over the same period (Fox et al., 2023). Additional information on each species present in the data are provided in Table 2, including GB Red List status (as of 2022), abundance and distribution trends in England and habitat preferences.

2.4 | Modelling

To test the effect of management on butterfly abundance, species richness and abundance of rare or declining species, a series of generalised linear mixed models (GLMMs) were used. Abundance models were fitted using a Tweedie distribution to accommodate non-integer values, and species richness models were fitted with a Poisson distribution, both using the glmmTMB package (Brooks et al., 2017).

The models tested included various combinations of main effects and interaction terms. To account for variability in butterfly populations between and across years, the variables of Year and RelativeWeek were included in all models. Year was included as a random effect and RelativeWeek as a continuous fixed effect. RelativeWeek is the number of weeks from the week commencing 15th July which is the midpoint of the UK's meteorological summer and the peak of butterfly abundance at the study sites. Additional variables included in the models were mean temperature per survey (Temperature) and mean percentage sunlight per survey (%Sun), to account for their ecological influence on butterfly activity (Wikström et al., 2009). These variables

TABLE 1 Summary of butterfly survey transect characteristics, where length refers to the total length of transect sections analysed and survey effort is the average number of surveys per year.

Transect	Management	Year sheep were removed	Length (m)	Survey effort (surveys year^{-1})	Years surveyed
High Brae	Cattle	2004	2424	7	2014–2023
Scar Close	Ungrazed	1977	2433	14	2004–2024
Crook Sike	Sheep	N/A	1409	11	2021–2024
Gauber	Sheep	N/A	2596[a]	9	2021–2023

Note: In UKBMS records transect names are Ingleborough High Brae, Scar Close NNR, Crook Sike, Gauber (retired).
[a]Gauber transect was 2101 m in 2023 surveys due to management change for section 1 from sheep to cattle grazing.

TABLE 2 Butterfly species recorded on study sites since 2004 with conservation status (Fox et al., 2022), average 10-year percentage change in abundance and distribution in England (data periods range between 1970 and 2019) (Fox et al., 2023), habitat (Chinery, 2012) and subset groups: (a) GB Red List species; (b) habitat specialists; (c) species with declining distribution; (d) species with declining abundance.

			Avg. 10-year % change			Subset group(s)			
Common name	**Scientific name**	**GB Red List status**	**Distribution**	**Abundance**	**Habitat**	**A**	**B**	**C**	**D**
Comma	*Polygonia c-album*	Least Concern	**13*****	**26*****	Gardens, hedgerows, open woodland			✓	✓
Common Blue	*Polyommatus icarus*	Least Concern	**−8*****	−3	Grassland			✓	
Dark Green Fritillary	*Speyeria aglaja*	Near Threatened	**−12*****	**41*****	Coastal dunes, heathland, open woodland, rough grassland	✓	✓	✓	✓
Green-veined White	*Pieris napi*	Least Concern	**−2*****	−4	Damp areas, flowery meadows, gardens, hedgerows			✓	✓
Green Hairstreak	*Callophrys rubi*	Least Concern	**−7****	**−11***	Heathland, moorland, scrubby grassland		✓	✓	✓
Large Skipper	*Ochlodes sylvanus*	Least Concern	**−6*****	−5	Hedgerows, rough grassland with shrubs, woodland rides			✓	
Large White	*Pieris brassicae*	Least Concern	**−2*****	−8	Cultivated land, flower-rich areas			✓	
Meadow Brown	*Maniola jurtina*	Least Concern	**−3*****	−0.2	Grassland			✓	
Northern Brown Argus	*Aricia artaxerxes*	Vulnerable	**−20***	**−18****	Rough grassland in mountain areas	✓	✓	✓	✓
Orange Tip	*Anthocharis cardamines*	Least Concern	−0.4	3	Damp meadows, gardens, hedgerows				
Painted Lady	*Vanessa cardui*	Least Concern	**3*****	20	Flower-rich areas, gardens, parks			✓	
Peacock	*Aglais io*	Least Concern	1	−1	Flower-rich areas, gardens, wasteland				
Red Admiral	*Vanessa atalanta*	Least Concern	**3*****	**29*****	Flower-rich areas, gardens			✓	✓
Ringlet	*Aphantopus Bhyperantus*	Least Concern	**5*****	**38*****	Damp areas, hedgerows, woodland rides			✓	✓
Small Copper	*Lycaena phlaeas*	Least Concern	**−12*****	−9	Heathland, rough grassland, wasteland			✓	
Small Heath	*Coenonympha pamphilus*	Vulnerable	**−22*****	**−15*****	Heathland, rough grassland	✓		✓	✓
Small Pearl-bordered Fritillary	*Boloria selene*	Vulnerable	**−24*****	**−16*****	Damp grassland, moorland, open woodland	✓	✓	✓	✓
Small Skipper	*Thymelicus sylvestris*	Least Concern	**−3*****	**−23*****	Grassland, woodland rides			✓	✓
Small Tortoiseshell	*Aglais urticae*	Least Concern	**−2*****	**−28*****	Flower-rich areas, gardens			✓	✓
Small White	*Pieris rapae*	Least Concern	**−2*****	−4	Cultivated areas, flower-rich areas, gardens			✓	✓

Note: Statistically significant species trends are in bold, with level of significance denoted by: $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$.

were scaled to aid model convergence. Two-way interaction terms with a clear ecological basis were also tested, specifically between RelativeWeek and each of Temperature and %Sun. Models that were tested are outlined in Table 3. These models were tested on abundance and species richness separately as response variables.

To account for any temporal autocorrelation in the repeated weekly measures, an Ornstein–Uhlenbeck (OU) correlation structure, in the glmmTMB package (Brooks et al., 2017), was included in all models. Covariates were tested for collinearity using Spearman's rank correlation to ensure none were highly correlated. Moderate correlations were found between some covariates, but these did not affect the estimation of Management on abundance or species richness.

Model selection was guided by the corrected Akaike Information Criterion (AICc) (Burnham & Anderson, 2002), which adjusts for small sample sizes to prevent overfitting. To maintain consistency across abundance models, simpler models were selected when the reduction in AICc for a more complex model was small and did not justify the additional parameters. Using the emmeans package (Lenth, 2024), post hoc Tukey tests were performed on each model to determine the significance of pairwise comparisons.

To test for differences in butterfly species composition between management types a distance-based redundancy analysis (db-RDA) with Bray–Curtis dissimilarities was used (vegan package; Oksanen et al., 2024). Temporal variation was accounted for by including Year and WeekNumber as conditional effects, both treated as factors. WeekNumber corresponds to the survey week, ranging from 1 to 26. The model was run with and without Temperature and %Sun as conditional effects, but their contributions to explaining variation were negligible, and they were therefore excluded from the final model. The overall effect of Management was assessed using permutation tests with 999 iterations, and pairwise db-RDAs were performed between management types to identify specific contrasts.

Data analysis was conducted using R version 4.4.0 (R Core Team, 2024).

3 | RESULTS

In the data used for this study, a total of 9689 butterflies were recorded across 20 species. Small heath was the most recorded species with 1540 individuals across all sites collectively.

3.1 | Abundance

Figure 2 compares butterfly abundance across the different grazing treatments. Sheep-grazed sites had a mean abundance of 0.28 butterflies per 100 m (SD 0.33). The ungrazed site had a mean abundance of 0.88 butterflies per 100 m (SD 1.24), over three times greater than sheep-grazed sites. The cattle-grazed site had the highest abundance, with a mean of 1.95 butterflies per 100 m (SD 1.52), nearly seven times greater than sheep-grazed sites.

The most parsimonious model for comparing butterfly abundance per 100 m across management types included an interaction term between RelativeWeek and Temperature (Model 5, Table 3). This model showed that the abundance of butterflies varied across different grazing treatments, with a post hoc Tukey test revealing significant differences between all pairwise comparisons (Table 4). Both the cattle-grazed and ungrazed sites supported higher butterfly abundance than sheep-grazed sites, with 4.9 and 3.6 times as many butterflies, respectively. The cattle-grazed site also supported 1.4 times as many butterflies as ungrazed sites.

3.2 | Species richness

Figure 3 compares species richness of butterflies between the grazing treatments. The mean species richness was greatest at the cattle-grazed site (mean = 3.13, SD 1.72), with lower values at the ungrazed (mean = 1.79, SD 1.84) and sheep-grazed sites (mean = 1.45, SD 1.52).

TABLE 3 Model variations, with fixed and random effects, used for response variables: Abundance per 100 m, species richness, abundance per 100 m for each species subset groups, A, B, C and D (Table 1).

Model variation number	Fixed effects	Random effects
1	Management + RelativeWeek	Year
2	Management + RelativeWeek + Temperature	Year
3	Management + RelativeWeek + %Sun	Year
4	Management + RelativeWeek + Temperature + %Sun	Year
5	Management + RelativeWeek × Temperature	Year
6	Management + RelativeWeek × %Sun	Year
7	Management + RelativeWeek × Temperature + %Sun	Year
8	Management + RelativeWeek × %Sun + Temperature	Year
9	Management + RelativeWeek × %Sun × Temperature	Year

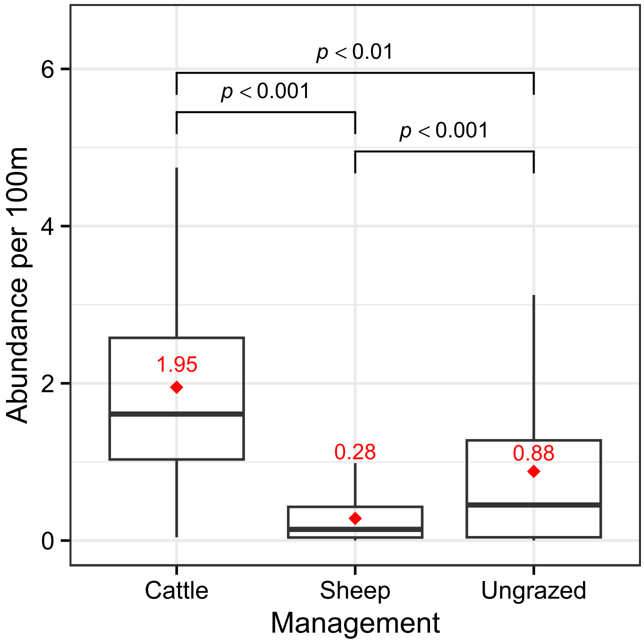

FIGURE 2 Comparison of butterfly abundance per 100 m per survey for different grazing treatments. Mean butterfly abundance per 100 m per survey (red points and labels), median (horizontal line), 25th and 75th percentiles (box) and 1.5 × IQR above and below lower and upper quartiles, respectively (whiskers). A linear model with a Tweedie distribution was used to investigate whether there was a significant difference in butterfly abundance per 100 m between grazing managements. *p*-value, derived from a post hoc Tukey test, are labelled showing a significant difference between all pairwise comparisons.

The most parsimonious model for comparing species richness between grazing management types included an interaction term between RelativeWeek and %Sun (Model 6, Table 3). Both the cattle-grazed and ungrazed sites had 1.7 times as many butterfly species as sheep-grazed sites (Table 4). There was no significant difference in butterfly species richness between cattle-grazed and ungrazed sites.

3.3 | Species composition

The composition of butterfly species differed significantly between grazing management types (Figure 4). The cattle-grazed site was dominated by small heath (GB Red List), with notable but lower numbers of common blue, northern brown argus (GB Red List) and meadow brown. Dark green fritillary, another species on the GB Red List, was also present at the cattle-grazed site, though less abundant. Most other species occurred at low densities, resulting in a community characterised by a small number of abundant open-habitat specialists and several scarce generalists.

In contrast, sheep-grazed sites supported a sparse and largely generalist assemblage, with consistently low abundances across all species. The most frequent species were small heath (GB Red List), meadow brown and green-veined white, but all occurred at substantially lower abundances than in the other management types. Dark green fritillary (GB Red List) was present at very low abundance, and no other specialist or Red List species were recorded.

TABLE 4 Pairwise comparisons of butterfly species abundance (per 100 m) and species richness among grazing treatments, for all species and species subsets.

Species subset	Response variable	Pairwise comparison	Rate ratio	95% CI	*p*
All species	Abundance	Cattle versus Sheep	4.88	3.51–6.78	<0.001
		Cattle versus Ungrazed	1.36	1.12–1.65	0.005
		Ungrazed versus Sheep	3.58	2.56–5.00	<0.001
All species	Species richness	Cattle versus Sheep	1.69	1.22–2.33	0.004
		Cattle versus Ungrazed	0.98	0.80–1.20	0.972
		Ungrazed versus Sheep	1.73	1.24–2.40	<0.003
GB Red List	Abundance	Cattle versus Sheep	8.91	5.57–14.26	<0.001
		Cattle versus Ungrazed	2.01	1.58–2.57	<0.001
		Ungrazed versus Sheep	4.42	2.71–7.25	<0.001
Declining distribution	Abundance	Cattle versus Sheep	4.97	3.55–6.95	<0.001
		Cattle versus Ungrazed	1.63	1.35–1.98	<0.001
		Ungrazed versus Sheep	3.04	2.15–4.29	<0.001
Declining abundance	Abundance	Cattle versus Sheep	8.39	5.56–12.66	<0.001
		Cattle versus Ungrazed	3.42	2.66–4.39	<0.001
		Ungrazed versus Sheep	2.46	1.59–3.77	<0.001
Habitat specialist	Abundance	Cattle versus Sheep	68.41	19.48–240.28	<0.001
		Cattle versus Ungrazed	0.49	0.38–0.65	<0.001
		Ungrazed versus Sheep	138.70	39.43–487.80	<0.001

Note: Rate ratios (with 95% confidence intervals) indicate the relative difference between the first and second management type in each comparison. *p*-values were derived from post hoc Tukey tests.

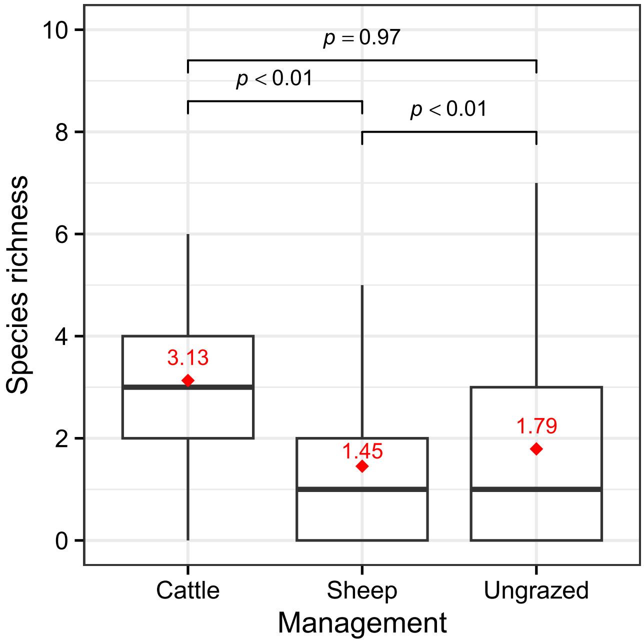

FIGURE 3 Comparison of butterfly species richness per survey for different grazing treatments. Mean butterfly species richness per survey (red points and labels), median (horizontal line), 25th and 75th percentiles (box) and 1.5 × IQR above and below lower and upper quartiles, respectively (whiskers). A linear model with a Poisson distribution was used to investigate whether there was a significant difference in butterfly species richness between grazing managements. *p*-values, derived from a post hoc Tukey test, are labelled showing a significant difference between sheep and cattle, and sheep and ungrazed, but no significant difference between cattle and ungrazed.

The ungrazed site supported a richer and more even community, including several moderately abundant species across both specialist and generalist groups. The most common species were dark green fritillary (GB Red List), common blue and green-veined white. The ungrazed site was the only management to support all Red List and habitat specialist species present in the dataset; notably, the small pearl-bordered fritillary (GB Red List) and green hairstreak, both habitat specialists, were recorded only at the ungrazed site.

We found significant differences in species abundance among management types for all subsets of rare and declining species (Table 4, Figure 5). The cattle-grazed site consistently supported the highest abundances, followed by the ungrazed site, with the exception of the habitat specialist group where the ungrazed site supported twice as many butterflies as the cattle-grazed site. Sheep-grazed sites supported the lowest abundances across all subset groups. The magnitude of each pairwise comparison is shown in Table 4.

It is notable that the trends in Red List species abundance were largely driven by the high density of small heath at the cattle-grazed site. Excluding small heath, the remaining three Red List species contributed 10%, 2% and 28% of total butterfly abundance at the cattle-, sheep- and ungrazed sites, respectively, compared to 63%, 36% and 30% when small heath was included. These results indicate that, although small heath strongly influences overall Red List abundance, cattle- and ungrazed sites still supported higher abundances of the rarer Red List species than sheep-grazed sites.

In addition, when considering habitat specialist species, there was also a much lower abundance on sheep-grazed (mean = 0.004, SD = 0.019 butterflies per 100 m) than both cattle-grazed (mean = 0.257, SD = 0.265) and ungrazed sites (mean = 0.285, SD = 0.646) (Figure 5). Statistical modelling confirmed this difference, with significantly lower abundances of habitat specialist butterflies at sheep-grazed sites than both cattle-grazed and ungrazed sites (Table 4). It is important to note that very low butterfly counts for habitat specialists on sheep-grazed sites means there is high uncertainty around the estimates of relative difference between sheep-grazed and the other managements. Therefore, exact magnitudes should be interpreted cautiously. The model also highlighted a positive effect of ungrazed sites relative to cattle-grazed sites, estimating that ungrazed sites supported approximately twice as many habitat specialist individuals, despite the similarity in the raw mean abundance values (Table 4).

4 | DISCUSSION

In this study we investigated the effect of different grazing managements on butterfly abundance, species richness and composition in calcareous habitats in the English uplands. Our results show that lightly cattle-grazed and ungrazed sites supported a significantly higher abundance of butterflies than lightly sheep-grazed sites. The ungrazed sites also had a higher butterfly abundance than the sheep-grazed sites, but lower abundance than the cattle-grazed sites. We also found that butterfly species richness was significantly higher on both the cattle-grazed and ungrazed sites compared to the sheep-grazed sites, with no significant difference between cattle-grazed and ungrazed sites.

The cattle-grazed sites also had higher abundances of Red List and declining butterfly species than both ungrazed and sheep-grazed sites. Sheep-grazed sites consistently had the lowest mean abundance of Red List and declining species, showing a significantly lower value than the ungrazed sites for two of the three species subset groups. While the cattle-grazed sites had the highest abundance, the ungrazed site supported the greatest number of Red List butterfly species, with all four of the Red List species present in the data recorded at the ungrazed sites, compared to three at the cattle-grazed sites and two at the sheep-grazed sites.

4.1 | Vegetation composition and structure

Our results show higher butterfly abundance and species richness at cattle-grazed sites compared with sheep-grazed sites, consistent with established effects of grazing on vegetation. Higher plant species richness, lower grass cover and less targeted grazing of flowering heads on cattle-grazed areas increase the availability of nectar sources and host plants supporting higher butterfly diversity and abundance (Milberg et al., 2016; Potts et al., 2009; Rook et al., 2004; Thomas et al., 1986).

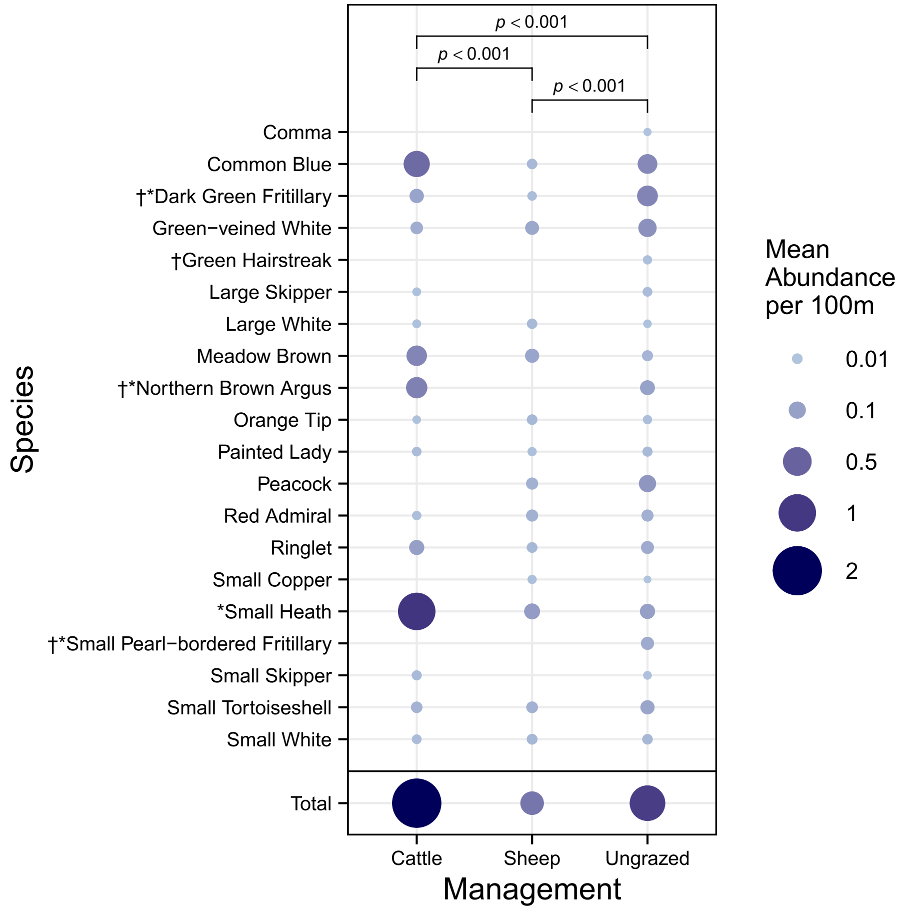

FIGURE 4 Butterfly species composition across management types. Each dot represents the mean abundance per 100 m per species, with total mean abundance per 100 m shown at the bottom. Dot size and shading both indicate mean abundance per 100 m, with larger and darker dots representing more abundant species. *p*-values shown are from a distance-based Redundancy Analysis (db-RDA), indicating significant differences in butterfly species composition among all management types. Species on the GB Red List are indicated with an asterisk (*) and habitat specialist species with a dagger (†).

The higher abundance and species richness of butterflies on ungrazed versus sheep-grazed sites is more likely driven by differences in vegetation structure than plant species richness (Lyons et al., 2017; Milligan et al., 2016). Reduced grazing pressure produces taller and more heterogeneous swards which increase nectar availability as well as creating microhabitats that facilitate basking, thermoregulation, egg-laying and shelter (Farruggia et al., 2012; Jerrentrup et al., 2014; Milberg et al., 2016; Morris, 2000; Öckinger et al., 2006). By broadening the range of available niches, this structural complexity supports higher butterfly diversity by providing the habitats and resources needed by both generalist and specialist species (Turlure et al., 2019).

Despite comparable butterfly species richness between the ungrazed and cattle-grazed sites, butterfly abundance was highest at the cattle-grazed site. Vegetation at the cattle-grazed sites at Ingleborough is considerably shorter than the optimal vegetation height for butterfly species richness (Porton et al., 2026; Pöyry et al., 2006). This pattern suggests that light cattle grazing creates favourable conditions for butterflies by maintaining high plant species richness, even in the absence of the taller, more structurally complex swards found in ungrazed areas (Milligan et al., 2016). These results indicate that the availability of host plants and nectar sources is a key driver of butterfly abundance, whereas the effects of vegetation structure and grazing management on butterfly species richness are more complex.

Changes to vegetation composition are one possible mechanism for the difference in butterfly populations between ungrazed and sheep-grazed sites. Although we don't have evidence at our sites, multiple studies have shown that livestock exclusion can drive shifts in vegetation composition (Alday et al., 2021; Kahmen et al., 2002; Marrs et al., 2020; Porton et al., 2024).

4.2 | Bioabundance

Sheep-grazed sites were shown to have the lowest butterfly abundance. Our results showed 4.9 times as many butterflies at the cattle-grazed site and 3.6 times as many at the ungrazed site compared to sheep-grazed sites. While the abundance of common species is not always the primary focus of conservation, with priority often given to rare or threatened species (Redford et al., 2013), it is important to note that cattle grazing had a positive effect on both rare and common butterfly species.

The substantially higher total butterfly abundance at cattle-grazed and ungrazed sites may have important ecosystem benefits. Butterflies, and their caterpillars, are important prey sources for other species such as birds (Ghazanfar et al., 2016). An increase in butterfly abundance is likely to benefit their predators, with the potential for trophic cascades, as observed at other upland sites following increases in invertebrate abundance (Evans et al., 2015).

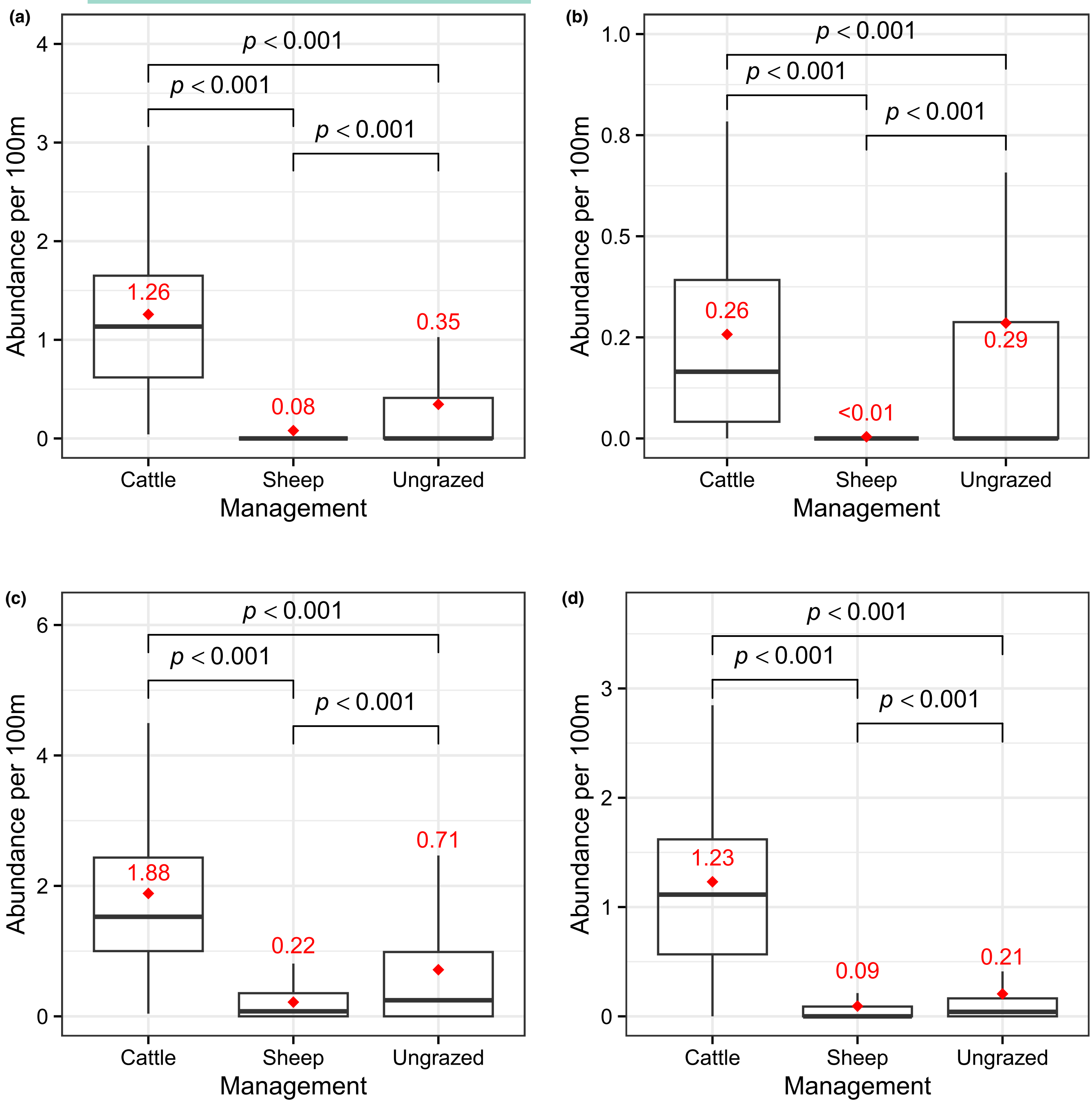

FIGURE 5 Abundance per 100 m for different grazing management types for species subset groups. (a) species on GB Red List as Vulnerable or Near Threatened (Fox et al., 2022); (b) habitat specialist species; (c) species showing a significant trend of decline in distribution across England from 1976 to 2019 (Fox et al., 2023); (d) species showing a significant trend of decline in abundance in England from 1976 to 2019 (Fox et al., 2023). Mean abundance per 100 m (red points and labels), median (horizontal line), 25th and 75th percentiles (box) and 1.5 × IQR above and below lower and upper quartiles, respectively (whiskers). Linear models, all with a Tweedie distribution, were used to investigate the difference in abundance per 100 m between grazing managements. *p*-values, derived from a post hoc Tukey test, are labelled showing a significant difference between all pairwise comparisons.

4.3 | Importance of habitat mosaics

At a site scale, and within the context of this study, light grazing by cattle was the most effective grazing management for supporting the highest butterfly species richness and abundance. However, each management type supported significantly different species compositions, with rarer species such as small pearl-bordered fritillary and green hairstreak only recorded at the ungrazed site. Different species compositions between grazing treatments have also been observed in beetles and spiders in similar habitats (Lyons et al., 2017, 2018). This suggests that, despite higher butterfly abundance at the cattle-grazed sites, there is a benefit in having a combination of cattle-grazed and ungrazed areas to maximise butterfly species richness at a landscape scale.

It is important to note that the ungrazed site in this study has been ungrazed for around 55 years and is not yet a climax community. Consequently, we cannot say what effect ungrazed areas may have on butterflies when a climax community is reached. One possibility is that these areas could provide habitats suited to woodland specialist butterflies, further expanding butterfly species richness across all sites combined.

Heterogenous landscapes are crucial to biodiversity (Hackett et al., 2024). For butterflies, it allows them to move between different habitats and select areas with the most suitable conditions as climatic factors fluctuate (Oliver et al., 2010). For example, during drier years, butterflies can utilise more drought resistant habitats, such as areas of taller vegetation or woodland, which tend to be cooler and retain more moisture (Sutcliffe et al., 1997). This means that butterfly populations can persist in a landscape during years with unfavourable conditions. Further to buffering the impacts of environmental change, a more heterogeneous landscape provides a broader range of resources from different habitat patches, facilitating the needs of butterflies in various life stages simultaneously. This includes supporting the requirements of adults, who alone utilise a range of habitat patches for thermoregulation, oviposition, nectaring and shelter (Dennis & Shreeve, 2003), as well as earlier life stages through the provision of larval food plants. This is especially beneficial for species that have multiple generations present within a single year (Roy & Thomas, 2003).

While this study provides insights into the effects of different grazing management types, it does not consider how variation in surrounding habitats could influence butterfly diversity and abundance. For instance, habitat mosaics in the broader landscape, such as areas of moorland, scrub or woodland, could provide additional resources and corridors that support butterfly populations and influence species composition.

Although maintaining sheep grazing as part of a mixed grazing system has been found to benefit butterfly numbers in some cases (Fraser et al., 2014), our findings show that sheep-grazed calcareous grasslands do not support the abundance or diversity of butterflies that is possible at either cattle-grazed or ungrazed sites. In addition, sheep-grazed sites were found to have low value in supporting rarer butterfly species, both in richness and abundance.

4.4 | Limitations

The primary limitations of our study are the restricted spatial replication and variation in survey years between sites. Greater spatial replication would allow any conclusions about the effect of grazing management to be applied to the wider uplands, rather than just the sites surveyed. This monitoring will also be continued long-term, improving the robustness of the dataset and the reliability of any conclusions drawn. Ongoing monitoring of butterfly populations at Ingleborough NNR will also allow analysis of temporal changes, capturing both the effects of restoration across the sites as a whole and changes resulting directly from a transition in grazing management.

4.5 | Implications for management

Our findings demonstrate that light cattle grazing on upland calcareous grasslands can be highly beneficial for butterfly abundance and diversity. The diverse vegetation, resulting from low-intensity cattle grazing, is likely a key driver of this (Porton et al., 2026). In contrast, sites lightly grazed by sheep resulted in lower abundance and diversity of butterflies, despite comparative site conditions. The stocking rates of sites in this study were substantially lower than typical stocking rates in the English uplands, suggesting that even light grazing by sheep can be detrimental to butterfly populations on upland calcareous grasslands. Stock exclusion supported greater abundance and diversity of butterflies than lightly sheep-grazed sites and showed comparative levels of diversity but lower abundance than the lightly cattle-grazed site. The dominance of sheep grazing as the current management option for upland calcareous grasslands in the UK therefore presents a challenge for butterfly conservation.

Our work provides evidence to justify agri-environment payments to farmers and land managers for switching from sheep grazing to light cattle grazing of upland calcareous grasslands. Importantly, shifts in grazing regimes provide ecological benefits beyond increasing butterfly diversity and abundance. Cattle grazing increases soil organic carbon (Su et al., 2023) as well as facilitating the development of scattered scrub (Porton et al., 2024). Although agri-environment payments aimed at reducing sheep stocking rates may benefit some species groups, our findings suggest that such reductions may not be as effective in increasing butterfly abundance and diversity in upland calcareous grasslands as low-intensity cattle grazing.

Therefore, for effective butterfly conservation in these areas, a shift towards light cattle grazing or stock exclusion should be considered, taking into account site-specific conditions. Given the potential for ecological benefits, agri-environment schemes that support low-intensity cattle grazing are a promising mechanism for improving the state of butterfly populations in upland calcareous landscapes in the UK.

AUTHOR CONTRIBUTIONS

Robyn Wrigley, George Porton and Dominick Spracklen conceived the ideas and designed methodology; George Porton, Terry Whitaker, Colin Newlands, Andrew Hinde, Frank Morgan, Anna-Marie Waters, Rachel Benson, Judith Greaves, Clare Leigh, Chloe Lumsdon, Kay Andrews, Kathleen Shaw, Edward Easton, Eve Pegler, Dwayne Martindale and Kathryn James collected the data; Robyn Wrigley analysed the data; Robyn Wrigley and George Porton led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.70210.

DATA AVAILABILITY STATEMENT

Data made available on Zenodo https://zenodo.org/records/18387648 (Wrigley et al., 2026). In addition, raw data used in this study are UKBMS data, which are managed by the Biological Records Centre and are available on request for research purposes at varying scales and resolutions: https://ukbms.org/request-data.

STATEMENT OF INCLUSION

Our study brings together authors from multiple organisations, including both staff and volunteers with extensive knowledge of the study area. We worked in conjunction with Natural England and Yorkshire Wildlife Trust to design the surveys used in this study. This ensured that the perspectives and expertise of all collaborators were integrated throughout the study.

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REFERENCES

Alday, J., O'Reilly, J., Rose, R. J., & Marrs, R. H. (2021). Effects of long-term removal of sheep-grazing in a series of British upland plant communities: Insights from plant species composition and traits. *Science of the Total Environment*, *759*, 143508.

Botham, M. S., Fernandez-Ploquin, E. C., Brereton, T., Harrower, C. A., Roy, D. B., & Heard, M. S. (2015). Lepidoptera communities across an agricultural gradient: How important are habitat area and habitat diversity in supporting high diversity? *Journal of Insect Conservation*, *19*(2), 403–420.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). SpringerVerlag.

Bussan, S. K. (2022). Can cattle grazing benefit grassland butterflies? *Journal of Insect Conservation*, *26*(3), 359–374.

Butterfly Conservation. (2025). *UK Conservation Strategy 2025*. Butterfly Conservation. https://butterfly-conservation.org/sites/default/files/2024-02/bc_2025_conservation_strategy.pdf

UK Butterfly Monitoring Scheme. (n.d.). *Methods*. https://ukbms.rg/methods

Chinery, M. (2012). *Butterflies*. HarperCollinsPublishers.

Chowdhury, S., Dubey, V. K., Choudhury, S., Das, A., Jeengar, D., Sujatha, B., Kumar, A., Kumar, N., Semwal, A., & Kumar, V. (2023). Insects as bioindicator: A hidden gem for environmental monitoring. *Frontiers in Environmental Science*, *11*, 1146052.

Demment, M. W., & Van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist*, *125*(5), 641–672.

Dennis, R. L. H., & Shreeve, T. G. (2003). Towards a functional resource-based concept for habitat: A butterfly biology view-point. *Oikos*, *10*, 417–426.

Department for Environment, Food and Rural Affairs. (2025). *Livestock-populations-in-england-20250828*. GOV.UK.

Department for Environment, Food and Rural Affairs. (2011). *defra-stats-foodfarm-landuselivestock-june-results-england-1900series111129*. The National Archives.

Evans, D. M., Villar, N., Littlewood, N. A., Pakeman, R. J., Evans, S. A., Dennis, P., Skartveit, J., & Redpath, S. M. (2015). The cascading impacts of livestock grazing in upland ecosystems: A 10-year experiment. *Ecosphere*, *6*(3), 1–15.

Farruggia, A., Dumont, B., Scohier, A., Leroy, T., Pradel, P., & Garel, J. P. (2012). An alternative rotational stocking management designed to favour butterflies in permanent grasslands. *Grass and Forage Science*, *67*(1), 136–149.

Fox, R., Dennis, E. B., Brown, A. F., & Curson, J. (2022). A revised Red List of British butterflies. *Insect Conservation and Diversity*, *15*(5), 485–495.

Fox, R., Dennis, E. B., Purdy, K. M., Middlebrook, I., Roy, D. B., Noble, D. G., Botham, M. S., & Bourn, N. A. D. (2023). *The state of the UK's butterflies 2022*. Butterfly Conservation.

Fraser, M. D., Davies, D. A., Vale, J. E., Hirst, W. M., & Wright, I. A. (2007). Effects on animal performance and sward composition of mixed and sequential grazing of permanent pasture by cattle and sheep. *Livestock Science*, *110*(3), 251–266.

Fraser, M. D., Moorby, J. M., Vale, J. E., & Evans, D. M. (2014). Mixed grazing systems benefit both upland biodiversity and livestock production. *PLoS One*, *9*(2), e89054.

Ghazanfar, M., Malik, M. F., Hussain, M., Iqbal, R., & Younas, M. (2016). Butterflies and their contribution in ecosystem: A review. *Journal of Entomology and Zoology Studies*, *4*(2), 115–118.

Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, *4*(4), 379–391.

Goulson, D. (2019). The insect apocalypse, and why it matters. *Current Biology*, *29*(19), R967–R971.

Hackett, T. D., Sauve, A. M., Maia, K. P., Montoya, D., Davies, N., Archer, R., Potts, S. G., Tylianakis, J. M., Vaughan, I. P., & Memmott, J. (2024). Multi-habitat landscapes are more diverse and stable with improved function. *Nature*, *633*, 114–119.

Harvey, D., & Scott, C. (2021). Farm Business Survey 2019/2020 Hill Farming in England, Rural Business Research. https://www.ruralbusinessresearch.co.uk/wp-content/uploads/2023/05/Hill-farming-in-England-2019-20.pdf

Jerrentrup, J. S., Wrage-Mönnig, N., Röver, K. U., & Isselstein, J. (2014). Grazing intensity affects insect diversity via sward structure and heterogeneity in a long-term experiment. *Journal of Applied Ecology*, *51*(4), 968–977.

Johansson, V., Kindvall, O., Askling, J., & Franzén, M. (2019). Intense grazing of calcareous grasslands has negative consequences for the threatened marsh fritillary butterfly. *Biological Conservation*, *239*, 108280.

Kahmen, S., Poschlod, P., & Schreiber, K. F. (2002). Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. *Biological Conservation*, *104*(3), 319–328.

Lenth, R. (2024). emmeans: Estimated marginal means, aka least-squares means. R package version 1.10.5, https://CRAN.R-project.org/package=emmeans

Lyons, A., Ashton, P. A., Powell, I., & Oxbrough, A. (2017). Impacts of contrasting conservation grazing management on plants and carabid beetles in upland calcareous grasslands. *Agriculture, Ecosystems & Environment*, *244*, 22–31.

Lyons, A., Ashton, P. A., Powell, I., & Oxbrough, A. (2018). Epigeal spider assemblage responses to vegetation structure under contrasting grazing management in upland calcareous grasslands. *Insect Conservation and Diversity*, *11*(4), 383–395.

Maes, D., Verovnik, R., Wiemers, M., Brosens, D., Beshkov, S., Bonelli, S., Buszko, J., Cantú-Salazar, L., Cassar, L. F., Collins, S., & Dincă, V. (2019). Integrating national Red Lists for prioritising conservation actions for European butterflies. *Journal of Insect Conservation*, *23*(2), 301–330.

Magurran, A. E. (2013). *Ecological diversity and its measurement*. Springer Science & Business Media. https://link.springer.com/book/10.1007/978-94-015-7358-0

Marrs, R. H., Lee, H., Blackbird, S., Connor, L., Girdwood, S. E., O'Connor, M., Smart, S. M., Rose, R. J., O'Reilly, J., & Chiverrell, R. C. (2020). Release from sheep-grazing appears to put some heart back into upland vegetation: A comparison of nutritional properties of plant species in long-term grazing experiments. *Annals of Applied Biology*, *177*(1), 152–162.

Milberg, P., Bergman, K. O., Cronvall, E., Eriksson, Å. I., Glimskär, A., Islamovic, A., Jonason, D., Löfqvist, Z., & Westerberg, L. (2016). Flower abundance and vegetation height as predictors for nectar-feeding insect occurrence in Swedish semi-natural grasslands. *Agriculture, Ecosystems & Environment*, *230*, 47–54.

Milligan, G., Rose, R. J., & Marrs, R. H. (2016). Winners and losers in a long-term study of vegetation change at Moor House NNR: Effects of sheep-grazing and its removal on British upland vegetation. *Ecological Indicators*, *68*, 89–101.

Morris, M. G. (2000). The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. *Biological Conservation*, *95*(2), 129–142.

Natural England. (2009). *Grazing livestock in the uplands. Environmental impacts of land management (NERR030)*. Natural England. https://publications.naturalengland.org.uk/file/62084

New, T. R. (1997). Are lepidoptera an effective 'umbrella group' for biodiversity conservation? *Journal of Insect Conservation*, *1*(1), 5–12.

Öckinger, E., Eriksson, A. K., & Smith, H. G. (2006). Effects of grassland abandonment, restoration and management on butterflies and vascular plants. *Biological Conservation*, *133*(3), 291–300.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., … Weedon, J. (2024). vegan: Community ecology package. R package version 2.6–8, https://CRAN.R-project.org/package=vegan

Oliver, T., Roy, D. B., Hill, J. K., Brereton, T., & Thomas, C. D. (2010). Heterogeneous landscapes promote population stability. *Ecology Letters*, *13*(4), 473–484.

Porton, G., Wrigley, R., Carr, J., Martindale, D., Morgan, F., Ryder, S., Coates, L., Shaw, K., Kelly, C., Birnie, R., Perry, J., Pegler, E., Thom, T., Scott, C. E., & Spracklen, D. V. (2026). Contrasting vegetation restoration responses from cattle grazing and livestock exclusion following sheep removal at a calcareous upland site. Unpublished Manuscript.

Porton, G., Wrigley, R., Scott, C. E., & Spracklen, D. V. (2024). Natural colonisation rates in a UK upland landscape under different conservation management approaches following sheep removal. *Ecological Solutions and Evidence*, *5*(2), e12338.

Poschlod, P., & Wallis de Vries, M. F. (2002). The historical and socio-economic perspective of calcareous grasslands–lessons from the distant and recent past. *Biological Conservation*, *104*, 361–376.

Potts, S. G., Woodcock, B. A., Roberts, S. P. M., Tscheulin, T., Pilgrim, E. S., Brown, V. K., & Tallowin, J. R. (2009). Enhancing pollinator biodiversity in intensive grasslands. *Journal of Applied Ecology*, *46*(2), 369–379.

Pöyry, J., Luoto, M., Paukkunen, J., Pykälä, J., Raatikainen, K., & Kuussaari, M. (2006). Different responses of plants and herbivore insects to a gradient of vegetation height: An indicator of the vertebrate grazing intensity and successional age. *Oikos*, *115*(3), 401–412.

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Redford, K. H., Berger, J., & Zack, S. (2013). Abundance as a conservation value. *Oryx*, *47*(2), 157–158.

Rook, A. J., Harvey, A., Parsons, A. J., Orr, R. J., & Rutter, S. M. (2004). Bite dimensions and grazing movements by sheep and cattle grazing homogeneous perennial ryegrass swards. *Applied Animal Behaviour Science*, *88*(3–4), 227–242.

Roy, D. B., & Thomas, J. A. (2003). Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. *Oecologia*, *134*, 439–444.

Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J. C., Linsenmair, K. E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E. D., Vogt, J., Wöllauer, S., & Weisser, W. W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, *574*, 671–674.

Spitzer, L., Benes, J., Dandova, J., Jaskova, V., & Konvicka, M. (2009). The large blue butterfly, Phengaris [Maculinea] arion, as a conservation umbrella on a landscape scale: The case of the Czech Carpathians. *Ecological Indicators*, *9*(6), 1056–1063.

Su, J., Xu, F., & Zhang, Y. (2023). Grassland biodiversity and ecosystem functions benefit more from cattle than sheep in mixed grazing: A meta-analysis. *Journal of Environmental Management*, *337*, 117769.

Sutcliffe, O. L., Thomas, C. D., Yates, T. J., & Greatorex-Davies, J. N. (1997). Correlated extinctions, colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation. *Oecologia*, *109*, 235–241.

Thomas, J. A., Thomas, C. D., Simcox, D. J., & Clarke, R. T. (1986). Ecology and declining status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain. *Journal of Applied Ecology*, *23*(2), 365–380.

Turlure, C., Schtickzelle, N., Dubois, Q., Baguette, M., Dennis, R. L., & Van Dyck, H. (2019). Suitability and transferability of the resource-based habitat concept: A test with an assemblage of butterflies. *Frontiers in Ecology and Evolution*, *7*, 127.

van Noordwijk, C. G. E., Flierman, D. E., Remke, E., WallisDeVries, M. F., & Berg, M. P. (2012). Impact of grazing management on hibernating caterpillars of the butterfly *Melitaea cinxia* in calcareous grasslands. *Journal of Insect Conservation*, *16*, 909–920.

Wagner, D. L. (2020). Insect declines in the anthropocene. *Annual Review of Entomology*, *65*(1), 457–480.

Wallis de Vries, M. F., Poschlod, P., & Willems, J. H. (2002). Challenges for the conservation of calcareous grasslands in north-western Europe: Integrating the requirements of flora and fauna. *Biological Conservation*, *104*, 265–273.

Wikström, L., Milberg, P., & Bergman, K. O. (2009). Monitoring of butterflies in semi-natural grasslands: Diurnal variation and weather effects. *Journal of Insect Conservation*, *13*, 203–211.

Wrigley, R., Porton, G., Whitaker, T., Newlands, C., Hinde, A., Morgan, F., Waters, A., Benson, R., Greaves, J., Leigh, C., Lumsdon, C., Andrews, K., Shaw, K., Easton, E., Pegler, E., Martindale, D., James, K., & Spracklen, D. V. (2026). The effect of different grazing managements on butterfly abundance, diversity and composition at a calcareous upland site. [data set]. *Zenodo*. https://doi.org/10.5281/zenodo.18387648

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1: Summary of species-level butterfly abundance across grazing management treatments and years. Transect length and total weeks surveyed are reported for each entry.

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