1   **Grazing impacts on ground beetle (Coleoptera: Carabidae) abundance and diversity on a semi-** 2   **natural grassland**

3   Gabor Pozsgai^{1,2*}, Luis Quinzo-Ortega^{1,2}, Nick A. Littlewood^{1,4}

4   1. The James Hutton Institute, Craigiebuckler, Aberdeen, AB15 8QH, UK

5   2. Department of Applied Ecology, Fujian Agriculture and Forestry University, 15 Shangxiadian
6   Road, Cangshan District, Fuzhou, Fujian, 350002, China

7   3. School of Biological and Environmental Sciences, James Parsons Building, Liverpool John
8   Moores University, Byrom Street, Liverpool L3 3AF

9   4. Department of Rural Land Use, SRUC North Facility, SRUC Aberdeen, Ferguson Building,
10   Craibstone Estate, Bucksburn, Aberdeen AB21 9YA, UK

11   *Corresponding author email address: pozsgaig@coleoptera.hu

12

13   **Abstract**

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

20   We investigated the responses of ground beetles to different grazing regimes within a long-term
21   grazing experiment on upland semi-natural grassland in Scotland. Although there was substantial
22   overlap between ground beetle assemblages in different grazing treatments, species richness, mean
23   abundance and Shannon diversity of ground beetles were significantly lower in ungrazed plots than
24   in plots subject to high- or low-intensity sheep grazing. Ground beetle abundance (but not species

richness or diversity) were 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.

Our results suggest that ground beetles may show different responses to grazing compared to responses of some other invertebrate groups and demonstrates the difficulty of carrying out management for a multi-taxon benefit.

Keywords:

Grazing pressure; insect assemblages; livestock; sustainable habitat management; upland grassland

1 Introduction

Semi-natural grasslands around the world are valued for their unique biodiversity (e.g. WallisDeVries et al., 2002). Recently, they have also been recognised as being important carbon stores (e.g. Conant et al., 2017). The nature of these grasslands, which have not suffered deleterious effects of fertilizer or herbicide application, varies with geographic location and factors such as altitude. However, semi-natural grasslands from across their range are under threat (e.g. 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 grasslands areas has gained considerable attention in recent decades (Evans et al., 2015; McGovern et al., 2011). 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 UK, 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 (e.g. 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) and may vary with livestock type (Tóth et al., 2018) but evidence is gradually emerging that

50 such land-use changes are having a marked impact on a range of biodiversity, including birds (Evans
51 et al., 2015) and invertebrates (Dennis et al., 2007). The extent of such impacts, however, varies
52 widely amongst different invertebrate groups (Bonari et al., 2017; García et al., 2009).

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

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

71 Ground beetles are among the more common of surface feeding arthropods and have important
72 functional roles to play in grasslands as predators of smaller invertebrates (e.g. Lövei and
73 Sunderland, 1996) in addition to being prey items themselves, including for upland birds (Buchanan
74 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 grazing experiment. In particular, we hypothesised that, as reduced grazing leads to increased vegetation density, which may impede ground beetle foraging ability, the abundance (as measured by activity density), species richness and diversity of ground beetles would be 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.

84

2 Methods

2.1 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. It extends to 4,085 ha in area. Large parts of the estate remain open ground, dominated by acid grassland and mire. The most represented National Vegetation Classification (NVC) communities (Rodwell, 1992, 1991) in the study areas were M23 (*Juncus effusus/acutiflorus*–*Galium palustre* rush-pasture), M25 (*Molinia caerulea*–*Potentilla erecta* mire), U4 (*Festuca ovina*–*Agrostis capillaris*–*Galium saxatile* grassland) and U5 (*Nardus stricta*–*Galium saxatile* grassland). Some areas were covered by bracken (*Pteridium aquilinum*, NVC U20). Sample sites ranged in altitude from approximately 200 m to 500 m.

96

97 2.2 *Treatments*

98 Six replicate blocks (labelled A to F) of four grazing treatment plots were established in 2003. Each
 99 plot measured 3.3 ha. Plots were located at three sites, each containing two replicate blocks of each
 100 treatment (so a total of eight plots in each of three sites). There sites were each separated by
 101 approximately 5 km. The grazing treatments were high-intensity sheep grazing, with nine sheep per
 102 plot (Treatment I), low-intensity sheep grazing with three sheep per plot (Treatment II), low-intensity
 103 mixed grazing with two sheep per plot and, for four weeks in August/September, two cows per plot,
 104 each with a suckling calf (Treatment III) and ungrazed by domestic herbivores (Treatment IV). Sheep
 105 were removed from plots during severe weather over winter and for routine farming practices, such
 106 as shearing. Grazing treatments were assigned randomly at the outset across the four plots for each
 107 block (Figure 1).

108

109 2.3 *Ground beetle sampling*

110 Sampling was carried out from 2009 to 2013. Each year, five points were chosen randomly from a
 111 pre-established grid of 25 sampling points within each plot. A 500-ml cup, with a diameter of 8 cm,
 112 was used as a pitfall trap and was placed within 1 m of each of these five points. Each cup was part-
 113 filled with ethylene-glycol that served as a preservative. Chicken wire, with a mesh size of 2 cm, was
 114 attached over the top of each trap to minimise capture of small vertebrates and to deter
 115 interference by sheep and a chicken wire dome was placed in each cup to aid escape of any
 116 vertebrates that did fall in the trap. Traps were set in May each year and emptied and reset at
 117 approximately three-week intervals through to September. Trap contents were stored in a freezer
 118 until sorting and identification in the laboratory. Subsequently, they were transferred to 70%
 119 ethanol and stored at the James Hutton Institute, Aberdeen, UK. Specimens were identified to
 120 species by reference primarily to (Lindroth, 1986, 1985) and Luff (2007). Species taxonomy follows
 121 Luff (2007).

122

123 2.4 Data analysis

124 The mean number of each ground beetle species captured was calculated across sampling dates
125 within a year, resulting in a data matrix showing sampling point/year/treatment/block in rows and
126 species in columns. Commonly used diversity measures, namely abundance and species richness per
127 trap, and Shannon-Wiener diversity were calculated, and differences between treatments were
128 investigated using Kruskal-Wallis test. When significant differences were found, post-hoc pairwise
129 Wilcoxon tests were conducted to compare individual treatments. In order to address multiple
130 comparison issues, *p*-values were corrected using Holm's method.

131 Non-metric multidimensional scaling (NMDS) was used on a Bray-Curtis distance matrix to show the
132 similarities of species composition among treatments and to visualize multivariate patterns in two
133 dimensions. Permutational Multivariate Analysis of Variance Using Distance Matrices (ADONIS),
134 implemented in the vegan R package (Oksanen et al., 2010), was used to detect the main drivers of
135 ground beetle assemblage composition, with treatment as a fixed variable and sampling block and
136 sampling year as grouping factors. *P*-values were calculated through a permutation process with 999
137 iterations. Species that were the most important in discriminating between treatments were
138 selected using similarity percentages (Clarke, 1993) with the help of the `simper()` function in the
139 vegan package. Indicator value analysis, `IndVal` (De Cáceres et al., 2010; De Cáceres and Legendre,
140 2009), was used to investigate whether any specific species were strongly associated with particular
141 treatments, experimental blocks or years. Prior to the multivariate analysis, ground beetle numbers
142 were transformed using Hellinger's method as suggested by O'Hara and Kotze (2010).

143 The impact of grazing pressure on the activity-density of the seven most common ground beetle
144 species was analysed using linear mixed effect models, where grazing treatment and sampling year
145 were considered as fixed, and sampling block as random effects. Sampling year was considered as a
146 fixed effect because climate change (Pozsgai et al., 2015) and altered land use (Déri et al., 2011;

York, 2000) can cause a directional shift in insect assemblages 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 amongst the fixed effects.

All analyses were carried out with the R statistical software, using *vegan* (Oksanen et al., 2010), *indicspecies* (De Cáceres and Legendre, 2009), and *nlme* (Pinheiro et al., 2017) packages.

3 Results

Thirty-six species of ground beetle were recorded (Figure 2). These comprised 5,120 individual ground beetles (Supplementary Material 1). The most frequently caught species were *Pterostichus nigrita* (1,217 individuals), *Pterostichus madidus* (1,050 individuals) and *Pterostichus niger* (545 individuals). Thirteen species were represented by fewer than ten individuals each. The mean number of beetles caught per trap per collection was relatively low, at 7.02 ± 7.00 (mean $\pm$ IQR).

3.1 Ground beetle abundance and diversity

Species richness, mean abundance and Shannon diversity were significantly lower in treatment IV (ungrazed) than in treatments I (high-intensity sheep) and II (low-intensity sheep). Both species richness and Shannon diversity were greater in treatment I than in III (low intensity sheep and cows) and mean abundance was significantly higher in treatment III than in treatment IV (Figure 3). 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 2).

3.2 Ground beetle assemblages

Multidimensional scaling showed that there was a large overlap between ground beetle assemblages in the four grazing treatments (Figure 3). 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 treatment I and the ungrazed treatment IV ($F = 3.98$, $R^2 = 0.064$, adjusted p -value = 0.006) but none of the other treatments were significantly different in pairwise comparison. When data were separated to blocks, the treatment effect was only significant in three of the six blocks, one from each block pair. The difference was mostly caused by treatment IV, which was well separated from all other treatments. Treatments I, II and III showed little separation from each other (Figure 4).

Although ADONIS indicated a significant effect of sampling year, no temporal trends were apparent in the assemblages overall (Supplementary Material 3). Data suggested, though, that assemblages in treatments II, III and IV were changing over time in some treatment blocks. In particular the ecological distance between samples increased over the years within treatment block B, and also treatment IV of block A and in treatment III of block F. The ecological distance between treatments I and IV showed an increase only in block E. Simper analysis indicated that the two most important species in shaping differences in ground beetle assemblages between treatments were *Pterostichus nigrita* and *Pterostichus madidus*. Further species played important roles in shaping differences between assemblages, notably *Pterostichus niger* (in differences between treatments I and II and between I and IV), *Carabus arvensis* (differences between treatments I and III) and *Carabus glabratus* (differences between treatments II and III, treatments II and IV and treatments III and IV) (Supplementary material 4).

Common, habitat generalist species dominated all treatments. Among the species that are commonly associated with wet peatlands (e.g. *Agonum ericeti*, *Patrobis 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 the ungrazed treatment IV plots and, indeed, IndVal analysis pinpointed this species as an indicator for treatment IV (IndVal $g = 0.231$, $p = 0.012$). In contrast, *Pterostichus adstrictus* (IndVal $g = 0.224$, $p = 0.001$) was typically found in the most heavily grazed treatment I. No other species were identified by this analysis as being significant indicators of any single grazing treatment (Table 2).

The regression of the mean abundances of the eight most commonly caught species showed a significant treatment effect (Block was included as a random effect) only for *Carabus arvensis* ($p = 0.042$). Sampling year caused a significant difference in abundance between treatments for *Pterostichus nigrita* ($p = 0.002$), *Carabus 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 5).

4 Discussion

Overall, there was substantial overlap between ground beetle assemblages in different grazing treatments. We did find that 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 hypothesis, our results also showed that there were fewer ground beetles caught, fewer species recorded and lower diversity in the ungrazed treatment IV than in the two sheep-grazed treatments (treatments I and II) and that fewer were caught in treatment IV than in the mixed grazing treatment III. However, no differences were identified in abundance, species richness or diversity between the three grazed treatments.

219

220 4.1 Grazing impact on ground beetle abundance

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

231 This effect of grazing may be replicated by other forms of vegetation removal. For example,
 232 Gimingham (1985) showed that ground beetles were most abundant in the pioneer (youngest) stage
 233 of growth of the dwarf shrub, *Calluna vulgaris*, (under a rotational burning regime), when vegetation
 234 complexity was at its lowest. In parallel, Sanderson et al. (2020) found more ground beetles in areas
 235 of *C. vulgaris* that were mechanically cut between one and seven years previously compared to
 236 areas cut eight or more years previously. Although dwarf shrubs were not dominant in our study
 237 plots, these results are consistent with our finding that ground beetle activity density was lower in
 238 the ungrazed treatment, which had the tallest vegetation with the greatest biomass (Evans et al.,
 239 2015) and most extensive areas of dense grassy tussocks (Smith et al., 2014), than in the grazed
 240 treatments. This observation may be at least partly driven by the two species that occurred in the
 241 highest numbers in our study, namely *Pterostichus nigrita* and *Pterostichus madidus*. These have
 242 previously been shown to display trends of decreasing abundance with increasing vegetation height
 243 (e.g. 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 (e.g. Brown and Matthews, 2016) whilst captures may also be biased by ground beetle body size (Hancock and Legg, 2011), 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 (e.g. 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.

4.2 *Grazing impact on ground beetle diversity*

Similarly to abundance, species richness of ground beetles has been shown in some studies 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 a similar lack of significant impact was reported from British Columbia, Canada (Bassett and Fraser, 2015). An opposite finding to ours was that, on heather moorland in Scotland, ground beetle species richness was reduced on sites that were the most heavily grazed by deer and sheep (Gardner et al., 1997). 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.

Metrics of ground beetle diversity may also be positively correlated to vegetation removal. Grandchamp et al. (2005), for example, found that intensive management of grasslands (through mowing, grazing and fertilisation) 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 *C. vulgaris*, may enhance ground beetle diversity (Gardner et al., 1991).

4.3 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 and 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 UK (e.g. Luff et al., 1992) and shown that these differ between different upland habitats (Butterfield and Coulson, 1983). In particular, ground beetle assemblages have been shown

to be substantially shaped by environmental conditions, including both vegetation structure and soil conditions (e.g. Luff et al., 1992, 1989). 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 or different management treatments within habitat mosaics (e.g. 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 apparent among ground beetle assemblages (Bonari et al., 2017; García et al., 2009; Lengyel et al., 2016), 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.

4.4 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 three years following the application of grazing treatments (Dennis et al., 2007). Studies of both moths (Littlewood, 2008) and Auchenorrhyncha (Littlewood et

al., 2012), sampled five 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 treatment plots compared with the high-intensity sheep grazing treatment. Overall arthropod abundance, measured at intervals over the first nine 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 whilst 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 and Tschamntke, 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.

5 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.

Acknowledgements

We thank the Woodland Trust and their Glen Finglas staff for hosting the grazing experiment and providing logistical support. The work was funded by the Scottish Government's Rural and Environment Science and Analytical Services' Strategic Research Programme.

6 References

- Bassett, E.R.L., Fraser, L.H., 2015. Effects of Cattle on the Abundance and Composition of Carabid Beetles in Temperate Grasslands. *Journal of Agricultural Studies* 3, 36–47. <https://doi.org/10.5296/jas.v3i1.6731>
- Batáry, P., Báldi, A., Szél, G., Podlussány, A., Rozner, I., Erdős, S., 2007. Responses of grassland specialist and generalist beetles to management and landscape complexity. *Diversity and Distributions* 13, 196–202. <https://doi.org/10.1111/j.1472-4642.2006.00309.x>
- Blake, S., McCracken, D.I., Eyre, M.D., Garside, A., Foster, G.N., 2003. The relationship between the classification of Scottish ground beetle assemblages (Coleoptera, Carabidae) and the National Vegetation Classification of British plant communities. *Ecography* 26, 602–616. <https://doi.org/10.1034/j.1600-0587.2003.03491.x>
- Bonari, G., Fajmon, K., Malenovský, I., Zelený, D., Holuša, J., Jongepierová, I., Kočárek, P., Konvička, O., Uříčář, J., Chytrý, M., 2017. Management of semi-natural grasslands benefiting both plant and insect diversity: The importance of heterogeneity and tradition. *Agriculture, Ecosystems & Environment* 246, 243–252. <https://doi.org/10.1016/j.agee.2017.06.010>
- Brooks, D.R., Bajer, J.E., Clark, S.J., Monteith, D.T., Corbett, S.J., Beaumont, D.A., Chapman, J.W., 2012. Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. *Journal of Applied Ecology* 49, 1009–1019. <https://doi.org/10.1111/j.1365-2664.2012.02194.x>
- Brown, G.R., Matthews, I.M., 2016. A review of extensive variation in the design of pitfall traps and a proposal for a standard pitfall trap design for monitoring ground-active arthropod biodiversity. *Ecology and Evolution* 6, 3953–3964. <https://doi.org/10.1002/ece3.2176>
- Buchanan, G.M., Grant, M.C., Sanderson, R.A., Pearce-Higgins, J.W., 2006. The contribution of invertebrate taxa to moorland bird diets and the potential implications of land-use management. *Ibis* 148, 615–628. <https://doi.org/10.1111/j.1474-919X.2006.00578.x>

390 Butterfield, J., Coulson, J.C., 1983. The carabid communities on peat and upland grasslands in
391 northern England. *Holarctic Ecology* 6, 163–174.

392 Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure.
393 *Australian Journal of Ecology* 18, 117–143.

394 Coates, P.S., Ricca, M.A., Prochazka, B.G., Brooks, M.L., Doherty, K.E., Kroger, T., Blomberg, E.J.,
395 Hagen, C.A., Casazza, M.L., 2016. Wildfire, climate, and invasive grass interactions negatively
396 impact an indicator species by reshaping sagebrush ecosystems. *PNAS* 113, 12745–12750.
397 <https://doi.org/10.1073/pnas.1606898113>

398 Cole, L.J., Morton, R., Harrison, W., McCracken, D.I., D, R., 2008. The influence of riparian buffer
399 strips on carabid beetle (Coleoptera, Carabidae) assemblage structure and diversity in
400 intensively managed grassland fields. *Biodiversity Conservation* 17, 2233–2245.
401 <https://doi.org/10.1007/s10531-007-9304-1>

402 Cole, L.J., Pollock, M.L., Robertson, D., Holland, J.P., Mccracken, D.I., 2006. Carabid (Coleoptera)
403 assemblages in the Scottish uplands: the influence of sheep grazing on ecological structure.
404 *October*.

405 Conant, R.T., Cerri, C.E.P., Osborne, B.B., Paustian, K., 2017. Grassland management impacts on soil
406 carbon stocks: a new synthesis. *Ecological Applications* 27, 662–668.
407 <https://doi.org/10.1002/eap.1473>

408 De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and
409 statistical inference. *Ecology* 90, 3566–3574. <https://doi.org/10.1890/08-1823.1>

410 De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining
411 groups of sites. *Oikos* 119, 1674–1684. <https://doi.org/10.1111/j.1600-0706.2010.18334.x>

412 Dennis, P., Skartveit, J., McCracken, D.I., Pakeman, R.J., Beaton, K., Kunaver, A., Evans, D.M., 2007.
413 The effects of livestock grazing on foliar arthropods associated with bird diet in upland
414 grasslands of Scotland. *Journal of Applied Ecology* 45, 279–287.
415 <https://doi.org/10.1111/j.1365-2664.2007.01378.x>

416 Dennis, P., Young, M.R., Howard, C.L., Gordon, I.J., 1997. The response of epigeal beetles (Col.:
417 Carabidae, Staphylinidae) to varied grazing regimes on upland *Nardus stricta* grasslands.
418 Journal of Applied Ecology 34, 433–443. <https://doi.org/10.2307/2404888>

419 Déri, E., Magura, T., Horváth, R., Kisfali, M., Ruff, G., Lengyel, S., Tóthmérész, B., 2011. Measuring the
420 short-term success of grassland restoration: the use of habitat affinity indices in ecological
421 restoration. Restoration Ecology 19, 520–528. [https://doi.org/10.1111/j.1526-](https://doi.org/10.1111/j.1526-100X.2009.00631.x)
422 100X.2009.00631.x

423 Evans, D.M., Villar, N., Littlewood, N.A., Pakeman, R.J., Evans, S.A., Dennis, P., Skartveit, J., Redpath,
424 S.M., 2015. The cascading impacts of livestock grazing in upland ecosystems: a 10-year
425 experiment. Ecosphere 6, 42. <https://doi.org/10.1890/ES14-00316.1>

426 Eyre, M.D., Luff, M.L., Rushton, S.P., Topping, C.J., 1989. Ground beetles and weevils (Carabidae and
427 Curculionoidea) as indicators of grassland management practices. Journal of Applied
428 Entomology 107, 508–517. <https://doi.org/10.1111/j.1439-0418.1989.tb00285.x>

429 García, R.R., Jáuregui, B.M., García, U., Osoro, K., Celaya, R., 2009. Effects of livestock breed and
430 grazing pressure on ground-dwelling arthropods in Cantabrian heathlands. Ecological
431 Entomology 34, 466–475. <https://doi.org/10.1111/j.1365-2311.2008.01072.x>

432 Gardner, S.M., Hartley, S.E., Davies, A., Palmer, S.C.F., 1997. Carabid communities on heather
433 moorlands in northeast Scotland: The consequences of grazing pressure for community
434 diversity. Biological Conservation 81, 275–286. [https://doi.org/10.1016/S0006-](https://doi.org/10.1016/S0006-3207(96)00148-6)
435 3207(96)00148-6

436 Gardner, S.M., Hartley, S.E., Davies, A., Palmer, S.C.F., 1991. Ground beetle (Coleoptera: Carabidae)
437 communities on upland heath and their association with heathland flora. Journal of
438 Biogeography 18, 281–289. <https://doi.org/10.2307/2845398>

439 Gimingham, C.H., 1985. Age-related interactions between *Calluna vulgaris* and phytophagous
440 insects. Oikos 44, 12–16. <https://doi.org/10.2307/3544036>

Grandchamp, A.-C., Bergamini, A., Stofer, S., Niemelä, J., Duelli, P., Scheidegger, C., 2005. The influence of grassland management on ground beetles (Carabidae, Coleoptera) in Swiss montane meadows. *Agriculture, Ecosystems & Environment* 110, 307–317. <https://doi.org/10.1016/j.agee.2005.04.018>

Hancock, M.H., Legg, C.J., 2011. Pitfall trapping bias and arthropod body mass. *Insect Conservation and Diversity* no-no. <https://doi.org/10.1111/j.1752-4598.2011.00162.x>

Jung, J.-K., Jeong, J.-C., Lee, J.-H., 2019. Effects of pitfall trap size and sampling duration on collection of ground beetles (Coleoptera: Carabidae) in temperate forests. *Entomological Research* 49, 229–236. <https://doi.org/10.1111/1748-5967.12358>

Koivula, M., 2011. Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. *ZooKeys* 100, 287–317. <https://doi.org/10.3897/zookeys.100.1533>

Kruess, A., Tschardtke, T., 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation* 106, 293–302. [https://doi.org/10.1016/S0006-3207\(01\)00255-5](https://doi.org/10.1016/S0006-3207(01)00255-5)

Lengyel, S., Déri, E., Magura, T., 2016. Species richness responses to structural or compositional habitat diversity between and within grassland patches: a multi-taxon approach. *PLoS ONE* 11, 0149662. <https://doi.org/10.1371/journal.pone.0149662>

Lindroth, C.H., 1986. The Carabidae (Coleoptera) of Fennoscandia and Denmark, *Fauna Entomologica Scandinavica*. E.J. Brill, Leiden, Netherlands.

Lindroth, C.H., 1985. The Carabidae (Coleoptera) of Fennoscandia and Denmark. E.J. Brill, Leiden, Netherlands.

Littlewood, N.A., 2008. Grazing impacts on moth diversity and abundance. *Society* 151–160.

Littlewood, N.A., Pakeman, R.J., Pozsgai, G., 2012. Grazing impacts on Auchenorrhyncha diversity and abundance on a Scottish upland estate. *Insect Conservation and Diversity* 5, 67–74. <https://doi.org/10.1111/j.1752-4598.2011.00135.x>

467 Lövei, G.L., Magura, T., 2011. Can carabidologists spot a pitfall? The non-equivalence of two
468 components of sampling effort in pitfall-trapped ground beetles (Carabidae. Community
469 Ecology 12, 18–22. <https://doi.org/10.1556/ComEc.12.2011.1.3>

470 Lövei, G.L., Sunderland, K.D., 1996. Ecology and behavior of ground beetles. Annual Review of
471 Entomology 41, 231–256.

472 Luff, M.L., 2007. The Carabidae (ground beetles) of Britain and Ireland (Handbooks for the
473 Identification of British Insects). Royal Entomological Society, St. Albans [England].

474 Luff, M.L., Eyre, M.D., Rushton, S.P., 1992. Classification and prediction of grassland habitats using
475 ground beetles (Coleoptera, Carabidae. Journal of Environmental Management 35, 301–315.
476 [https://doi.org/10.1016/S0301-4797\(11\)80012-5](https://doi.org/10.1016/S0301-4797(11)80012-5)

477 Luff, M.L., Eyre, M.D., Rushton, S.P., 1989. Classification and Ordination of Habitats of Ground
478 Beetles (Coleoptera, Carabidae) in North-East England. Journal of Biogeography 16, 121.
479 <https://doi.org/10.2307/2845086>

480 Luff, M.L., Rushton, S.P., 1989. The ground beetle and spider fauna of managed and unimproved
481 upland pasture. Agriculture, Ecosystems and Environment 25, 195–205.
482 [https://doi.org/10.1016/0167-8809\(89\)90051-0](https://doi.org/10.1016/0167-8809(89)90051-0)

483 Lyons, A., Ashton, P.A., Powell, I., Oxbrough, A., 2017. Impacts of contrasting conservation grazing
484 management on plants and carabid beetles in upland calcareous grasslands. Agriculture,
485 Ecosystems and Environment 244, 22–31. <https://doi.org/10.1016/j.agee.2017.04.020>

486 Martin, D., Fraser, M.D., Pakeman, R.J., Moffat, A.M., 2013. Natural England Review of Upland
487 Evidence 2012 - Impact of moorland grazing and stocking rates. Natural England Evidence
488 Review Number 006.

489 Martin, G., Barth, K., Benoit, M., Brock, C., Destruel, M., Dumont, B., Grillot, M., Hübner, S., Magne,
490 M., Moerman, M., Mosnier, C., Parsons, D., Ronchi, B., Schanz, L., Steinmetz, L., Werne, S.,
491 Winckler, C., Primih, R., 2020. Potential of multi-species livestock farming to improve the

492 sustainability of livestock farms: A review. *Agricultural Systems* 181, 102821.
493 <https://doi.org/10.1016/j.agsy.2020.102821>

494 McGovern, S., Evans, C.D., Dennis, P., Walmsley, C., McDonald, M.A., 2011. Identifying drivers of
495 species compositional change in a semi-natural upland grassland over a 40-year period.
496 *Journal of Vegetation Science* 22, 346–356. [https://doi.org/10.1111/j.1654-](https://doi.org/10.1111/j.1654-1103.2011.01256.x)
497 [1103.2011.01256.x](https://doi.org/10.1111/j.1654-1103.2011.01256.x)

498 Nijssen, M., Alders, K., van der Smitten, N., Esselink, H., 2001. Effects of grass-encroachment and
499 grazing management on carabid assemblages of dry dune grasslands. *Proceedings of the*
500 *Section Experimental and Applied Entomology of the Netherlands Entomological Society*
501 (N.E.V.) 12, 113–120.

502 Oakleaf, J.R., Kennedy, C.M., Baruch-Mordo, S., West, P.C., Gerber, J.S., Jarvis, L., Kiesecker, J., 2015.
503 A world at risk: Aggregating development trends to forecast global habitat conversion. *PLoS*
504 *ONE* 10, 0138334. <https://doi.org/10.1371/journal.pone.0138334>

505 O’Hara, R.B., Kotze, D.J., 2010. Do not log-transform count data. *Methods in Ecology and Evolution* 1,
506 118–122. <https://doi.org/10.1111/j.2041-210X.2010.00021.x>

507 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O’Hara, R.G., Simpson, G.L., Solymos, P., Stevens,
508 M.H.H., Wagner, H., 2010. *vegan: Community ecology package*.

509 Pakeman, R.J., Fielding, D.A., Everts, L., Littlewood, N.A., 2019. Long-term impacts of changed
510 grazing regimes on the vegetation of heterogeneous upland grasslands. *Journal of Applied*
511 *Ecology* 56, 1794–1805. <https://doi.org/10.1111/1365-2664.13420>

512 Pétillon, J., Georges, A., Canard, A., Ysnel, F., 2007. Impact of cutting and sheep grazing on ground –
513 active spiders and carabids in intertidal salt marshes (Western France). *Animal Biodiversity*
514 *and Conservation* 2, 201–209.

515 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2017. {nlme}: Linear and Nonlinear Mixed
516 Effects Models.

517 Pozsgai, G., Baird, J., Littlewood, N.A., Pakeman, R.J., Young, M.R., 2018. Phenological changes of the
518 most commonly sampled ground beetle (Coleoptera: Carabidae) species in the UK
519 environmental change network. *International Journal of Biometeorology* 62, 1063–1074.
520 <https://doi.org/10.1007/s00484-018-1509-3>

521 Pozsgai, G., Baird, J., Littlewood, N.A., Pakeman, R.J., Young, M.R., 2015. Long-term changes in
522 ground beetle (Coleoptera: Carabidae) assemblages in Scotland. *Ecological Entomology* 41,
523 157–167. <https://doi.org/10.1111/een.12288>

524 Pozsgai, G., Littlewood, N.A., 2014. Ground beetle (Coleoptera: Carabidae) population declines and
525 phenological changes: Is there a connection? *Ecological Indicators* 41, 15–24.
526 <https://doi.org/10.1016/j.ecolind.2014.01.029>

527 Pozsgai, G., Littlewood, N.A., 2011. Changes in the phenology of the ground beetle *Pterostichus*
528 *madidus* (Fabricius, 1775). *Insect Science* 18, 462–472. [https://doi.org/10.1111/j.1744-](https://doi.org/10.1111/j.1744-7917.2011.01416.x)
529 [7917.2011.01416.x](https://doi.org/10.1111/j.1744-7917.2011.01416.x)

530 Pravia, A., Andersen, R., Artz, R.E., Pakeman, R.J., Littlewood, N.A., 2019. Restoration trajectory of
531 carabid functional traits in a formerly afforested blanket bog. *Zoologica Academiae*
532 *Scientiarum Hungaricae* 65, 33–56. <https://doi.org/10.17109/AZH.65.Suppl.33.2019>

533 Ridding, L.E., Redhead, J.W., Pywell, R.F., 2015. Fate of semi-natural grassland in England between
534 1960 and 2013: A test of national conservation policy. *Global Ecology and Conservation* 4,
535 516–525. <https://doi.org/10.1016/j.gecco.2015.10.004>

536 Rodwell, J.S., 1992. Grasslands and montane communities, *British Plant Communities*. Cambridge
537 University Press, Cambridge, UK.

538 Rodwell, J.S., 1991. Mires and heaths, *British Plant Communities*. Cambridge University Press,
539 Cambridge, UK.

540 Sanderson, R., Newton, S., Selvidge, J., 2020. Effects of vegetation cutting on invertebrate
541 communities of high conservation value Calluna upland peatlands. *Insect Conservation and*
542 *Diversity* 13, 239–249. <https://doi.org/10.1111/icad.12384>

543 Smith, S.W., Vandenberghe, C., Hastings, A., Johnson, D., Pakeman, R.J., Wal, R., Woodin, S.J., 2014.
544 Optimizing carbon storage within a spatially heterogeneous upland grassland through sheep
545 grazing management. *Ecosystems* 17, 418–429. <https://doi.org/10.1007/s10021-013-9731-7>

546 Söderström, B., Svensson, B., Vessby, K., Glimskär, A., 2001. Plants, insects and birds in semi-natural
547 pastures in relation to local habitat and landscape factors. *Biodiversity and Conservation* 10,
548 1839–1863. <https://doi.org/10.1023/A:1013153427422>

549 Suominen, O., Niemelä, J., Martikainen, P., Niemelä, P., Kojola, I., 2003. Impact of reindeer grazing
550 on ground-dwelling Carabidae and Curculionidae assemblages in Lapland. *Ecography* 26,
551 503–513. <https://doi.org/10.1034/j.1600-0587.2003.03445.x>

552 Thomas, C.F.G., Brown, N.J., Kendall, D.A., 2006. Carabid movement and vegetation density:
553 Implications for interpreting pitfall trap data from split-field trials. *Agriculture, Ecosystems*
554 *and Environment* 113, 51–61. <https://doi.org/10.1016/j.agee.2005.08.033>

555 Török, P., Valkó, O., Deák, B., Kelemen, A., Tóth, E., Tóthmérész, B., 2016. Managing for species
556 composition or diversity? Pastoral and free grazing systems in alkali steppes. *Agriculture,*
557 *Ecosystems and Environment* 234, 23–30. <https://doi.org/10.1016/j.agee.2016.01.010>

558 Török, P., Valkó, O., Deák, B., Kelemen, A., Tóthmérész, B., 2014. Traditional cattle grazing in a
559 mosaic alkali landscape: effects on grassland biodiversity along a moisture gradient. *PloS one*
560 9, e97095. <https://doi.org/10.1371/journal.pone.0097095>

561 Tóth, E., Deák, B., Valkó, O., Kelemen, A., Migléc, T., Tóthmérész, B., Török, P., 2018. Livestock type
562 is more crucial than grazing intensity: traditional cattle and sheep grazing in short-grass
563 steppes. *Land Degradation and Development* 29, 231–239. <https://doi.org/10.1002/ldr.2514>

564 Twardowski, J.P., Pastuszko, K., Hurej, M., Gruss, I., 2017. Effect of different management practices
565 on ground beetle (Coleoptera: Carabidae) assemblages of uphill grasslands. *Polish Journal of*
566 *Ecology* 65, 400–409. <https://doi.org/10.3161/15052249PJE2017.65.3.007>

567 WallisDeVries, M.F., Poschlod, P., Willems, J.H., 2002. Challenges for the conservation of calcareous
568 grasslands in northwestern Europe: Integrating the requirements of flora and fauna.
569 Biological Conservation 104, 265–273. [https://doi.org/10.1016/S0006-3207\(01\)00191-4](https://doi.org/10.1016/S0006-3207(01)00191-4)
570 Wang, L., Delgado-Baquerizo, M., Wang, D., Isbell, F., Liu, Jun, Feng, C., Liu, Jushan, Zhong, Z., Zhu,
571 H., Yuan, X., Chang, Q., Liu, C., 2019. Diversifying livestock promotes multidiversity and
572 multifunctionality in managed grasslands. Proc Natl Acad Sci USA 116, 6187–6192.
573 <https://doi.org/10.1073/pnas.1807354116>
574 York, A., 2000. Long-term effects of frequent low-intensity burning on ant communities in coastal
575 blackbutt forests of southeastern Australia. Austral Ecology 25, 83–98.
576 <https://doi.org/10.1046/j.1442-9993.2000.01014.x>
577

578 Table 1: The effects of treatment, sampling block, and sampling year on carabid assemblages. The
579 results of the Permutational Multivariate Analysis of Variance Using Distance Matrices (ADONIS) on
580 species assemblage distance matrix. df: degrees of freedom, SS: sum of squares.

	Df	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 x Year	12	1.428	1.050	0.377
Treatment x Year	15	2.611	1.536	0.004
Residual	78	8.840		

581

582 Table 2: Indicator values and bootstrapped p-values of ground beetle species with high fidelity to
583 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

584

585

Figure 1: Location of sampling points at Glen Finglas, Scotland. The overview map in the topleft corner shows the location within the UK, 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.

Figure 2: Ground beetle species recorded at Glen Finglas, 2009-2013, showing log abundance in each grazing treatment.

Figure 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. Adjusted p -values are indicated as *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$; NS: not significant ($p > 0.05$).

Figure 4: Multidimensional scaling of ground beetle samples from Glen Finglas Numerals I, II, III and IV show grazing treatments 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.

Figure 5: Multidimensional scaling of ground beetle samples from Glen Finglas. Each plot, A to E, represents a treatment block. Numerals I, II, III and IV show grazing treatments 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.

609 **Supplementary Material 1:** List of all recorded Carabidae species with their full taxonomic name, the
610 subfamily they belong to, and their unique identifier for both the Global Biodiversity Information
611 Facility (GBIF) and for the National Center for Biotechnology Information (NCBI) taxonomy
612 backbones.

613

614 **Supplementary Material 2:** Temporal trends in species richness and log abundance of ground
615 beetles at Glen Finglas. Letters A to F represent sampling blocks whilst grazing treatments are shown
616 by numerals I, II, III and IV.

617

618 **Supplementary Material 3:** Ecological distances of ground beetle assemblages collected in Glen
619 Finglas. Distances between treatment-years are calculated using Bray-Curtis dissimilarity indices on
620 untransformed mean species abundance matrices. Heatmaps are grouped by sampling blocks.
621 Letters A to F represent sampling blocks whilst grazing treatments are shown by numerals I, II, III and
622 IV.

623

624 **Supplementary Material 4:** Results of Simper analysis – species contributing most on the differences
625 between treatments.

626

627 **Supplementary material 5:** The effect of treatment and sampling year on the mean abundances of
628 the 16 most common carabid species collected in Glen Finglas. *P*-values of the linear mixed effect
629 models are shown under each plot, and sampling years are colour coded according to the legend.

0 1000 2000 3000 4000 m

log abundance

20
15
10
5
0

AKruskal–Wallis, $p = 9.6\text{e-}06$

abundance

BKruskal–Wallis, $p = 1.3\text{e-}05$

richness

CKruskal–Wallis, $p = 2.6\text{e-}05$

Shannon

A

Adonis p-value = 0.524

D

Adonis p-value = 0.222

B

Adonis p-value = 0.004

C

Adonis p-value = 0.024

F

Adonis p-value = 0.002

E

Adonis p-value = 0.229