Title: Impacts of Contrasting Conservation Grazing Management on Plants and Carabid Beetles in Upland Calcareous Grasslands

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Abstract

Calcareous grassland is among the most species rich and diverse habitat in Europe, but has faced decline due to agricultural intensification and abandonment. In recent years, conservation organisations have changed grazing practices in this habitat in an attempt to maintain characteristic vegetation. However, there has been little consideration of the effects of changes in grazing practices on invertebrate communities or their relationship with plant communities. This study determines the impacts of commonly used grazing practices in internationally rare upland calcareous grasslands on vegetation and on carabid beetles, a diverse group that are known to respond to environmental change. Typical conservation management regimes (light cattle grazing, light sheep grazing and ungrazed), established for over ten years, were examined in three regions of Britain. Carabid beetles were sampled using pitfall traps from late April – early September 2013 and per cent cover of plant species was recorded in 2m x 2m quadrats paired with pitfall traps sequentially throughout the sample period. Plant and beetle species composition differed significantly between regimes, as did plant species richness where ungrazed sites had significantly fewer species than sheep or cattle grazed sites. In contrast, beetle species richness did not differ by grazing type. Three beetle species were significantly associated with grazing management regimes: *Carabus arvensis* with light cattle grazing, and *Carabus violaceaus* and *Synchus vivalis* with light sheep grazing, the former two having undergone major population declines in the UK. Grazing regime affects both plant and carabid beetle communities and is important in supporting distinct species compositions as well as rare and declining species. Carabid beetles did not always respond in the same way as plants to grazing regime, suggesting that conservation managers should exercise caution when using plant species composition or broad measures of plant diversity to indicate biodiversity value, identify priority habitats or select grazing regimes to support a particular habitat condition.

Key words: Community, Carabid beetle, Livestock, Ungrazed, Upland, Vegetation.

1. Introduction

Calcareous grassland is one of the most species rich and diverse habitats in Europe (Wallis de Vries et al. 2002). Their exceptional diversity of plants and invertebrates render them of great conservation interest (Boschi and Baur 2007; Krauss et al. 2003; van Swaay 2002; Wallis de Vries et al. 2002). In Europe, large areas have been lost since the 1950s due to changes in management practices, such as increased use of fertilisers, greater stocking densities and occasionally abandonment (Fischer and Stocklin 1997; Poschlod et al. 2005; Roesch et al. 2013; Wallis de Vries et al. 2002). This has resulted in a dramatic decline in plant species richness (Poschlod and Wallis de Vries 2002). Consequently, calcareous grassland is now protected in national and international legislation (e.g. EU Habitats Directive).

Semi-natural grasslands are sub-climax communities that require intervention to prevent succession to scrub or woodland (Rook et al. 2004) and to maintain plant diversity (Roesch et al. 2013; Wallis de Vries et al. 2002). Grazing is commonly used as a conservation tool for maintaining diversity within these plant communities. Through grazing the removal of plant biomass alters competitive relationships amongst plants which drives both heterogeneity within a landscape and preserves diversity (Bullock and Marriott 2000; Rook et al. 2004; Scimone et al. 2007). Dietary choice of livestock, determined by adaptations such as dental anatomy (Ferreira et al. 2013), is the principle factor influencing habitat heterogeneity, diversity and composition (Rook et al. 2004). For instance, sheep exhibit more selectivity in their diet than cattle, resulting in increased cover of less desirable grasses (Grant et al. 1985). Additionally, the intensity of grazing also impacts upon vegetation, as suggested by the intermediate grazing optimisation model (Grime, 1973), with high stocking densities or abandonment resulting in a decline in plant species richness and structural complexity, whilst moderate stocking densities lead to increased plant species richness (Deng et al. 2013: Grime, 1973; Vickery et al. 2001). Further, at low densities, the above ground biomass of grass increases whilst that of forbs decreases (Deng et al. 2013); the resulting encroachment of dominant grasses reduces species richness and the increased litter deposition results in eutrophication (Calaciura and Spinelli 2008; Jacquemyn et al. 2011; Wallis de Vries et al. 2002; Woodcock et al. 2005).

Selection of grazing regime has implications for invertebrate communities directly through disturbance or provision of resources, such as dung or carrion, and indirectly through its effects on plant species composition, plant architecture and heterogeneity (Dennis et al. 2001; Morris 2000; Vickery et al. 2001; Woodcock et al. 2005). The *habitat heterogeneity hypothesis* predicts that the greater the heterogeneity of a habitat the more species can coexist in that habitat (Pianka 1966). Thus, it follows that under grazing conditions that produce a more heterogeneous sward, such as low intensity grazing with cattle or sheep compared to no grazing, invertebrate species richness will be enhanced as there is greater niche availability.

There are currently an estimated 595973ha of calcareous grassland within Europe, of which around 33419ha is in the United Kingdom (Calaciura and Spinelli 2008) and an estimated 60 – 75 per cent of this occurs in the British uplands (Maddock 2008). As elsewhere in Europe, upland areas within Britain experienced decline in this habitat due to intensive grazing, typically with sheep (Dennis et al. 2008; Fuller and Gough 1999). Indeed, between 1990 and 1998 there was an 18% decline in calcareous grassland in the UK (Haines-Young et al. 2000). To conserve the characteristic vegetation of this habitat there has been a reduction in stocking levels within the last decade. This typically involves a shift from grazing with high numbers of sheep to a lower stocking density of cattle, though occasionally lower stocking densities of sheep or no grazing occurs. These so-called ‘conservation grazing regimes’ are based on suggested appropriate annual stocking rates of 0.25 LU ha-1 yr-1 for maintaining biodiversity (Backshall et al. 2001). However, there have been few studies which address the impact of these established low stocking conservation grazing regimes and compare ungrazed regimes, on plants and fewer still on invertebrates in these internationally important habitats (Wallis de Vries et al. 2002, 2016). Previous studies of grazing impacts on calcareous grassland have examined small experimental plots (e.g. Barbaro et al. 2001; Woodcock et al. 2005; Jacquemyn et al. 2011). The present study is the first to present an evidence base for the impacts of established (>10 years) conservation grazing management on biodiversity in upland calcareous grasslands, using plants and carabid beetles as models. This study aims to determine the impact of low intensity sheep grazing, low intensity cattle grazing and ungrazed regimes on plant and carabid beetle communities and tests the following hypotheses:

1. In low intensity conservation grazing regimes with either cattle or sheep, there will be greater plant species richness compared to ungrazed regimes.   
   This follows the intermediate grazing optimisation model where plant species richness reaches a maximum at intermediate biomass as a product of optimum grazing levels (Grime, 1973). According to this model, species richness will increase or decrease depending on grazing intensity, since this directly alters the amount of biomass and hence alters competition. It is expected that even below recommended optimum stocking levels, low intensity cattle or sheep grazing will lead to greater plant species richness compared to ungrazed regimes as a consequence of reduced biomass.   
   Supplementary to hypothesis one, it is expected that owing to equal stocking densities, plant species richness will not differ between low intensity cattle and sheep grazing regimes.
2. It is further expected that in line with plant species richness, and following the *habitat heterogeneity* hypothesis, there will be greater carabid beetle species richness in low intensity conservation grazing regimes with either cattle or sheep than ungrazed regimes.   
   Supplementary to hypothesis two, it is expected that due to the disturbance action of grazing livestock, greater habitat heterogeneity in grazed compared to ungrazed regimes will result in a greater range of food resources available through seeds or prey, thus providing a greater range of niches for more carabid beetle species to occur. Again, it is expected that due to comparable stocking densities, no difference in carabid beetle species richness will be observed between sheep and cattle regimes.
3. There will a distinct species composition among the three grazing types for both plants and carabid beetles due to the different grazing actions of cattle and sheep, as discussed above, even at low intensities.

Plants are directly impacted by grazing and are the target of conservation efforts. Conversely, invertebrates are very rarely considered when grazing management decisions are made for upland calcareous grassland, despite their importance for the functioning of ecosystems. Carabid beetles, for instance, play an important role in grasslands through their roles such as predators, as granivores and as a food source for other animals (Lövei and Sunderland 1996) yet are overlooked in management decisions. Management is typically focused on maintaining particular plant communities and condition of sites is always assessed based on vegetation characteristics. Results from this study, weighed against other evidence, will inform management recommendations for enhancing biodiversity through grazing regimes in rare calcareous grasslands and determine whether plant species composition can be used to indicate carabid beetle species composition, a useful tool in the context of conservation management in these habitats.

1. Methods

2.1 Study Sites

Three grazing types were selected for study within the most extensive upland limestone areas within the UK: ungrazed, cattle grazed and sheep grazed regimes (with a negligible number of cattle (<0.02 Livestock Units per Hectare per Year (LU ha-1 yr-1) and herein referred to as sheep grazed). The current grazing regime had been in place for at least ten years prior to investigation across all locations. Grazed regimes were deemed as being lightly grazed for upland calcareous grassland as they had a grazing intensity of less than 0.24 LU ha-1 yr-1 (Backshall et al. 2001) calculated as: Annual Equivalent Stocking Density = ((N\*GLU/H)\*(M/12)

Where: N = Number of individuals, GLU = Grazing Livestock Unit (taken from Nix, 2004), H = Hectares and M = Number of months grazed. Detail of stocking densities and duration of grazing is provided in table 1.

Each grazing regime was replicated across three geographically distinct regions separated by 20-37km in Northern England (54°29′18.55″N, 002°32′33.00″W) (54°11′43.30″N, 002°21′00.13″W) (54°06′29.41″N, 002°03′55.04″W) (Fig. 1). In each region three extensive areas of limestone grassland (size 15 ha – 525.68 ha, median 82.75) were selected within which three sampling locations were established. These were separated by a minimum of 150m (median 330m) to ensure statistical independence of samples (Digweed et al. 1995), and a minimum of 50m from the edge and away from disturbance e.g. footpaths, water troughs etc. Spatial independence of samples was confirmed with Moran’s I based on nearest neighbour distances using the spdep package in R (Bivand et al. 2014) (see appendix A1 in Supplementary material).

In each of the three regions there were three gazing types giving a total of 27 areas selected for study (three replicates per grazing type nested within region).  Elevation ranged from 288 – 396m, median 335m. Soil across the sites was generally base rich with some deposits of glacial till and peat.

All areas were characterised by a mix of calcareous grassland, upland heath and limestone pavement, and were surrounded by a mix of extensively and intensively grazed open grassland. Typical areas of calcareous grassland were selected for study through the use of detailed habitat maps and aerial photographs. Within each location, surveys of vascular plants, bryophytes and epigeic carabid beetles were conducted between April – September 2013.

2.2 Vegetation Sampling

To incorporate changes in plant communities across the sampling period one 2m x 2m quadrat was recorded at each sampling location at approximately three weekly intervals to achieve a total of six quadrats per sample location for the duration of the sampling season, between 27th May 2013 and 20th September 2013. For three of the sample locations in the sheep grazed regime permission was restricted for the first two sampling rounds, so two quadrats were recorded in each of the final two rounds of sampling to ensure the same sampling effort. Per cent cover of all vascular plants and bryophytes was estimated to the nearest five per cent. Vascular plants were identified to species using Poland and Clement (2009) and Rose (2006) and bryophytes identified using Smith (2004). Nomenclature follows Stace (2010) for vascular plants and Smith (2004) for bryophytes.

2.3 Invertebrate Sampling

Within each sampling location a line of six pitfall traps, spaced 2m apart and 1m from vegetation quadrats, was set up to capture carabid beetles (Gardner et al. 1997; Haysom et al. 2004; Oxbrough et al. 2012). The sixth trap was kept as a spare in case of loss or damage. Each trap consisted of a plastic cup approximately 7cm in diameter and 9cm deep and was covered with a square plastic lid suspended 1cm from the ground by pegs to prevent flooding. 1cm depth of ethylene glycol was used in traps as a killing and preserving agent. To prevent traps being trampled or interfered with by livestock, in grazed areas each trap was protected by a secured cage made from 2.5cm x 2.5cm gauge mesh. These cages do not affect the trapping rates of ground-dwelling invertebrates (Oxbrough et al., 2012). In all but one grazing regime at one region, traps were set between 29/04/2013 and 04/09/2013 and were changed every 21 days, giving a total of 127 trap days. Due to restrictions in permission to sample in one of the sheep grazed regimes traps were set from 01/07/2013 and 02/09/2013 in this site, giving a total of 64 trap days. Samples from five of the traps within each location were pooled for analysis, with the sixth kept as a spare in case of trap loss.

Pitfall traps are a widely used sampling method to catch active ground dwelling invertebrates in grasslands and heathlands (Gardner et al. 1997; Haysom et al. 2004). They do not provide measures of absolute abundance, but rather a relative count based on a species’ density and activity (Greenslade 1964) and are less likely to capture species that are more sedentary. Nevertheless, their high catch rate and ease of setting up render their use appropriate in large scale studies with multiple sites (e.g. Oxbrough et al. 2012; Taboada et al. 2010). Species identification and nomenclature follows Luff (2007). Carabid beetle reference specimens are housed at the Edge Hill University Department of Biology arthropod collection.

3. Data Analysis

For vegetation, per cent cover data collected at each sampling location for the duration of the sampling period was averaged, giving a single measurement of vegetation cover from the six quadrats recorded at each location. For carabid beetles, the five traps in each sampling location were pooled across the full sampling period. To account for differences in trapping effort all samples were standardised by trap day by calculating the abundance of each species at each location and dividing it by the number of actual trap days at that location and then multiplying it by the maximum number of trap days across all locations (127), a standard method used in studies using pitfall trapping (Bergeron et al. 2013; Blanchet et al. 2012: Pinzon et al. 2013).

Statistical analyses were carried out with R statistical software (version 3.2.0.) (R Core team 2015) and EstimateS (version 9.1.0) (Colwell 2013).

To address hypothesis one species richness was calculated for vegetation across all grazing regimes using the specnumber function in the vegan package (Oksanen et al. 2015) in R. Generalised Linear Mixed Models (GLMM) were performed with Poisson errors to analyse the differences of grazing regime (cattle, sheep and ungrazed) on vegetation species richness with the glmer function of the lme4 package (Bates et al. 2015). Grazing regime was modelled as a fixed factor with region modelled as a random factor. The model was tested for over dispersion of Poisson errors and was found to be under dispersed (vegetation = 0.68). To correct for under dispersion individual level variability was included as a random variable. Results indicated that the individual level variable did not account for any variance and as such was omitted from the final model. Tukey pairwise comparisons were used to test for differences among grazing regimes, correcting p values for multiple comparisons with the Holm method using the ghlt function of the multcomp package (Hothorn et al. 2008). To determine if plant per cent cover or vegetation height were different among grazing regimes GLMMs were again performed using the method described above, to compare the proportion of cover that was grass among grazing regimes a GLMM was performed with Binomial errors and over dispersion dealt with as above (Crawley, 2012).

To address hypothesis two, differences in carabid beetle species richness were examined with raw species data (not standardised by trap day) using sample based rarefaction calculated using EstimateS, version 9.1.0 (Colwell 2013) with rarefaction curves produced in R and scaled by the number of individuals. This technique accounts for differences in sampling effort by standardising species richness for the number of individuals within a sample. Rarefaction estimates the number of species expected in a random sub-sample extracted from a larger sample (Chao 2005; Magurran 1988, 2004). Indicator species analysis (Dufrene and Legendre 1997) was used on both taxon groups to determine species that were strongly associated (both common and frequent) with each grazing regime using the indval function of the labdsv package (Roberts 2015). Indicator Species Analysis produces indicator values between 0 – 1, a value of 1 represents a perfect indicator that is always present in a particular treatment and is exclusive to that treatment (McCune et al. 2002). Significance of indicator values was assessed using a Monte Carlo randomisation procedure with 4999 iterations. Significant indicator values infer species associations with each grazing regime as a mechanism to characterise habitat use by plants and carabid beetles.

To address hypothesis three Principal Components Analysis was computed on Hellinger transformed species data using the RDA function in the vegan package in R. Region was included as a covariable and its effects removed from the community matrix with the residuals submitted to the next stage. Ordinarily this would produce a partial redundancy analysis but as the constraining variable ‘grazing’ was omitted the model produced a Principle Components Analysis for which the effects of region were partialled out. To determine differences in plant or carabid beetle species compositions between grazing types Permutational Multivariate Analysis of Variance (PERMANOVA) was used with 9999 permutations using the adonis function of the vegan package. Differences in multivariate dispersion among groups was explored using between grazing regime beta diversity results with the Anova function of the Car package (Fox and Weisberg 2011) as PERMANOVA is sensitive to these differences. Results of this are only discussed where significant.

To determine if plant species composition can be used as a tool in conservation management to indicate carabid beetle species composition, similarities in community composition between plants and carabid beetles were explored using the Procrustes rotation method (Jackson 1995: Peres-Neto and Jackson 2001) with the protest function in the vegan package. This measures concordance between two matrices by subjecting one matrix to reflection, rotation, translation and dilation in order to minimise the sum of squared residuals between observations in the original matrix and the identical observations in the target matrix (Jackson 1995). PCA axes one and two scores of both groups (plants and carabid beetles) were best fitted to find a suitable superimposition using the protest function in vegan which uses randomisation tests to assess the statistical significance of concordance between matrices (Jackson 1995). Using a correlation like statistic, comparable to Pearson correlation r2 (Peres-Neto and Jackson 2001), Protest produces a correlation value between 0 and 1, with larger values indicating better concordance. To determine if there were any differences in concordance amongst grazing regimes coordinates for both vegetation and carabid beetle points were taken from a procrustean superimposition plot and distance between points was calculated using Pythagorean Theorem and significance analysed using analysis of variance using the aov function. The relationship between plant species richness and carabid beetle species richness was also examined using Spearmen’s rho correlation using the cor.test function in the Hmisc package (Harrell 2015).

4. Results

A total of 102 plant species were recorded, (79 species of vascular plants and 22 species of bryophytes). 54.1% of total plant abundance was made up by two species; *Sesleria caerulea* (37.3%) and *Festuca ovina* (16.8%). These were the only species that individually made up more than 10% of total plant abundance. A total of 5866 individual carabid beetles from 23 species were collected. Taken across all locations two species made up 80.2% of the total abundance of individuals; *Pterostichus madidus* (69.3%) and *Pterostichus melanarius* (10.9%). A full list of species is given in the Supplementary material Table A1.

4.2 Plant and carabid beetle species diversity among grazing regimes

Plant species richness was significantly different among grazing regimes (*X*2 (2, *N* = 27) = 14.03, p<0.001) being greater in both cattle grazed and sheep grazed than ungrazed locations (z = -3.24, p<0.01; z = -3.39, p<0.01 respectively) (Fig. 2a). Total plant per cent cover was significantly different (*X*2 (2, *N* = 27) = 11.57, p<0.01) and was driven by the greater cover in cattle grazed compared to ungrazed (z = -3.38, p<0.01) (Fig. 2b). Further, the proportion of cover of grasses was significantly different among grazing regimes (*X*2 (2, *N* = 27) = 59.61, p<0.01), with greater cover in ungrazed than either cattle grazed or sheep grazed (z = 7.42, p<0.01, z = 2.40, p<0.05 respectively) and greater cover in sheep grazed than cattle grazed (z = 5.11, p<0.01) (Fig. 2c). Vegetation height was significantly different among grazing regimes (*X*2 (2, *N* = 27) = 19.62, p<0.001), with the difference greatest between cattle grazed and ungrazed (z= 4.34, p<0.01), sheep grazed and ungrazed (z = 2.48, p<0.05) and marginally significant between cattle grazed and sheep grazed (z= 1.98, p=0.05) (Fig. 2d).

For carabid beetles, rarefaction curves indicated that species richness did not differ among grazing regimes (Fig. 3), as indicated by the overlap in confidence intervals.

4.3 Plant and carabid beetle species compositions among grazing regimes

Seven plant species were strongly associated with cattle grazing, one with sheep grazing and one with ungrazed regimes (Table 2). All were patch forming and of the six vascular plants the vegetative spread of three species was creeping, two species were tussock forming and one showed no vegetative spread. Of the carabid beetle species two were strongly associated with sheep grazing (*C. violaceaus* indicator value = 0.64, p = 0.004; *Synchus vivalis* indicator value = 0.65, p = 0.004) and one associated with cattle grazing (*C. arvensis* indicator value = 0.74, p = 0.0002). The declining *C. violaceaus* (Brooks et al. 2012) had a strong association with sheep grazing, whilst the nationally scarce *Pterostichus cristatus* (1 individual) and *Pterostichus aethiops* (5 individuals) were also present in this regime, though not identified as being significantly associated with it. In addition, the only carabid beetle species associated with cattle grazing, *C. arvensis*, is in decline in Britain (Brooks et al. 2012).

There were significant differences in species composition of plants amongst grazing regimes. (F2, 24 = 2.60, p <0.001). The covariable of region accounted for 24.8% of the variability in the overall model. The first two PCA axes accounted for 41.2% of variability in the unconstrained species data (represented in the ordination biplot; Fig. 4), and cumulatively PCA axes 1-4 accounted for 57.1% of the variability in the unconstrained species data (Table 3). Cattle grazed and sheep grazed regimes display overlap along both axes whilst ungrazed regimes are separated in ordination space from cattle grazed regimes on PCA2. Further, cattle grazed and ungrazed regimes have an even spread along PCA1 with sheep grazed regimes displaying a tighter cluster. The tighter clustering of sheep grazed regimes along PCA1 reflects greater homogeneity than both cattle grazed and ungrazed regimes.

Carabid beetle species compositions also differed significantly amongst grazing regimes (F2, 24 = 2.16, p <0.001). Multivariate dispersion was also significant amongst regimes (*X*2 (2, *N* = 27) = 6.14, p<0.05) though a post hoc test revealed no differences. However, significant differences in carabid beetle species composition among grazing regimes found by PERMANOVA are supported by the PCA plot (Fig. 5) where there is overlap of sheep grazed sites and cattle grazed sites on both axes, whilst ungrazed sites are mostly separated from cattle grazed sites on PCA2. The covariable of region accounted for 36.6% of the variability in the overall model. The first two PCA axes accounted for 44.6% of variability in the unconstrained species data (represented in the ordination biplot; Fig. 5), and cumulatively PCA axes 1-4 accounted for 70% of the variability in the unconstrained species data (Table 4).

4.4 Concordance between plant and carabid beetle species compositions

There was significant concordance between species composition ordinations (Correlation in a symmetric Procrustes rotation = 0.42, p = 0.015). However, this was not sufficiently strong (>0.7) to regard vegetation as a proxy for carabid beetles (Heino 2010; Sauberer 2004). Examination of distance between coordinates revealed no significant difference amongst grazing regimes (F2, 24 = 0.345, p = 0.71) indicating that the pattern of concordance in the overall model holds true across all regimes. There was no significant correlation between plant species richness and carabid beetle species richness (rs (N= 25)= -0.08, p = 0.67).

5. Discussion

5.1 Plant and carabid beetle species diversity among grazing regimes

This study found reduced plant species richness in ungrazed locations, supporting hypothesis one that grazed locations would have greater plant species richness than ungrazed locations. This is in accord with the intermediate grazing optimisation model which suggests that plant species richness reaches a maximum at intermediate biomass as a product of optimum grazing levels (Grime 1973; Oba et al. 2001). Deviation either side of this, through increased grazing or reduced grazing, results in reduction in plant species richness as observed in ungrazed regimes in the present study. This is likely to be a result of reduced light in ungrazed regimes due to increased vegetation height and encroachment of grasses (Bakker et al. 2003; Jacquemyn et al. 2003; Jaquemyn et al. 2011). Further, reduced plant species richness may be a result of decreased germination opportunities from a reduction in gaps in the sward (Grubb 1977; Jacquemyn et al. 2003; Jaquemyn et al. 2011). In contrast, and in line with previous studies (Partel et al. 1998; Pykala 2003), plant species richness was greater in grazed regimes, whilst vegetation height was lower.

Among grazing types plant species richness did not differ between sheep grazing and cattle grazing. However, the proportion of cover of grasses was higher under sheep grazing than cattle grazing. Grant et al. (1985) found that sheep diet was more varied and contained more forbs and less grass stems than that of cattle. This may explain the increased cover of grasses in sheep grazed locations in the present study and the strong association of *Anthoxanthum odoratum*, a competitive grass that is grazed less preferentially by sheep when other more palatable grasses are available (Lopez et al. 2003) such as *Sesleria caerulea* and *Agrostis capillaris* in this case.

The results did not support hypothesis two that carabid beetle species richness would be greater in grazed compared to ungrazed regimes as a product of greater habitat heterogeneity. Instead, carabid beetle species richness did not differ among grazing regimes, despite differences in plant species richness and vegetation height between grazed and ungrazed regimes. There were, however, differences in carabid beetle abundance between grazed and ungrazed regimes, which may reflect greater breadth of resources. In contrast, similarity in species richness may be reflective of little niche differentiation among grazing regimes. Kaltas et al. (2013) found that carabid species richness was greater at intermediate rather than low intensity grazing. Indeed, increased carabid beetle richness may require greater disturbance than the low intensity grazing regimes in the present study.

5.2 Plant and carabid beetle species compositions among grazing regimes

There was a distinct difference in species composition for both taxon groups, supporting hypothesis three. Species composition of plants differed among grazing regimes (Fig. 4) as hypothesised, matching results of previous studies (Tahmasebi Kohyani et al. 2008; Veen et al. 2010). The removal of plant biomass through grazing alters competitive relationships amongst plants which drives both heterogeneity and preserves diversity (Bullock and Marriott 2000; Rook et al. 2004; Scimone et al. 2007). It is likely that differences in plant species composition among grazing regimes in the present study are a product of this altered competitive relationship. Indeed, plant species that were strongly associated with cattle grazing are all patch forming and of these, all but one of the vascular indicator species favoured method of propagation is vegetative. This enables them to colonise bare gaps left when cattle indiscriminately remove tufts of vegetation, even when seed germination is not possible as in Bullock et al. (2001).

In ungrazed regimes, the species composition of carabid beetles was distinct from those in grazed regimes, akin to the vegetation results. Differences in carabid beetle species composition among grazing regimes in the present study may be a product of different plant species compositions and vegetation height. Indeed, such small-scale vegetation differences influence available resources for carabid beetles including prey and other food, microclimate etc. (Thiele 1977).

Species that had strong associations with grazing included those from the genus *Carabus*. Under both grazing regimes tussock forming grasses were identified as associated species (*A. odoratum* and *Danthonia decumbens*) which may act as places of refuge for both *Carabus* species found to be associated with grazing here. Dennis et al. (1997) found that *C. violaceaus* was associated with short term ungrazed *Nardus stricta* grassland which had an average sward height of 8 – 12cm. However, the present study found an association of *C. violaceaus* with extensively grazed sheep calcareous grassland rather than those which had been ungrazed long term, whilst *C. arvensis* was associated with cattle grazing. Grazing produces more spatially heterogeneous vegetation (Grandchamp et al. 2005; van Wieren 1995) and associations of *Carabus* species with grazing in this study may be due to greater plant spatial heterogeneity. The removal of selected plant species during sheep grazing, or larger tufts under cattle grazing, often results in patches of shorter vegetation containing taller tufts, which are preferred conditions for many *Carabus* species (Butterfield et al. 1995; Cole et al. 2010). This may account for the greater abundance of *Carabus* species in grazed regimes (146 individuals) than in ungrazed regimes (11 individuals).

5.3 Conservation significance and management recommendations

The present study demonstrates the differing impacts of three commonly used grazing regimes in upland calcareous grassland, sheep grazing, cattle grazing and no grazing on vegetation and carabid beetles and indicates that both taxonomic groups respond differently to grazing and no grazing. Under no grazing and sheep grazing the plant species composition becomes more homogeneous, with dominance of grass. While there are no associations between any rare plant species and any particular grazing regime there are important implications for carabid beetle diversity.

Interestingly, despite the absence of forest cover in the upland landscapes studied, several carabid beetle species recorded in the present study are usually associated with forest habitats in mainland Europe e.g. *Abax parallelpipedus, P. aethiops, Harpalus latus, Stomis pumicatus*. Forests occupy 13% of the total UK land area (Forestry Commission, 2013) though this figure was as low as 5% in 1900 (Atkinson and Townsend, 2011). It has been suggested that forest carabid species have adapted to occupy dwarf shrub communities in Britain (Anderson et al. 2000). It may also be the case that such species have adapted to inhabit grasslands due to appropriate microclimatic conditions. Within the present study the calcareous grassland occurs within a matrix of upland heath and limestone pavement, the former of which has a relict woodland floor plant community, carabid communities may be influenced by these neighbouring habitats and their management should also be considered.

Species composition of plants influences structural characteristics within grasslands (Woodcock et al. 2007) which in turn influences invertebrate composition by providing refuge, food resources and suitable hunting grounds (Dennis et al. 2001; Morris 2000; Vickery et al. 2001). Woodcock et al. (2005) found a positive correlation between plant diversity and grass cover with beetle diversity. Results from the present study identify a statistical correlation between species composition of plants and carabid beetles. However, this could not be considered to be ecologically valid as the correlation coefficient was less than 0.7, the level above which one taxonomic group may be considered as an indicator of another (Heino 2010; Sauberer et al. 2004). In addition, there was no relationship between plant species richness and carabid beetle species richness, concurrent with previous studies (Finch and Löffer 2010; Jonsson and Jonsell 1998; Sauberer et al. 2004). Results for both community composition and species richness suggest that neither are appropriate indicators of carabid beetle diversity

Populations of both *C. violaceus* and *C. arvensis* have declined by 10-20% and 60-70% respectively in the past decade (Brooks et al. 2012). The association of *C. violaceaus* and the presence of the nationally scarce *P. cristatus* and *P. aethiops* with sheep grazing warrants the recommendation of continuation of this management regime. The importance of cattle grazing is also highlighted by the heterogeneous nature of the plant species composition and the association of the declining *C. arvensis*. The unique nature of the carabid beetle species composition in ungrazed regimes, including the presence of the nationally scarce *P. aethiops*, is also noted. Hence, it is recommended that conservation organisations consider a landscape scale approach to these high nature value grasslands that incorporates low intensity cattle grazing, low intensity sheep grazing and ungrazed areas as an alternative to high intensity sheep grazing.

Plant species composition and richness did not indicate change in that of carabid beetles. Further, carabid beetles did not always respond in the same way as plants to grazing regime, suggesting that conservation managers should exercise caution when using plant species composition or broad measures of plant diversity to indicate biodiversity value, identify priority habitats or select grazing regimes to support a particular habitat condition.

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**Table 1** Annual stocking intensities and duration of grazing for each grazing regime within each region.

**Table 2** Vascular plant and bryophyte species associated with grazing regime. Indicator Species Analysis produces an Indicator Value between 0 – 1, with values closest to 1 signifying a perfect indictor (always present in a particular treatment and exclusive to that treatment). P values signify significance of Indicator Values for each species based on Monte Carlo randomisation procedure with 4999 iterations. Selected vascular plant traits were gathered from Peat, Fitter and Ford (2015).

**Table 3** Summary of plant species PCA results. Eigenvalues and their contribution to total variance is after the removal of the conditioning variable ‘region’. Total Variance\* is after removal of the conditioning variable ‘region’.

**Table 4** Summary of carabid beetle species PCA results. Eigenvalues and their contribution to total variance is after the removal of the conditioning variable ‘region’. Total Variance\* is after removal of the conditioning variable ‘region’.

**Fig 1** Map displaying the location of the three sample regions within mainland Britain. The highlighted box displays the sample sites within one sample region. Sample site locations within the two other regions are comparable to the one highlighted here. Grazing types are identified as triangles = cattle, squares = sheep, circles = ungrazed.

**Fig 2** Boxplot of (a) plant species richness, (b) total plant per cent cover, (c) per cent cover of grass and (d) vegetation height among grazing regimes. The letters indicate significance of post hoc Tukey test, where letters are the same this indicates no significant difference.

**Fig 3** Sample based rarefaction curves scaled by the number of individuals, indicating carabid beetle species richness. U=ungrazed, S=sheep grazed and C=cattle grazed. Grey bars indicate 95% confidence intervals

**Fig 4** Principle Components Analysis of vegetation species data with the effects of location partialled out. Indicator species with significance of <0.05 are displayed as weighted species scores. Circles are ungrazed, triangles are cattle grazed and squares are sheep grazed. Numbers represent indicator species as follows: 1 – *Betonica officinalis*, 2 – *Carex panicea*, 3 – *Carex flacca*, 4 – *Danthonia decumbens*, 5 – *Anthoxanthum odoratum*, 6 – *Thymus polytrichus*, 7 – *Pseudoscleropodium purum*, 8 – *Dicranum scoparium*, 9 – *Racomitrium lanuginosum*

**Fig 5** Principle Components Analysis of carabid beetle species data with the effects of geographical location partialled out. Indicator species with significance of <0.05 are displayed as weighted species scores. Circles are ungrazed, triangles are cattle grazed and squares are sheep grazed. Numbers represent indicator species as follows: 1 – *Carabus arvensis*, 2 – *Synchus vivlais*, 3 – *Carabus violaceus*