




Grazing impacts on ground beetle (Coleoptera: Carabidae) abundance and diversity on semi-natural grassland

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Abstract. 1. Semi-natural grasslands are commonly managed as a grazing resource for domestic livestock but, due to their unique biodiversity, they are also of conservation interest. Numerous drivers have impacted on the status of these grasslands in recent decades, most importantly changing grazing management strategies. These changes have the potential to affect the biodiversity associated with these habitats, including on some rich invertebrate assemblages. Responses, however, are often dissimilar between different invertebrate taxa.

2. We investigated the responses of ground beetles to different grazing regimes within a replicated, controlled, long-term grazing experiment on upland semi-natural grassland in Scotland.

3. Although there was substantial overlap of species composition of ground beetle assemblages in different grazing treatments, species richness, abundance and Shannon diversity of ground beetles were significantly lower in ungrazed plots than in plots subject to high- or low-intensity sheep grazing. Ground beetle abundance (but not species richness or diversity) was lower in ungrazed plots compared to those with low-intensity mixed grazing by sheep and cattle. However, no differences were identified in abundance, species richness or diversity between the three grazed treatments.

4. Our results suggest that ground beetles may show different responses to grazing compared to responses of some other invertebrate groups and demonstrate the difficulty of attempting to manage grazing to optimise conditions for a wide range of invertebrates.

Key words. Carabid assemblages, grazing pressure, livestock, sustainable habitat management, upland grassland.

Introduction

Semi-natural grasslands are valued for their unique biodiversity (WallisDeVries *et al.*, 2002) and are recognised as being important carbon stores (Conant *et al.*, 2017). The condition and extent of these grasslands, which have not suffered deleterious effects of fertiliser or herbicide application, varies with geographic location and factors such as elevation. However, semi-natural grasslands from across their range are under threat

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(Oakleaf *et al.*, 2015; Ridding *et al.*, 2015), with drivers of change including altered livestock grazing, land use changes (Török *et al.*, 2016), biological invasions, and wildfires (Coates *et al.*, 2016).

Among semi-natural grasslands that have a long-term history of grazing by domestic herbivores, the condition of upland grassland areas has gained considerable attention in recent decades (McGovern *et al.*, 2011; Evans *et al.*, 2015). In Europe, for example, recent changes in agricultural policy have driven substantial shifts in the way that semi-natural upland habitats are managed. In some areas, such as in the United Kingdom, this has manifested in the number of grazing livestock declining markedly since the start of the twentieth century and many areas

that were formerly grazed now have no grazing by domestic herbivores (Martin *et al.*, 2013). Resultant changes in vegetation structure and composition may be slow to become apparent in these low-productivity systems (Pakeman *et al.*, 2019; Pakeman & Fielding, 2020) and may vary with livestock type (Tóth *et al.*, 2018) but evidence is gradually emerging that such land-use changes are having a marked impact on a range of biodiversity, including birds (Evans *et al.*, 2015) and invertebrates (Dennis *et al.*, 2007). The extent of such impacts, however, varies widely among different invertebrate groups (García *et al.*, 2009; Bonari *et al.*, 2017).

Ground beetles (Coleoptera: Carabidae) populations have suffered large-scale declines in the United Kingdom over recent decades (Brooks *et al.*, 2012; Pozsgai & Littlewood, 2014) and there is evidence of increased homogeneity of assemblages (Pozsgai *et al.*, 2015) at systematically monitored sites. The causes of these declines are not well understood. Some declines may be linked to agricultural intensification, including, for example, improvement of grassland for grazing animals (Luff *et al.*, 1989). Evidence of detrimental effects of climate change is also growing. For example, changing phenologies of some ground beetle species have been linked with climate change (Pozsgai & Littlewood, 2011, 2014; Pozsgai *et al.*, 2018) and changes in upland ground beetle assemblages and an increased prevalence of generalist species have been linked to decreasing maximum temperatures and increasing rainfall (Pozsgai *et al.*, 2015).

The extent to which differences in grazing management may impact on ground beetle abundances and assemblages has been studied in upland heathland (Gardner *et al.*, 1997) and in upland calcareous grassland (Lyons *et al.*, 2017) but rather less so in acidic grasslands that dominate much of the upland vegetation in the United Kingdom (though see Cole *et al.*, 2006). There is some evidence from acid grasslands elsewhere that ground beetle abundance and, especially, species richness may be reduced by relaxation or cessation of grazing (Grandchamp *et al.*, 2005). However, such trends may be site and context specific with, for example, Twardowski *et al.* (2017) reporting more ground beetles in sites that were less intensively grazed.

Ground beetles in their adult stage are among the more abundant ground-dwelling arthropods and have important functional roles to play in grasslands as predators of smaller invertebrates (Lövei & Sunderland, 1996) in addition to being prey items themselves, including for upland birds (Buchanan *et al.*, 2006). Given the reported declines in ground beetle abundances and ongoing changes in upland management, it is desirable to understand what forms of management may best support populations. To investigate the influence of the intensity of one aspect of management, livestock grazing, on ground beetle assemblages of semi-natural upland acidic grassland, we sampled ground beetles within a replicated, controlled, long-term grazing experiment. In particular, as reduced grazing leads to increased structural complexity of the vegetation (e.g., a higher density of grassy tussocks per plot with reduced grazing; Smith *et al.*, 2014), we considered that this may impede ground beetle foraging ability. To test this, we hypothesised that:

- 1 ground beetle abundance (as measured by activity density) is positively correlated with grazing intensity;

- 2 ground beetle species richness is positively correlated with grazing intensity; and
- 3 ground beetle diversity is positively correlated with grazing intensity.

Furthermore, we assessed whether or not any such differences that we identified between grazing treatments resulted in differences in the overall ground beetle assemblage structure.

Methods

Field site

Sampling was carried out on the estate of Glen Finglas, in Perthshire, Scotland (56°16'N, 4°24'W). This estate is owned and managed by a conservation charity, the Woodland Trust, with a long-term aim of restoring a semi-natural woodland/grassland mosaic (see: www.woodlandtrust.org.uk/visiting-woods/woods/glen-finglas). It extends to 4085 ha in area. Most of the estate, including the study plots, remains open ground, dominated by acid grassland and mire. The most represented National Vegetation Classification (NVC) communities (Rodwell, 1991, 1992) in the study plots were M23 (*Juncus effusus*–*Galium palustre* rush-pasture), M25 (*Molinia caerulea*–*Potentilla erecta* mire), U4 (*Festuca ovina*–*Agrostis capillaris*–*Galium saxatile* grassland) and U5 (*Nardus stricta*–*G. saxatile* grassland). Some areas were covered by bracken (*Pteridium aquilinum*, NVC U20). Sample sites ranged in elevation from approximately 200 to 500 m. Treatment effects on vegetation within this experiment were investigated in detail by Pakeman *et al.* (2019) and Pakeman and Fielding (2020).

Treatments

Six replicate blocks (labelled A–F) of four grazing treatment plots were established in 2003. Each plot measured 3.3 ha. Plots were located at three sites, each containing two replicate blocks of each treatment (a total of eight plots in each of three sites). Blocks were arranged across a hillside such that plots within a block generally covered similar elevational ranges and had similar aspect. The sites were each separated by approximately 5 km. The grazing treatments were high-intensity sheep grazing, with nine sheep per plot (treatment I), low-intensity sheep grazing with three sheep per plot (treatment II), low-intensity mixed grazing with two sheep per plot and, for 4 weeks in August/September, two cows per plot, each with a suckling calf (treatment III) and ungrazed by domestic herbivores (treatment IV). These treatments approximated to historic management up to around 1996 (treatment I), grazing management that prevailed when the plots were established (treatment II), and alternative conservation-focussed mixed grazing regime (treatment III) and grazing abandonment, as had increased in the Scottish Highlands since around 2001 (treatment IV). Sheep were removed from plots during severe weather over winter and for routine farming practices, such as shearing. Grazing treatments were assigned randomly at the outset across the four plots for each block (Fig. 1). Hereafter, treatments are generally referred to as

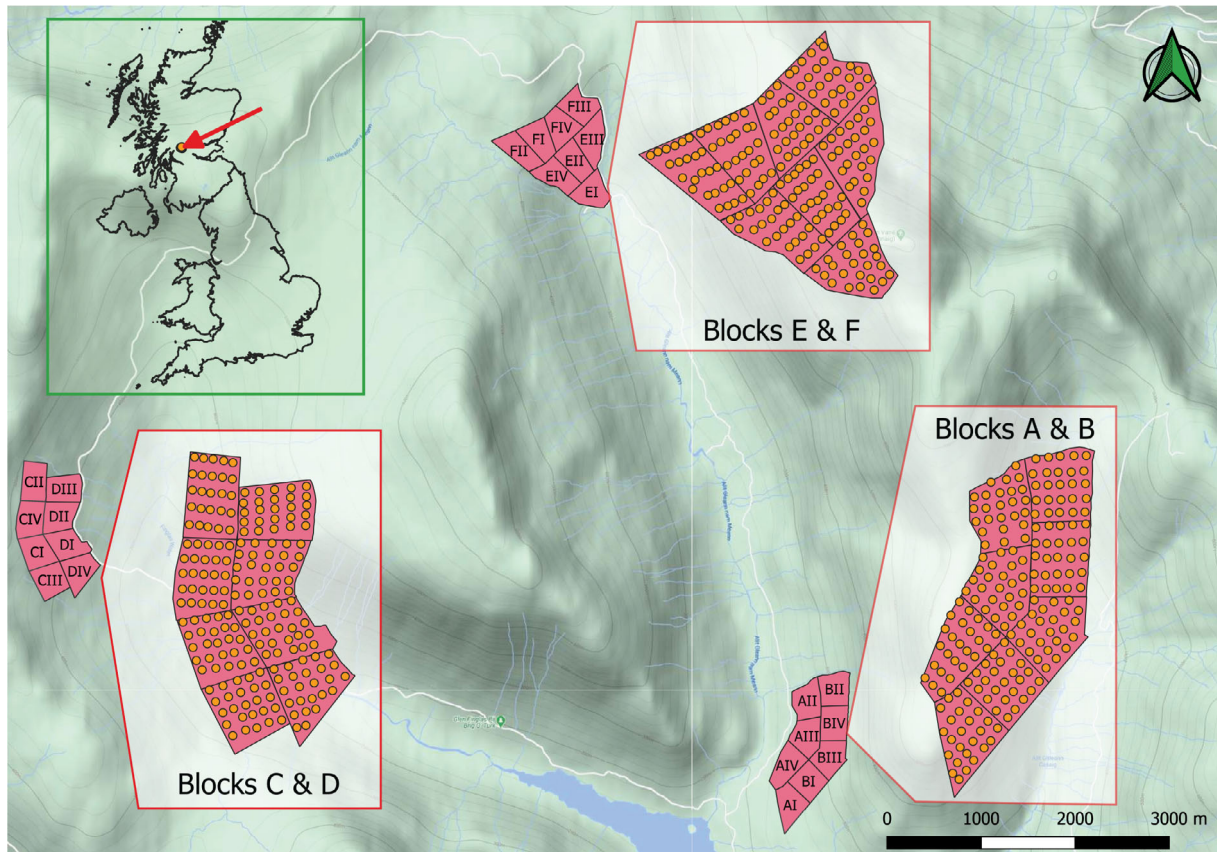


Fig 1. Location of sampling points at Glen Finglas, Scotland. The overview map in the top-left corner shows the location within the United Kingdom, the main map shows the arrangement of sample blocks within the glen and the larger scale maps show the arrangement of sample points within these blocks. From the 25 points, 5 were randomly selected each year in each plot for pitfall trap placement. Capital letters indicate the replicates, while grazing treatments are shown by numerals I, II, III, and IV referring to high-intensity sheep grazing, low-intensity sheep grazing, low-intensity mixed cattle and sheep grazing, and no grazing, respectively.

high sheep (TI), low sheep (TII), low mixed (TIII) and ungrazed (TIV).

Ground beetle sampling

Sampling was carried out from 2009 to 2013. Five points were randomly assigned from a pre-established grid of 25 sampling points (minimum 7.2 m from the plot edge) within each of the 24 plots. A new selection of five points per plot was made each year, to minimise potential bias from trap placement in these heterogeneous plots. In all cases, the minimum distance between two traps exceeded 20 m (range: 20.6–265.6 m, median: 93.4 m). Although dispersal distances for carabids can be large, movements for foraging do not normally exceed 15 m (Wallin & Ekblom, 1988; Riecken & Raths, 1996; Charrier *et al.*, 1997; Holland *et al.*, 2004), and thus our traps are likely to represent independent catches. A 500-ml cup, with a diameter of 8 cm, was used as a pitfall trap (Hohbein & Conway, 2018) and was placed within 1 m of each selected sample point. Each cup was part-filled with ethylene-glycol that served as a preservative.

Wire netting, with a mesh size of 2 cm, was attached over the top of each trap to minimise capture of small vertebrates and to deter interference by sheep and a wire mesh dome was placed in each cup to aid escape of any vertebrates that did fall in the trap. Traps were set in May each year and were emptied and reset at approximately 3-week intervals through to September each year. Trap contents were stored in a freezer until sorting and identification in the laboratory. Subsequently, they were transferred to 70% ethanol and stored at the James Hutton Institute, Aberdeen, UK. Specimens were identified to species by reference primarily to Lindroth (1985, 1986) and Luff (2007). Species taxonomy follows Luff (2007).

Data analysis

The mean number of each ground beetle species captured was calculated across sampling dates within a year, resulting in a data matrix showing sampling point/year/treatment/block in rows and species in columns. Frequent flooding events precluded calculations of standard trap-days but yearly mean catches were used to

address this issue. Although, in theory, this could reduce the robustness of the study, our models including floodedness as a random variable did not show significant differences from those presented here. A simulation-based sensitivity analysis on the effect of flooded pitfall traps (Supplementary Material S1) further confirmed the low influence of flooding events.

Commonly used diversity measures, namely abundance and species richness per trap, and Shannon-Wiener diversity were calculated and used as response variables. Since residuals, even after transformation, were not normally distributed and neither were variances homogenous, we fitted robust linear mixed models (Koller, 2016). Treatments and sampling years were included as fixed effects and blocks/treatment (sampling plot) as random effects. The inclusion of plots among random effects addresses the potential effect of within-plot pseudoreplication. Huber function was used for fitting the model with a $k = 2.18$ tuning parameter. P -values were calculated from the degrees of freedom estimations in fitted non-robust linear mixed models using Satterthwaite's method. Model fit was tested using graphical methods. Pairwise comparisons were made by estimating marginal means using the `emmeans()` function in the `emmeans` R package (Lenth, 2021), with P -values adjusted according to the Benjamini and Hochberg (1995) procedure.

To fully address the potential effects of the reduced catch in the flooded traps we estimated sampling coverage from abundances (Roswell *et al.*, 2021) using the `iNEXT` R package

(Hsieh *et al.*, 2020), and compared the extrapolated Hill numbers ($q = 0$ as species richness and $q = 1$ as the exponential of the Shannon-Wiener diversity) between treatments.

Carabid numbers were summarised for each plot and non-metric multidimensional scaling was used on a Bray–Curtis distance matrix to show the similarities of species composition among treatments and to visualise multivariate patterns in two dimensions. Permutational multivariate analysis of variance using distance matrices (ADONIS), implemented in the `vegan` R package (Oksanen *et al.*, 2010), was used to detect the main drivers of ground beetle assemblage composition, with treatment as a fixed variable and sampling block and sampling year as grouping factors. P -values were calculated through a permutation process with 999 iterations. Species that were the most important in discriminating between treatments were selected using similarity percentages (Clarke, 1993) with the help of the `siprer()` function in the `vegan` package. Indicator value analysis, `IndVal` (Dufrene & Legendre, 1997; De Cáceres & Legendre, 2009; De Cáceres *et al.*, 2010), was used to investigate whether any specific species were strongly associated with particular treatments, experimental blocks or years. Prior to the multivariate analysis, counts of ground beetles were transformed using Hellinger's method as suggested by O'Hara and Kotze (2010).

The impact of grazing pressure on the activity-density of the seven most common ground beetle species was analysed using linear mixed-effect models, where grazing treatment and

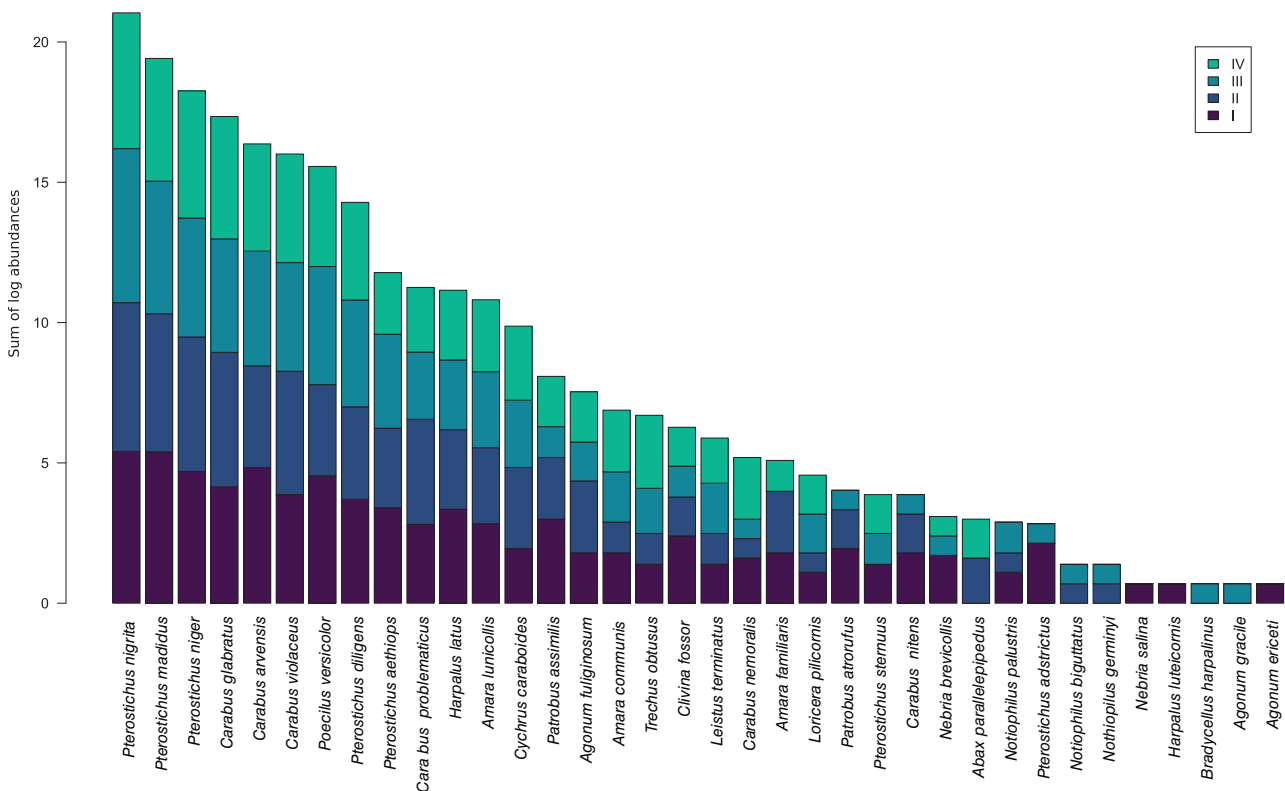


Fig 2. Ground beetle species recorded at Glen Finglas, 2009–2013, showing log abundance in each grazing treatment. Since log abundances are calculated for each treatment separately, Y-axis values show the sum of log abundances. Grazing treatments are shown by numerals I, II, III, and IV, referring to high-intensity sheep grazing, low-intensity sheep grazing, low-intensity mixed cattle and sheep grazing, and no grazing, respectively.

sampling year were considered as fixed, and treatment/sampling block as random effects. Sampling year was considered as a fixed effect because climate change (Pozsgai *et al.*, 2015) and altered land use (York, 2000; Déry *et al.*, 2011) can cause a directional shift in insect assemblage composition over time. Thus, temporal trends in the abundance of species in our samples were also expected. Moreover, these abundance trends could also be of ecological interest (e.g., common species declining with less common, habitat specialists, increasing) which further supports the inclusion of sampling year among the fixed effects. Tukey HSK correction was used to adjust *P*-values when multiple comparisons were made.

All analyses were carried out with the R statistical software (R Core Team, 2012), using the nlme (Pinheiro *et al.*, 2017) packages.

Results

Thirty-six species of ground beetle were recorded (Fig. 2), comprising 5120 individual ground beetles. See Supplementary Material S2 for details of species and their conservation statuses. The most frequently caught species were *Pterostichus nigrita* (1,217 individuals; 24% of the total number of ground beetles caught), *Pterostichus madidus* (1050 individuals; 21%) and *Pterostichus niger* (545 individuals; 11%). Thirteen species were represented by fewer than 10 individuals each. The median number of beetles caught per trap per collection was relatively low, at 5.00 ± 7.00 (median \pm IQR, range: 0.3–438.5).

Ground beetle abundance and diversity

Species richness, mean abundance and Shannon diversity were significantly lower in the ungrazed plots (treatment IV)

than in high-intensity sheep-grazed plots (treatment I) and low-intensity sheep-grazed plots (treatment II). All three measures were greater in high sheep (TI) than in the low-intensity mixed plots (treatment III) and mean abundance was significantly higher in low mixed (TIII) than in ungrazed (TIV) (Fig. 3; Supplementary Material S3). There were no significant overall temporal trends in mean abundances and species richness but some individual plots showed signs of decline in species richness (Supplementary Material S4).

All treatments had a high observed coverage (TI, TII, TIII, TIV: 0.998, 0.996, 0.993, 0.999, respectively) and yearly catches in each treatment also showed high coverage (Supplementary Material S5). At a 0.993 coverage level, the 95% confidence intervals did not overlap between T1 and T4 and between TIII and TIV for either Hill number $q = 0$ (estimated species number) or Hill number $q = 1$ (exponential of the Shannon-Wiener diversity). Additionally, confidence intervals of Hill number $q = 1$ did not overlap between TIV and TII (Supplementary Material S5).

Ground beetle assemblages

Multidimensional scaling showed that there was a large overlap between ground beetle assemblages in the four grazing treatments (Fig. 4). The ADONIS model, however, demonstrated a significant treatment effect, along with significant effects from sampling year, sampling block, and the combination of these (Table 1). The ADONIS model explained 36.3% of the total variance, of which the most important was the block effect (7.4%). Only a small proportion of variance, 2.3%, was explained purely by the treatment effect. Pairwise ADONIS showed a significant difference in assemblages between high sheep (TI) and ungrazed (TIV) plots ($F = 3.98$, $R^2 = 0.064$, adjusted *P*-value = 0.006)

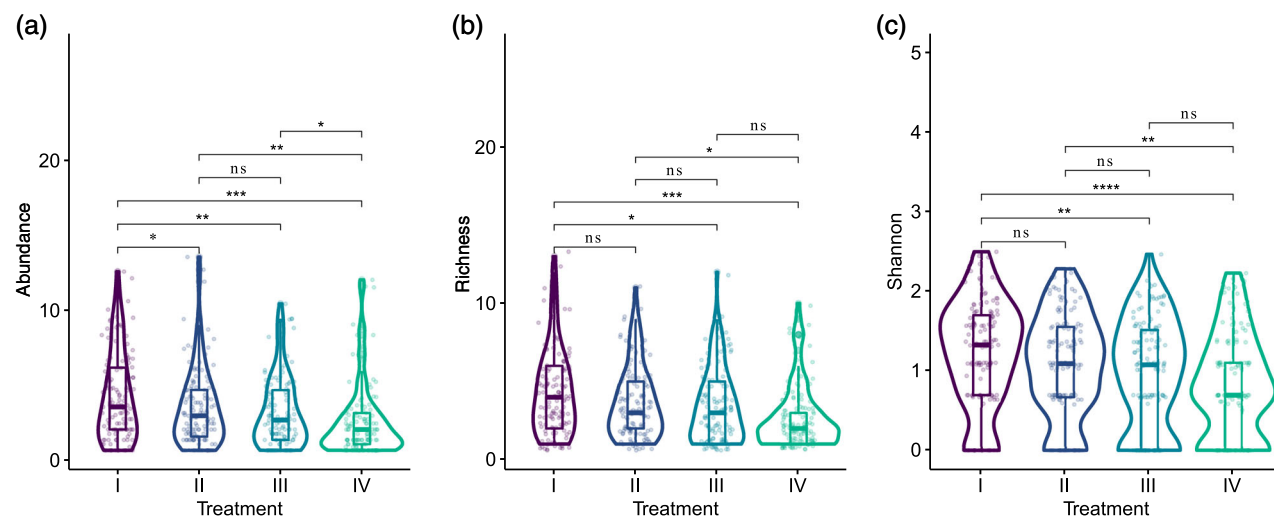


Fig 3. The effect of grazing treatments on ground beetle diversities. Violin plots show probability densities of (a) log-transformed abundance, (b) species richness, and (c) Shannon diversity. Boxplots inside violins represent the distribution of measured data and show the median, and the lower and upper quartiles. Individual data points are also displayed. Results of pairwise comparisons are indicated on the top of the lines connecting violins. Grazing treatments are shown by numerals I, II, III, and IV referring to high-intensity sheep grazing, low-intensity sheep grazing, low-intensity mixed cattle and sheep grazing, and no grazing, respectively. Adjusted *P*-values are indicated as * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant ($P > 0.05$).

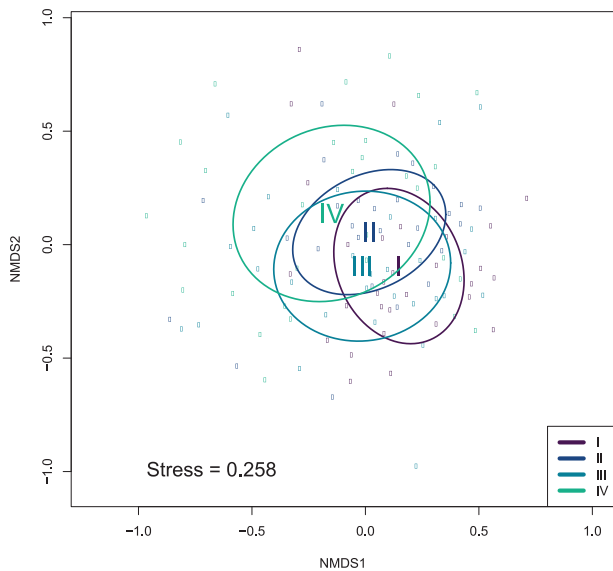


Fig 4. Multidimensional scaling of ground beetle samples from Glen Finglas numerals I, II, III, and IV show grazing treatments (high-intensity sheep grazing, low-intensity sheep grazing, low-intensity mixed cattle and sheep grazing, and no grazing, respectively) and are positioned precisely centrally relative to the ellipse for that treatment. Ellipses indicate areas within which 95% of the site points belonging to one treatment are located.

Table 1. The effects of treatment, sampling block, and sampling year on carabid assemblages. The results of the permutational multivariate analysis of variance using distance matrices (ADONIS) on species assemblage distance matrix. d.f., degrees of freedom; SS, sum of squares.

	d.f.	SS	F-value	P-value
Treatment	3	1.002	2.946	0.001
Year	4	1.029	2.271	0.001
Block	5	4.062	7.168	0.001
Treatment × year	12	1.428	1.050	0.377
Treatment × year	15	2.611	1.536	0.004
Residual	78	8.840		

but none of the other treatments were significantly different in pairwise comparison.

Although ADONIS indicated a significant effect of sampling year, no temporal trends were apparent in the assemblages overall (Supplementary Material S6). Data suggested, though, that

assemblages in low sheep (TII), low mixed (TIII) and ungrazed (TIV) plots were changing over time in some treatment blocks (Supplementary Material S4). In particular the ecological distance (measured as the Bray–Curtis distance between abundance-based community matrices) between samples increased over the years within treatment block B, and also ungrazed (TIV) plots of block A and in low mixed (TIII) plots of block F. The ecological distance between high sheep (TI) and ungrazed (TIV) plots showed an increase only in block E. Similarity percentage analysis indicated that the two most important species in shaping differences in ground beetle assemblages between treatments were *P. nigrita* and *P. madidus*. Further species played important roles in shaping differences between assemblages, notably *P. niger* [in differences between high sheep (TI) and low sheep (TII) plots and between high sheep (TI) and ungrazed (TIV) plots], *Carabus arvensis* [differences between high sheep (TI) and low mixed (TIII) plots] and *Carabus glabratus* [differences between low sheep (TII) and low mixed (TIII) plots, between low sheep (TII) and ungrazed (TIV) plots and between low mixed (TIII) and ungrazed (TIV) plots] (Supplementary Material S7).

Common, habitat generalist species dominated all treatments. Among the species that are commonly associated with wet peatlands (e.g., *Agonum ericeti*, *Patrobus atrorufus*, *Trechus obtusus*; Blake *et al.*, 2003) only a few that are also tolerant of drier soils, such as *T. obtusus* (Eyre *et al.*, 1989) were found in ungrazed (TIV) plots and, indeed, IndVal analysis pinpointed this species as being associated with ungrazed (TIV) plots (IndVal $g = 0.231$, $P = 0.012$). In contrast, *Pterostichus adstrictus* (IndVal $g = 0.224$, $P = 0.001$) was typically found in high sheep (TI) plots. In both cases, this was based on a relatively low overall number of individuals (23 for *T. obtusus* and 11 for *P. adstrictus*). No other species were identified by this analysis as being significantly associated with any single grazing treatment (Table 2).

The linear mixed-effect models fitted for mean abundances of the eight most commonly caught species showed a significant treatment effect only for *C. arvensis* ($P = 0.042$). Sampling year caused a significant difference in abundance between treatments for *P. nigrita* ($P = 0.002$), *C. arvensis* ($P = 0.048$) and *Pterostichus diligens* ($P = 0.001$). Differences, however, were not significant for *C. arvensis*, when years were pairwise compared and the Tukey HSK correction was applied (Supplementary Material S8).

Discussion

Overall, there was substantial overlap between ground beetle assemblages in different grazing treatments. We did find that

Table 2. Indicator values and bootstrapped p-values of ground beetle species with high fidelity to treatments or treatment groups.

Group	Species	IndVal G	P-value
Treatment I	<i>Pterostichus adstrictus</i>	0.224	0.001
Treatment IV	<i>Trechus obtusus</i>	0.231	0.012
Treatment I + II	<i>Carabus problematicus</i>	0.351	0.037
	<i>Patrobus assimilis</i>	0.265	0.006
Treatment I + III	<i>Poecilus versicolor</i>	0.444	0.002
Treatment I + II + III	<i>Pterostichus aethiops</i>	0.382	0.004

there were significant differences between treatments, though these were small, with treatment explaining just a small portion of the variance in the complete dataset. Nonetheless, in partial support of our three hypothesis, our results also showed that there were fewer ground beetles caught, fewer species recorded and lower diversity in ungrazed (TIV) plots than in high sheep (TI) and low sheep (TII) plots and that fewer were caught in ungrazed (TIV) than in low mixed (TIII plots). However, no differences were identified in abundance, species richness or diversity between the three grazed treatments.

Grazing impact on ground beetle abundance

The finding that ground beetles were caught in lower overall numbers in ungrazed (TIV) plots give some support to our first hypothesis and is broadly consistent with results from several other studies from a variety of grassland habitats. For example, ground beetle abundance was higher in grazed compared to ungrazed sites in three different dune grassland types in the Netherland (Nijssen *et al.*, 2001). Similarly, Pétilon *et al.* (2007) reported higher ground beetle abundance (and species richness) in areas of saltmarsh in France that were subject to sheep grazing and grass cutting than in non-grazed and uncut areas, and this trend was driven by typical grassland species. In a study in Lapland, ground beetles were more numerous on plots grazed by reindeer *Rangifer tarandus* than on ungrazed plots but their numbers peaked under intermediate grazing levels (Suominen *et al.*, 2003), suggesting that there may be an optimum level of grazing at which ground beetle abundance is maximised.

This effect of grazing may be replicated by other forms of vegetation removal. For example, Gimingham (1985) showed that ground beetles were most abundant in the pioneer (youngest) stage of growth of the dwarf shrub, *Calluna vulgaris* (under a rotational burning regime), when vegetation complexity was at its lowest. In parallel, Sanderson *et al.* (2020) found more ground beetles in areas of *C. vulgaris* that were mechanically cut between one and 7 years previously compared to areas cut 8 or more years previously. Although dwarf shrubs were not dominant in our study plots, these results are consistent with our finding that ground beetle activity density was lower in the ungrazed (TIV) plots, which had the tallest vegetation with the greatest biomass (Evans *et al.*, 2015) and most extensive areas of dense grassy tussocks (Smith *et al.*, 2014), than in the grazed treatments. This observation may be at least partly driven by the two species that occurred in the highest numbers in our study, namely *P. nigrita* and *P. madidus*. These have previously been shown to display trends of decreasing abundance with increasing vegetation height (Dennis *et al.*, 1997). Thus, the response of these common species may drive the higher overall abundances in plots that were grazed, and thus had shorter vegetation (Pakeman *et al.*, 2019), than in the ungrazed plots.

Assessments of ground beetle abundance using pitfall traps can lead to bias in that more mobile species are more likely to encounter, and be caught by, the traps (Brown & Matthews, 2016) while captures may also be biased by ground beetle body size (Hancock & Legg, 2012), perhaps due to correlation between size and mobility. Thus, the results represent 'activity density' rather

than indices of absolute abundance. If mobility is reduced in denser vegetation, this might cause an apparent reduction in the number of individuals caught in our ungrazed treatment and an apparent increase in those in the highest grazing intensity treatment. Such an effect has been previously observed in an experimental set-up when there was no evidence of differences in absolute ground beetle density between areas of different vegetation structure (Thomas *et al.*, 2006). Other studies based on pitfall trap data have similarly found lower activity density in areas of denser vegetation (Cole *et al.*, 2008). However, as activity density cannot be directly translated into abundance, we are unable to demonstrate whether such a difference represents an actual abundance difference. Nonetheless our samples were taken using a sufficiently large trap and over sufficient timescales to meet requirements recommended by Jung *et al.* (2019) for promoting reliability of pitfall trapping programmes.

Grazing impact on ground beetle species richness

Similarly to abundance, and in partial support of our second hypothesis, ground beetle species richness was lower in ungrazed (TIV) plots than in high sheep (TI) and low sheep (TII) plots though there was no significant difference between ungrazed (TIV) and low mixed (TIII) plots. There was, however, a slight difference in the findings between the linear mixed models and the comparison of estimated species richnesses (Hill number $q = 0$): the overlap of the 95% confidence intervals indicated no difference between ungrazed (TIV) and low sheep (TII), whereas between ungrazed (TIV) and low mixed (TIII) non-overlapping confidence intervals indicated a difference. This difference between methods highlights that communities may not be easily ordered based on simple diversity indices (Tóthmérész, 1995). Yet, our results are at least partially consistent with several other studies that have shown ground beetle species richness to be enhanced by grazing. For example, in montane meadows in Switzerland, increased density of cattle grazing was associated with increased ground beetle species richness (Grandchamp *et al.*, 2005) and, in Sweden, species richness was positively (albeit weakly) associated with increased cattle grazing intensity (Söderström *et al.*, 2001). However, some studies have found no significant relationship, including on semi-natural grasslands in Hungary, where ground beetle species richness was not affected by grazing intensity of cattle (Batáry *et al.*, 2007) and similar lacks of significant impact were reported from British Columbia, Canada (Bassett & Fraser, 2015) and from calcareous grassland in the United Kingdom (Lyons *et al.*, 2017). Opposite findings to ours include ground beetle species richness being reduced on heather moorland sites in Scotland that were most heavily grazed by deer and sheep (Gardner *et al.*, 1997) and a reduction in species richness associated with vegetation removal (through mowing) on salt meadow sites in Hungary (Torma *et al.*, 2019). It is possible in this latter case that the highest intensity sheep-grazing treatment was higher, in terms of the quantity of forage that remained after grazing, than in our high-intensity sheep-grazing treatment and that more discrimination between treatments may have been apparent had we used a higher sheep stocking rate.

Grazing impact on ground beetle diversity

Like species richness, ground beetle diversity was lower in ungrazed (TIV) plots than in high sheep (TI) and low sheep (TII) plots though did not differ between ungrazed (TIV) and low mixed (TIII) plots. The non-overlapping confidence intervals of the estimated exponential of the Shannon-Wiener (Hill number $q = 1$) between low mixed (TIII) and ungrazed (TIV), however, do suggest some difference. Again, this provides a degree of support for our third hypothesis. Few studies have reported on ground beetle diversity responses to grazing intensity. However, metrics of ground beetle diversity may be positively correlated with vegetation removal and may thus be analogous to our study. Grandchamp *et al.* (2005), for example, found that intensive management of grasslands (through mowing and fertilisation in addition to grazing) helped to maintain ground beetle assemblages with higher diversity than of those in grasslands managed at a lower intensity. Similarly, rotational burning, which reduces biomass of the dwarf shrub, *C. vulgaris*, may enhance ground beetle diversity (Gardner *et al.*, 1991).

Grazing impact on ground beetle assemblage structure

Although, as discussed above, variation in species mobility may affect ground beetle captures, we utilised a substantial number of traps set across an extensive experimental site. This was on a scale reported to be sufficient to accurately sample the assemblage that was present (Lövei & Magura, 2011). This is further evidenced by the ground beetle assemblages at our site being broadly similar in the different treatments. Additionally, the fact that Simper analysis indicated that the most abundant species were responsible for the significant differences that we did identify between assemblages suggests that those differences were more quantitative rather than qualitative. Previously, work has documented distinct ground beetle assemblages associated with upland environments in the United Kingdom (Luff *et al.*, 1992) and shown that these differ between different upland habitats (Butterfield & Coulson, 1983). In particular, ground beetle assemblages have been shown to be substantially shaped by environmental conditions, including both vegetation structure and soil conditions (Luff *et al.*, 1989, 1992). In comparable habitat to that in our study, Cole *et al.* (2006) found that large flightless *Carabus* species favoured an extensive grazing regime over an intensive one. However, other research has failed to find species that are indicators of different management treatments within habitat mosaics (Pravia *et al.*, 2019). This is in line with our own findings in which we did not identify species or assemblages that were particularly associated with different intensities of grazing at our site, including no evidence that some species preferred the less intensively grazed plots that might equate to a more extensive grazing regime.

Inconsistent responses to grazing that are apparent among ground beetle assemblages (García *et al.*, 2009; Lengyel *et al.*, 2016; Bonari *et al.*, 2017) suggest that this group may not be suitable as an indicator taxon for grassland management, including in restoration projects. Lengyel *et al.* (2016), in their multi-taxon study, pointed out clear differences in the ways that a range of organism groups respond to vegetation diversity and structure. Some may more consistently show directional responses

to treatment. For example, plant communities appear to be positively affected by grazing (Török *et al.*, 2014). For ground beetles, although Koivula (2011) showed that European ground beetles may reflect management, the requirement for further research into the usefulness of these responses for conservation purposes was stressed and our own results suggest that their use as indicators may be limited, at least within the system that we studied.

Implications for upland grassland management

Previous studies, based on sampling within the same long-term experiment as this work, have shown a range of responses of invertebrate faunal groups to the four grazing treatments. Foliar invertebrates as a whole have been shown to respond positively to relaxation of grazing levels and cessation of grazing, over the first 3 years following the application of grazing treatments (Dennis *et al.*, 2007). Studies of both moths (Littlewood, 2008) and Auchenorrhyncha (Littlewood *et al.*, 2012), sampled 5 years on from the initiation of grazing treatments, likewise showed trends to greater abundance and species richness in less grazed compared to more grazed plots. In both cases, abundance and species richness were significantly higher in the ungrazed (TIV) plots compared with the high sheep (TI) plots. Overall arthropod abundance, measured at intervals over the first 9 years of the experiment, was also negatively related to grazing intensity (Evans *et al.*, 2015). Our results show only small differences between treatments but those that were identified contrasted with these previous results by showing the lowest abundance and species richness in ungrazed plots. This might suggest that while potential prey items for carabids may be more abundant with reduction in grazing pressures, ground beetles are not able to fully exploit this increased resource availability, perhaps due to those prey being less accessible in the denser vegetation. This demonstrates how environmental factors act quite differently compared to other taxa in shaping occurrences within this largely carnivorous group and indicates that management for a multi-taxon benefit may be difficult to achieve on sites under a single uniform management regime (Kruess & Tscharntke, 2002).

Multi-species livestock farming has been shown to benefit biodiversity (Martin *et al.*, 2020), and also to promote ecosystem multifunctionality (Wang *et al.*, 2019). Our results on carabid assemblages, however, were not supportive to these studies; abundances, species richnesses, as well as Shannon diversities were lower in plots grazed by a mix of cattle and sheep than in those with high-intensity sheep grazing and showed no difference from other treatments. Whereas these results highlight that optimising upland grazing for multi-taxon benefits with mixed-species grazing is unlikely to equally favour all species, knowing which taxa are 'winners' or 'losers' is essential for successfully managing diverse grasslands.

Conclusions

In this study, we demonstrate that ground beetle assemblages are affected by differences in livestock grazing in our upland experimental site. In particular, abundance, species richness and diversity of ground beetles were lower in the ungrazed treatment than in the high- or low-intensity sheep grazed treatments. These results contrast with previous studies of other invertebrate taxa and show, in particular, that a single management prescription

cannot benefit all species. Overall invertebrate species richness and abundance is likely to be promoted by a mosaic of grazing intensities. This can be difficult to achieve on unenclosed upland grassland, though topographical and habitat variation may drive unequal distribution of livestock.

In reality, upland areas are managed for multiple outputs, such as food production, recreation, and ecosystem services, including biodiversity. Within biodiversity management, maintaining specialised or characteristic species or assemblages of upland areas, such as through promoting mosaics of management types and intensities across landscapes, may be seen as a higher priority than maximising species richness, abundance or diversity of any particular taxa. To this end, our findings add to earlier evidence that grazing abandonment may be detrimental to some elements of biodiversity but find no evidence that ground beetle assemblages are detrimentally affected by grazing at a low-intensity compared to at a higher intensity.

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Author contributions

G.P. conceived the idea, designed the sampling protocol, collected, sorted and identified samples, conducted the formal analysis and wrote parts of the manuscript. L.Q-O collected, sorted and identified samples, and N.A.L. collected samples, wrote parts of the manuscript and supervised the project.

Conflict of interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available on request from the authors.

Supporting information

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

Supplementary Material S1 Sensitivity analysis showing the potential influence of pitfall trap floodedness on model outputs.

Supplementary Material S2 List of all recorded Carabidae species with their full taxonomic name, the subfamily they belong to, and their unique identifier for both the Global Biodiversity Information Facility (GBIF) and for the National Center for Biotechnology Information (NCBI) taxonomy backbones.

Supplementary Material S3 Results of robust linear mixed models and pairwise tests.

Supplementary Material S4 Temporal trends in species richness and log abundance of ground beetles at Glen Finglas. Letters A to F represent sampling blocks whilst grazing treatments are shown by numerals I, II, III and IV (high-intensity sheep grazing, low-intensity sheep grazing, low-intensity mixed cattle and sheep grazing, and no grazing, respectively).

Supplementary Material S5 Sampling coverage and Hill numbers estimated from yearly carabid catches. Estimates are given both for yearly treatment data and for treatment data with the years pooled.

Supplementary Material S6 Ecological distances of ground beetle assemblages collected in Glen Finglas. Distances between treatment-years are calculated using Bray–Curtis dissimilarity indices on untransformed mean species abundance matrices. Heatmaps are grouped by sampling blocks. Letters A to F represent sampling blocks whilst grazing treatments are shown by numerals I, II, III and IV, referring to high-intensity sheep grazing, low-intensity sheep grazing, low-intensity mixed cattle and sheep grazing, and no grazing, respectively.

Supplementary Material S7 Results of Simper analysis – species contributing most on the differences between treatments.

Supplementary Material S8 The effect of treatment and sampling year on the mean abundances of the 16 most common carabid species collected in Glen Finglas. *P*-values of the linear mixed effect models are shown under each plot, and sampling years are colour coded according to the legend.

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