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Progressively excluding mammals of different body size affects community and trait structure of ground beetles

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Mammalian grazing induces changes in vegetation properties in grasslands, which can affect a wide variety of other animals including many arthropods. However, the impacts may depend on the type and body size of these mammals. Furthermore, how mammals influence functional trait syndromes of arthropod communities is not well known.

We progressively excluded large (e.g. red deer, chamois), medium (e.g. alpine marmot, mountain hare), and small (e.g. mice) mammals using size-selective fences in two vegetation types (short- and tall-grass vegetation) of subalpine grasslands. We then assessed how these exclusions affected the community composition and functional traits of ground beetles (Coleoptera, Carabidae), and which vegetation characteristic mediated the observed effects.

Total carabid biomass, the activity densities of carabids with specific traits (i.e. small eyes, short wings), the richness of small-eyed species and the richness of herbivorous species were significantly higher when certain mammals were excluded compared to when all mammals had access, regardless of vegetation type. Excluding large and medium mammals increased the activity density of herbivorous carabid species, but only in short-grass vegetation. Similarly, excluding large mammals (ungulates) altered carabid species composition in the short-, but not in the tall-grass vegetation. All these responses were related to aboveground plant biomass, but not to plant Shannon diversity or vegetation structural heterogeneity.

Our results indicate that changes in aboveground plant biomass are key drivers of mammalian grazers' influence on carabids, suggesting that bottom–up forces are important in subalpine grassland systems. The exclusion of ungulates provoked the strongest carabid response. Our results, however, also highlight the ecological significance of smaller herbivorous mammals. Our study furthermore shows that mammalian grazing not only altered carabid community composition, but also caused community-wide functional trait shifts, which could potentially have a wider impact on species interactions and ecosystem functioning.

Keywords: biodiversity, vertebrate, arthropod

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Introduction

Mammalian herbivores can alter plant biomass (Fleischner 1994, Hulme 1996, Bardgett and Wardle 2003), vegetation structure (Morris 2000, Woodcock and Pywell 2010), plant species composition (Pykälä 2003, Hülber et al. 2005) and plant diversity (Olff and Ritchie 1998, Joern 2005) in grassland ecosystems through (selective) grazing (Hülber et al. 2005), trampling (van Klink et al. 2015b), burrowing (Bangert and Slobodchikoff 2006) and dung deposition (Schütz et al. 2006). These changes in vegetation characteristics can, in turn, have cascading effects on a wide variety of invertebrate taxa (Bardgett and Wardle 2003, van Klink et al. 2015a, Vandegehuchte et al. 2018), but usually depend on the intensity, timing, duration of grazing (O'Neill et al. 2003) and the productivity of the habitat (Daskin and Pringle 2016, Vandegehuchte et al. 2017).

A recent review by Daskin and Pringle (2016) showed that large mammalian herbivores tend to have a negative, but not significant impact on arthropod abundance. However, the response of arthropods to these large animals was highly dependent on the taxonomic group of arthropods considered (Foster et al. 2014). Arthropod diversity and richness, on the other hand, are usually negatively impacted by large herbivore grazing (reviewed by Foster et al. 2014, van Klink et al. 2015a, Daskin and Pringle 2016). Considerably fewer studies assessed how medium- or small-sized mammalian herbivores (e.g. rabbits, voles) affect invertebrates. For example, Barham and Stewart (2005) showed that rabbit grazing affected the community composition of leafhoppers, and studies in desert grassland in North America showed that medium- and small-sized mammalian herbivores (prairie dogs, banner-tailed kangaroo rats) could create habitats (e.g. burrows) beneficial for the abundance and/or richness of many invertebrate species, especially detritivores (Bangert and Slobodchikoff 2006, Davidson and Lightfoot 2007). In addition, rats and other omnivorous mammals that feed on invertebrate species may exert top–down control on invertebrate richness and/or abundance (Churchfield et al. 1991). Consequently, invertebrates with specific functional or ecological traits (e.g. dispersal ability, feeding habits, habitat preference) can differ in their responses to grazing of different sized mammals (Carvell 2002, Dennis 2003, Karen et al. 2008, Vandegehuchte et al. 2018) and thus modulate mammalian grazing effects on invertebrate community composition and structure (Dennis et al. 1997, Cole et al. 2006).

In this study, we assessed how the progressive exclusion of mammals of different body size affected the community structure and functional traits of ground beetles (Coleoptera, Carabidae) in two subalpine grassland vegetation types (short- and tall-grass vegetation, Risch et al. 2013, 2015). We focused on carabid beetles as these beetles are relatively abundant, functionally diverse, and sensitive to changes in the environment (Kotze et al. 2011). They also play key roles in trophic associations since a large proportion of carabid species are polyphagous predators and others are mainly phytophagous (Thiele 1977, Kotze et al. 2011). In addition, the distribution and species composition of carabid beetles are closely related to habitat diversity (Halme and Niemelä 1993), aboveground plant biomass (Bassett and Fraser 2015), and vegetation structure (Brose 2003, Cole et al. 2006), which, in turn, can all be strongly influenced by mammalian herbivores. Carabid species with specific morphological traits and ecological requirements often dominate specific habitat types within an ecosystem (Gardner et al. 1997, Karen et al. 2008). Larger-eyed species, for example, prefer open habitats (Bauer et al. 1977, Thiele 1977). A habitat with a high degree of disturbance generally supports a lower proportion of short-winged (Gobbi and Fontaneto 2008, Wamser et al. 2011), but a higher one of long-winged species (Ribera et al. 2001, Pétillon et al. 2007).

We hypothesize that bottom–up forces (Kagata and Ohgushi 2006) drive the responses of carabids to mammalian grazing. More specifically, we hypothesize that the exclusion of mammalian herbivores may generally positively influence available plant biomass (food availability) and thus overall carabid biomass and activity density. The exclusion may enhance the total species richness of carabids by increasing vegetation structural heterogeneity. We also expect that excluding both large and smaller mammals will have a stronger effect on carabids than the exclusion of large mammals alone. We hypothesize that carabid species with different functional traits may respond differently to the mammal exclusions. Specifically, because of lower disturbance levels, and higher food availability, we expected higher activity density and richness of short-winged carabids, more herbivorous and carnivorous carabids on plots with denser vegetation. We also expected higher activity density and richness of large-eyed carabids in short vegetation found in our control plots.

Material and methods

Study area

The study was conducted in subalpine grasslands in the Swiss National Park (SNP). The park is located in southeastern Switzerland at elevations ranging from 1350 to 3170 m a.s.l. The SNP covers an area of 172 km² with 50 km² occupied by forest, 33 km² by alpine and approximately 3 km² by subalpine grasslands (Risch et al. 2013). Mean annual precipitation and temperature (2009–2013; average ± SD) are 826 ± 112 mm and 0.9 ± 0.5°C, respectively (MeteoSchweiz 2014). Since the foundation in 1914, the SNP received minimal human disturbance (no livestock grazing, no hunting, no fishing, no off-trail hiking; Risch et al. 2013).

Homogeneous patches (usually >1 ha) of short- and tall-grass vegetation make up the subalpine grasslands. Short-grass vegetation, roughly 2 to 5 cm in height, dominated by the lawn grasses red fescue *Festuca rubra*, quaking grass *Briza media* and common bent grass *Agrostis capillaris*, has a history of intense mammalian grazing (Schütz et al. 2003, 2006).

Tall-grass vegetation, about 20 cm in height, dominated by tussocks of evergreen sedge *Carex sempervirens* and mat grass *Nardus stricta*, has been grazed less intensively in history (Schütz et al. 2003, 2006). A diverse herbivore community inhabits the subalpine grasslands, which can be divided into four groups based on their body size/weight: large (red deer *Cervus elaphus*, chamois *Rupicapra rupicapra*; 30–150 kg), medium (alpine marmot *Marmota marmota*, mountain hare *Lepus timidus*; 3–6 kg), small vertebrate herbivores (small rodents such as *Clethrionomys* spp., *Microtus* spp., *Apodemus* spp.; 30–100 g) and invertebrates (e.g. grasshoppers, caterpillars, leafhoppers, < 5 g) (Risch et al. 2013).

Experimental design

The mammal exclusion experiment started in spring 2009 (immediately after snowmelt, early May) and was designed as a split-plot design with vegetation type as whole-plot factor, exclusion treatment as split-plot factor and exclosure network (i.e. whole plots) blocked on grassland. Specifically, we selected eighteen study sites, nine on tall- and nine on short-grass vegetation in six subalpine grasslands spread throughout the park (two sites per vegetation type in three large grasslands, one per vegetation type in three small grasslands). All our study sites were located on dolomite parent material at altitudes between 1975 and 2300 m a.s.l. At each site, we established one exclosure network that progressively excludes the large, medium, and smaller vertebrates as well as invertebrates. For each network, a 2.1 m tall and 7 × 9 m main exclosure (electrical fence) was established to exclude large mammalian herbivores. Then we randomly established four 2 × 3 m plots within the main exclosure: (1) a 'M/S/I' plot (within exclosure but unfenced) permitted medium and small mammals and invertebrate herbivores to access, (2) a 'S/I' plot (electrical fence) excluded large and medium-sized mammals, (3) an 'I' plot (metal mesh) excluded all mammals and only permitted invertebrates to access, and (4) a 'None' plot (covered with a mosquito mesh roof) excluded all vertebrates and invertebrates. Located at least 5 m away from the main exclosure, we established the 'L/M/S/I' plot (unfenced 'control'; 2 × 3 m) that gave access to all vertebrate and invertebrate herbivores. We did not use any data collected in the 'None' plots for this study. The fences were dismantled every fall (late October; to protect them from snow pressure and avalanches) and reconstructed in the following year immediately after spring snowmelt (early May). A more detailed description of our experimental setup can be found in Risch et al. (2013, 2015).

Carabid sampling and trait determination

We installed two pitfall traps in the middle of each 2 × 3 m treatment plot in late May 2013 to collect invertebrates. The traps were partly filled with 20% propylene glycol to preserve the captured specimens. We emptied and refilled the traps with an interval of two weeks until late September 2013. Each pitfall trap consisted of a plastic cylinder (13 cm depth,

6.75 cm inner diameter), a 100 ml vial (6.70 cm outer diameter) placed in the cylinder and a plastic funnel suspended in the top part of the cylinder to guide invertebrates into the vial. Each trap was covered with a cone-shaped transparent plastic roof to protect it from rain. The pitfall trap counts are not a measure of density, but a function of both abundance (density) and activity of an invertebrate population (Woodcock 2005, Kotze et al. 2011). The small size of our treatment plots (2 × 3 m) implies that the pitfall-trap catches are more likely to reflect movement and habitat selection by carabids, rather than demographics (Englund 1997, Gil et al. 2016). We therefore use the term "activity density" (Kotze et al. 2011) throughout the paper and caution against extrapolating the pitfall-trap catches to population levels.

The invertebrates caught with the traps were rinsed with water and preserved in 70% ethanol. Carabids were identified to species level (with one exception, see Supplementary material Appendix 1 Table A1) following Freude et al. (2004). Morphological or functional traits for each carabid species were obtained from Homburg et al. (2014) and other sources (Supplementary material Appendix 1 Table A1). These traits represent the feeding guild (trophic level), visual acuity (eye/head proportion), movement and dispersal ability (hind wing development), and body size (average body length). Specifically, we followed Homburg et al. (2014) and classified carabids into herbivorous species (feeding on plants and seeds) and carnivorous species (predators). Regarding hind wing development characteristics, carabids were categorized into brachypterous (i.e. short-winged, mostly flightless), macropterous (long-winged), and wing-dimorphic species (short- and long-winged individuals within the same species). Carabids were also categorized into small-eyed (proportion of eye-to-head width: 10–25%) and large-eyed species (proportion of eye-to-head width: 25–50%). Estimated total carabid biomass (biomass of all individuals of all species collected within each plot) was defined as $T = \sum (p_i \times c_i)$, where p_i was the individual species mass of species i, while c_i was the number of individuals of species i. Individual species mass was determined using the weight ~ length formula proposed by Szyszko (1983).

Vegetation characteristics

We measured aboveground plant biomass (g m^{-2}; canopy intercept method, Frank and McNaughton 1990) every season at peak biomass (2009–2013) in a predetermined 1 × 1 m subplot in each treatment plot. For each subplot we identified the plant species and calculated plant Shannon diversity ($H' = -\sum p_i \ln(p_i)$, where p_i was relative frequency of species i. We used the average (2009–2013) for these two variables for our analyses. Vegetation structural heterogeneity, the standard deviation of the height profile (standard deviation (SD) of height), was assessed with parallel photography and image analysis as described in detail in Vandegehuchte et al. (2017). In short, a photograph was taken of a strip of vegetation (1 m long, 30 cm wide) against a blue background canvas from a fixed distance. The photograph was then converted

to a black-and-white image. The image was split into 100 columns of 1 cm width, and the height of the highest pixel in each column recorded. These 100 height values were used to calculate the SD of the vegetation height.

Statistical analyses

Changes in carabid beetle activity density, biomass and richness

We pooled carabid count data of both traps and all sampling dates per plot. We tested the effects of mammal exclusion and vegetation type on activity density and species richness of all carabid species and of carabids with specific traits (Table 1) using linear mixed-effects model (LMM; R package 'lmerTest', Kuznetsova et al. 2016). Each carabid response variable was modeled as a function of the fixed effects (exclusion treatment, vegetation type) and their interactions. Grassland and exclosure network were included in the model as a nested random effect. The response variables were log- transformed when necessary to achieve normality of the residuals. If the exclusion treatment effect was found to be significant for a carabid response variable, we performed post hoc comparisons between treatments (function 'glht' in R package 'multcomp', Hothorn et al. 2008). p-values were adjusted with the Benjamini–Hochberg (BH) method (Benjamini and Hochberg 1995).

If an initial LMM model was statistically significant with respect to exclusion treatment or vegetation type, we added one vegetation characteristic variable as a covariate to the model as explained below. We ran a separate LMM model for each vegetation characteristic variable, i.e. plant Shannon diversity, plant biomass and vegetation structural heterogeneity (Table 2), with exclusion treatment or vegetation type as fixed effect. The nested random effect remained unchanged. We then performed backward elimination (function 'step' in 'lmerTest' package) of non-significant effects to determine whether the covariate was significantly related with the response variable and whether the inclusion of the significant covariate rendered the original exclusion treatment or vegetation type effect non-significant. If the treatment or vegetation type effect became non-significant, this means that the change in the covariate explains the differences in the carabid response variable induced by exclusion treatment or vegetation type (see Risch et al. 2015 and Vandegehuchte et al. 2015 for applications of this statistic approach).

Changes in carabid species composition

We assessed community-level data for short- and tall-grass vegetation separately. We evaluated the exclusion treatment effects using a partial redundancy analysis (pRDA). A pRDA analysis can remove the effect of random (or 'background') variables before analyzing the effect of variables of interest, and allows for hierarchical (e.g. split-plot) designs (Legendre and Legendre 2012, Oksanen et al. 2016). We Hellinger transformed (Legendre and Gallagher 2001) carabid community data constrained by exclusion treatment and included grassland and exclosure network as conditioning variables (covariates; see a similar pRDA application in Speed et al. 2012). A global permutation test (999 permutations) of the pRDA model was performed to assess whether the exclusions significantly affected carabid community composition. The pRDA and the test of significance were performed using the function 'rda' and 'anova.cca' (both in 'vegan' package, Oksanen et al. 2016), respectively. We also plotted RDA biplots to exhibit the relationships between carabid species compositions and the herbivore exclusions. If a pRDA model

Table 1. The results of linear mixed-effect models (LMM) conducted on carabid response variables. Response variables were modeled as a function of the fixed effects (vegetation type and mammal exclusion treatment) and their interactions, with a nested random effect built with grassland and exclosure network. df = the numerator and denominator degrees of freedom. p-values in bold were statistically significant at the 0.05 level. †: as the interaction effect was significant, we further examined whether a treatment effect on the activity density of herbivorous carabids could be found in short- or tall-grass vegetation and the results are shown in Fig. 1h.

Carabid response variables	Vegetation			Exclusion			Vegetation: Exclusion		
	df	F	p	df	F	p	df	F	p
Total biomass	1,11.02	5.52	**0.04**	3,48	3.27	**0.03**	3,48	1.66	0.19
Total activity density	1,11.02	4.23	0.06	3,48	1.53	0.22	3,48	0.69	0.57
Total number of species	1,11.01	0.08	0.78	3,48	1.95	0.13	3,48	0.09	0.96
Activity density of short-winged species	1,11.16	5.37	**0.04**	3,48	3.96	**0.01**	3,48	1.28	0.29
Activity density of wing-dimorphic species	1,11.02	1.73	0.22	3,48	0.52	0.67	3,48	0.34	0.80
Activity density of long-winged species	1,11.02	3.96	0.07	3,48	1.87	0.15	3,48	2.53	0.07
Activity density of small-eyed species	1,11.04	6.90	**0.02**	3,48	4.33	**0.01**	3,48	1.94	0.14
Activity density of large-eyed species	1,11.02	1.14	0.31	3,48	0.53	0.66	3,48	0.39	0.76
Activity density of herbivores	1,11.02	3.33	0.10	3,48	2.26	0.09	3,48	3.39	**0.03†**
Activity density of carnivores	1,11.06	2.30	0.16	3,48	1.10	0.36	3,48	1.50	0.23
Richness of short-winged species	1,11.05	0.73	0.41	3,48	1.74	0.17	3,48	0.82	0.49
Richness of wing-dimorphic species	1,11.12	1.52	0.24	3,48	3.63	**0.02**	3,48	0.16	0.92
Richness of long-winged species	1,11.02	0.09	0.78	3,48	2.74	0.05	3,48	0.47	0.71
Richness of small-eyed species	1,11.02	0.51	0.49	3,48	4.14	**0.01**	3,48	0.56	0.65
Richness of large-eyed species	1,11.04	0.72	0.41	3,48	3.17	**0.03**	3,48	0.89	0.46
Richness of herbivores	1,11.02	0.11	0.75	3,48	3.13	**0.03**	3,48	0.64	0.59
Richness of carnivores	1,11.03	0.00	1.00	3,48	0.61	0.61	3,48	0.70	0.56

Table 2. Summary of effects of adding covariates individually to linear mixed-effect models (LMM) with vertebrate exclusion treatment or vegetation type as fixed effect and a nested random effect built with grassland and exclosure network. For each covariate a separate model was run. *#: inclusion of the significant covariate rendered the original vertebrate exclusion (or vegetation type) effect non-significant. NS: non-significant (p > 0.05) effect of the covariate on the response variable. * : indicated that the covariate was significantly correlated with the response variable, but it was not related to the significant treatment or vegetation type effect, suggesting that other environmental variables contributed to the effect on the response variable. †: the exclusion treatments had significant effects on the activity density of herbivorous species in short-grass but not in tall-grass vegetation.

| | | The vegetation characteristic variables as covariates | | |
LMM(s)	Carabid response variables	Plant biomass	SD of height	Shannon diversity
(a) Models with significant vegetation type effect on	total carabid biomass	*#	NS	NS
	activity density of short-wing species	*#	NS	NS
	activity density of small-eye species	*	NS	NS
(b) Models with significant exclusion treatment effect on	total carabid biomass	*#	NS	NS
	activity density of short-winged species	*#	NS	NS
	richness of wing-dimorphic species	NS	NS	NS
	activity density of small-eye species	*#	NS	NS
	richness of small-eye species	*#	*	NS
	richness of large-eye species	*#	NS	NS
	activity density of herbivores in short-grass†	*#	NS	NS
	richness of herbivores	*#	*	NS

was found to be significant, we calculated the Pearson correlations between vegetation characteristic variables and scores of ordination axes to assess whether and which of the vegetation variables related to the exclusion-induced carabid community change. All analyses were performed in R ver. 3.4.0 (<www.r-project.org>). We used an α level of 0.05 for all statistical tests.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.q5f2j75> (Wang et al. 2018).

Results

We collected a total of 5772 individuals of 37 carabid beetle species (Supplementary material Appendix 1 Table A1). The two most abundant species were *Pterostichus multipunctatus* (26.42% of total catch) and *Calathus melanocephalus* (17.05%). Eleven species were common, with proportional abundances of 1 to 10% of the total catch; 24 species were locally rare with abundances of less than 1% of all the individuals caught (Supplementary material Appendix 1 Table A1).

Total biomass of carabids was significantly higher in the tall-grass than in the short-grass vegetation (Table 1, Fig. 1a), and was significantly higher when both large and medium-sized mammalian herbivores were excluded ('S/I'), or when all mammals were excluded ('I') than when all mammalian herbivores were present ('L/M/S/I'). These differences were related to aboveground plant biomass, which was the only factor that explained the exclusion treatment and vegetation type effects (Table 2). Total activity density of carabids (Table 1, Fig. 1b) and overall species richness (Table 1,

Fig. 2a) were not significantly different between our exclusion treatments or the two vegetation types.

Several variables describing the activity density or richness of carabids with specific traits were significantly affected by exclusion treatments, and two of these variables, the activity densities of short-winged species and small-eyed species (Table 1), also differed between the vegetation types, with lower activity densities in short-grass compared to tall-grass vegetation. The activity density of short-winged beetles was significantly higher in all our exclosures ('M/S/I', 'S/I', 'I') compared to when all mammals were present ('L/M/S/I'; Fig. 1c). A higher number of small-eyed carabid individuals (Fig. 1f) and species (Fig. 2e) was captured in plots where large and medium ('S/I') or all mammalian herbivores ('I') were excluded. Conversely, the species richness of large-eyed carabids was lower when large mammalian herbivores were excluded ('M/S/I') compared to when all mammals were present ('L/M/S/I'; Fig. 2f).

Both the activity density (Fig. 1h) and richness (Fig. 2g) of herbivorous carabids were significantly higher when excluding large and medium mammals ('S/I') than when all mammals were present ('L/M/S/I'), with the activity density only differing between treatments in the short-grass vegetation. All the significant differences caused by our exclusion treatments were related to changes in aboveground plant biomass, with the exception of changes in richness of wing-dimorphic species (Table 2, also see Supplementary material Appendix 2 Table A2). All other carabid parameters (long-winged species' activity density and richness, wing-dimorphic species' activity density, short-winged species' richness, large-eyed species' activity density, carnivorous species' activity density and richness) did not significantly differ among the exclusion treatments or between the vegetation types (Table 1, Fig. 1, 2).
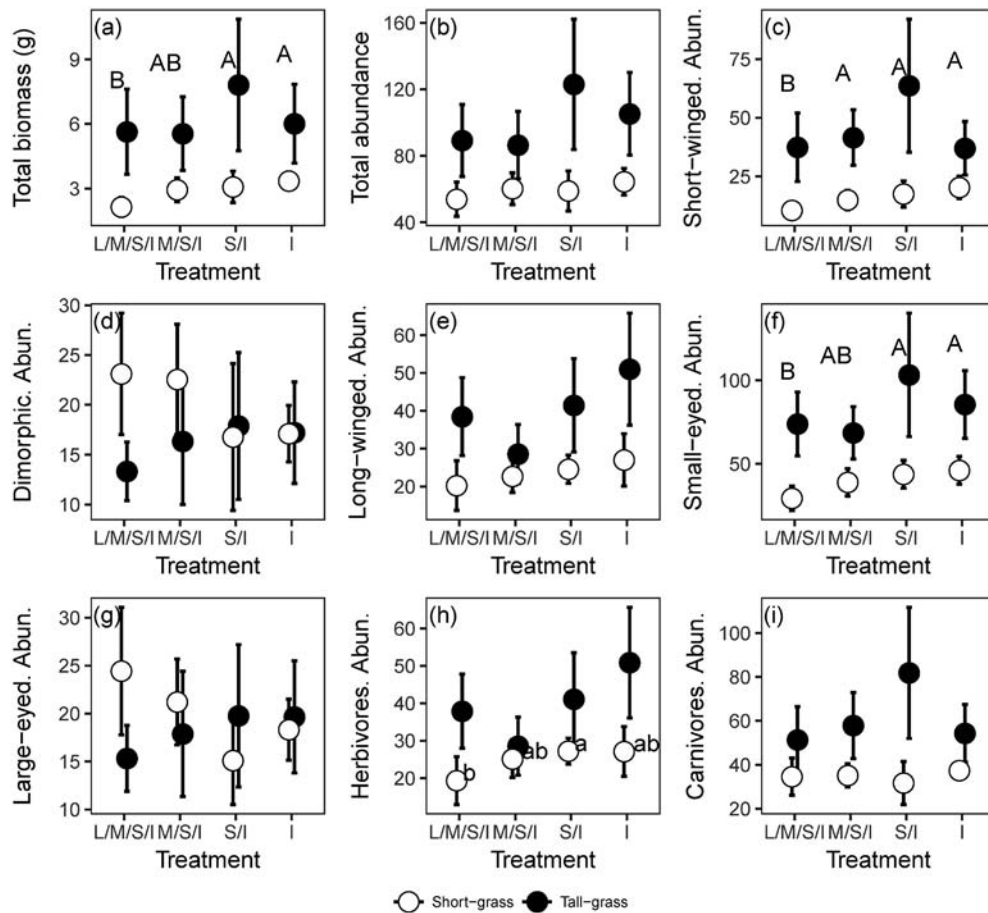
Figure 1. The effects of mammalian herbivore exclusions on (mean ± SE) total carabid biomass, total activity density of carabids and the activity densities of carabids with specific traits in the two vegetation types. Open circles: short-grass vegetation. Solid circles: tall-grass vegetation. The codes on the x-axis indicate which groups of mammalian herbivores had access to the plots: L/M/S/I, large mammals, medium mammals, small mammals and invertebrates had access; M/S/I, medium mammals, small mammals, and invertebrates had access; S/I, small mammals and invertebrates had access; I, only invertebrates had access. Different capital letters indicate the main effects of exclusions (i.e. differences between exclusion treatments, regardless of vegetation type). Different small letters in Fig. 1h indicate significant differences between treatments in short-grass (treatment effect was not found in tall-grass vegetation).

The partial redundancy analysis (pRDA) results indicated that our exclusion treatments significantly affected the carabid community composition in the short-grass vegetation (df = 3, F = 1.51, p = 0.03), but not in the tall-grass vegetation (df = 3, F = 1.06, p = 0.39; Fig. 3b). In the short-grass vegetation (Fig. 3a), species composition of carabids in plots where all mammalian herbivores could graze ('L/M/S/I') differed from all the exclosures ('M/S/I', 'S/I', 'I'), with no difference between 'M/S/I', 'S/I' and 'I'. Aboveground plant biomass in the short-grass vegetation was significantly correlated to the scores of the first axis of the pRDA (Pearson correlation r = 0.59, p < 0.01), but not to axis 2. Thus, plant biomass also helps to explain differences in the community composition of carabid beetles between the exclusion treatments. No correlation was found between the scores of neither axis and plant Shannon diversity or vegetation structural heterogeneity (Pearson correlations with p-values > 0.05), suggesting that these parameters do not help explain the treatment effects on carabid community composition.

Discussion

Responses of activity density and biomass of carabids

Total carabid biomass, but not the total carabid activity density, was significantly higher when large and medium-sized or all mammalian herbivores were excluded. These findings contrast Grandchamp et al. (2005) who found that the intensity of livestock grazing was positively related to the number of carabid individuals in grazed compared to ungrazed Swiss montane meadows. Yet, our findings are similar to those of Bassett and Fraser (2015), who also reported higher carabid biomass, but not activity density, in ungrazed compared to cattle-grazed upper elevation sites in temperate grasslands in British Columbia, Canada. Our result suggests that total carabid biomass is more sensitive than total carabid activity density for identifying the effects of short-term changes in mammalian grazing intensity (exclusion treatments) on carabids. It is argued that abundance and biomass of an
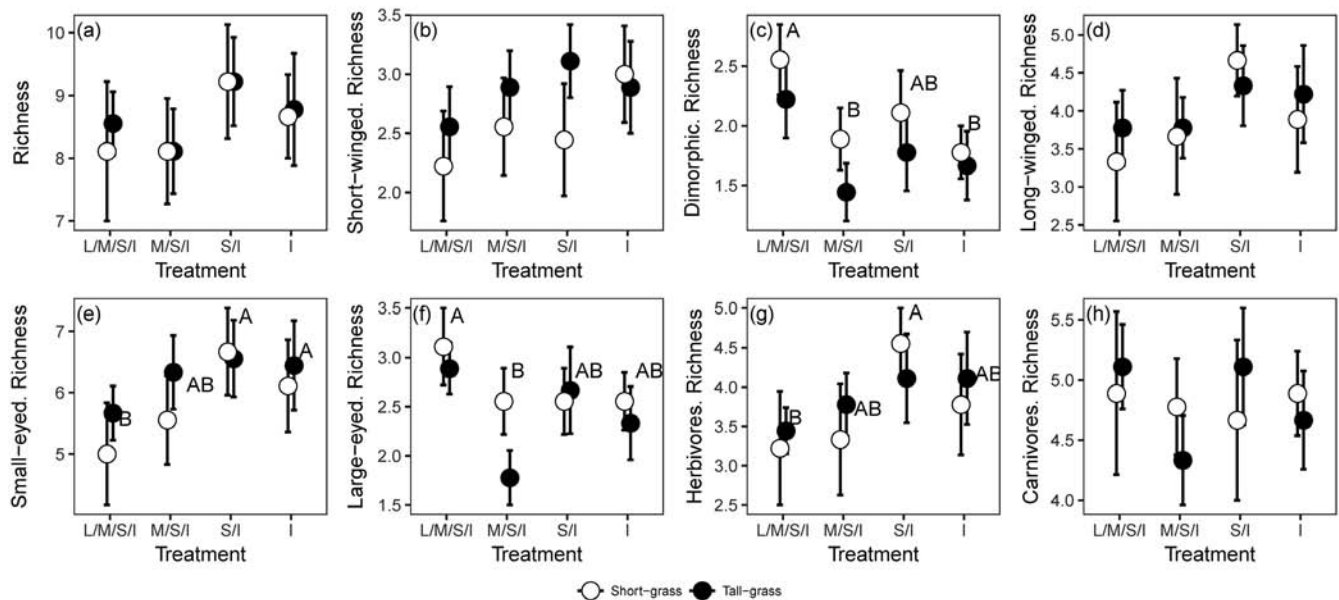
Figure 2. The effects of mammalian herbivore exclusions on (mean ± SE) total carabid species richness and the richness of carabids with specific traits in the two vegetation types. Open circles: short-grass vegetation. Solid circles: tall-grass vegetation. The codes on the x-axis indicate which groups of mammalian herbivores had access to the plots: L/M/S/I, large mammals, medium mammals, small mammals and invertebrates had access; M/S/I, medium mammals, small mammals, and invertebrates had access; S/I, small mammals and invertebrates had access; I, only invertebrates had access. Different capital letters indicate the main effects of exclusion treatments (i.e. differences between the exclusion treatments, regardless of vegetation type).

arthropod assemblage do not necessarily respond in the same way to disturbance or environmental gradients, and biomass should be used more often in arthropod community analyses, as it reflects functionality more accurately than abundance (Saint-Germain et al. 2007, Woodcock and Pywell 2010). The rationale behind this is that body weights of individual species within a community may be extremely different (see Blake et al. 1994 for the case with carabids), and species with different body size or body mass may have different

mobility and movement behaviours (Birkhofer et al. 2015). For example, larger carabid species were shown to prefer plots with dense vegetation as they are more likely to be predated on open plots compared to small species (Blake et al. 1994, Dennis et al. 1997, Brose 2003). In such a case, even minor shifts in these large species' activity densities may cause a remarked change in the overall carabid community biomass.

Consistent with our prediction, carabids that belong to different functional groups strongly differed in their
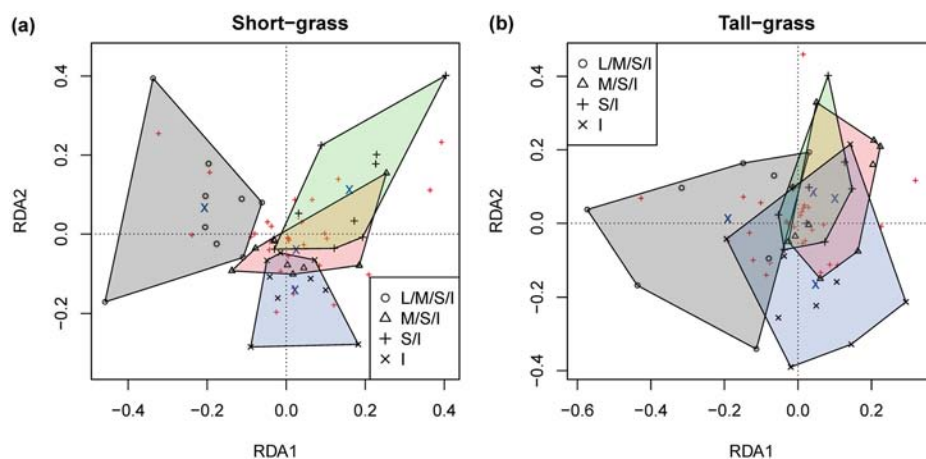

Figure 3. Redundancy analysis biplots (RDA; scaling = 3) showing the relationships between carabid species compositions and the mammalian herbivore exclusions: (A) for short-grass vegetation and (B) for tall-grass vegetation. Blue 'X'(s) represent treatment centroids. Red '+' (s) represent carabid species. Four exclosure types were included in this study, corresponding to which mammals had access to the plots: L/M/S/I, large mammals, medium mammals, small mammals and invertebrates had access; M/S/I, medium mammals, small mammals, and invertebrates had access; S/I, small mammals and invertebrates had access; I, only invertebrates had access.

responses to grazing. Large flightless *Carabus* species were more abundant in extensively compared to intensively managed Scottish uplands sites (Cole et al. 2006), which is similar to our results: short-winged carabids were more responsive to our mammalian herbivore exclusions and the alteration in grassland plant biomass than long-winged carabids. Taken together these results suggest that short-winged species, with limited dispersal ability, seem to be favoured in less disturbed habitats (Wamser et al. 2011). One possible explanation could be that short-winged species gain a reproductive advantage compared to long-winged ones as they do not have to set aside resources for flight dispersal (Kotze and O'Hara 2003). Long-winged carabid species, in contrast, are found across wide ecological amplitudes (de Vries 1994) as they can escape adverse habitat conditions by flight (Fournier and Loreau 2001). Consequently, they will be less affected by a local change in habitat quality (Kotze and O'Hara 2003).

We found higher activity densities of herbivorous carabids when large and medium-sized mammals were excluded from the short-grass vegetation. Unexpectedly, however, the activity density of carnivorous carabids was not affected by our exclusion treatments nor did they differ between the vegetation types. This is surprising, as we would have expected that changes in plant biomass (food availability) and the abundance of herbivorous invertebrates, for example, leafhoppers (Vandegehuchte et al. 2018) and other food items (Vandegehuchte et al. 2017) would have cascading positive effects on abundances of higher-trophic-level species. Herbivorous carabids that prefer seeds and other plant parts (e.g. pollen; Thiele 1977) may, to a large extent, show host plant specialization and high dependency on habitats where the host plant is abundant (Vanbergen et al. 2010). In contrast, predatory carabid species can generally be considered as generalists as they feed on a broad spectrum of prey (Thiele 1977). Consequently, predatory species may be less affected by variation in plant biomass due to their greater ability to switch to alternative prey (Vanbergen et al. 2010) in both treatment and control plots. In addition, activity density of carnivorous carabids did not significantly increase in fenced plots with higher aboveground plant biomass, probably because predacious species are less efficient at visually locating and hunting the prey in the denser vegetation (the hunting efficiency hypothesis; Morse 1980, Brose 2003).

Large-eyed carabids have better optical resolution to spot prey from afar (Bauer et al. 1998) and they are more likely to be the visual hunters (Bauer and Kredler 1993). They thus may benefit from short and sparse vegetation where prey can be seen and pursued easily (Bauer and Kredler 1993). However, contrary to our prediction, large-eyed beetles were not more abundant on the control plots, probably because they may expose themselves to higher risks of being predated (e.g. by vertebrate, Thiele 1977) in open or sparse vegetation. In such case, they are likely to travel at times to the adjacent (treatment) plots with dense vegetation to search for shelters or alternative food. In contrast, small-eyed beetles were more abundant on plots with higher plant biomass simply because

they are not able to survive and hunt well in open or sparse vegetation (Bauer et al. 1998, Homburg et al. 2014).

We are aware that our exclusion treatment effects on carabids may, at least partially, be caused by carabids' movement behaviour and not necessarily by their demographic (reproduction, mortality) responses (Englund 1997, Gil et al. 2016). The changes in the activity densities of carabids with specific traits can also be related to the "refuge effect" (Fournier and Loreau 2001), the resource concentration hypothesis (Root 1973) and the "enemy-free space" hypothesis (Price et al. 1980). For carabids, especially those species with a lower disturbance tolerance (Pöyry et al. 2006), the exclosure plots can be used as "refuges" where plant biomass, and therefore the availability of resources and hiding places is higher (van Klink et al. 2015a), but disturbance from vertebrates is lower (Pöyry et al. 2006).

We are also aware that pitfall-trap counts can be affected, independently of population size, by the behaviour of the animals. For example, trappability varies with the movement speed or difficulty of an individual to move through specific types of ground-cover (Greenslade 1973). Melbourne (1999) found that trappability increased as the grassland habitat structure became simpler and more open. However, we are positive that bias in the effect of grassland vegetation structure on pitfall traps was negligible in our study, as we generally captured higher numbers of carabid individuals in the more complex structure of the tall-grass compared to the short-grass vegetation (Fig. 1).

Responses of species richness and community composition of carabids

Several review papers showed that grassland arthropod diversity often decreases with increasing grazing intensity (Pöyry et al. 2006, van Klink et al. 2015a), but empirical studies on species richness and/or diversity of Carabidae showed negative (Bassett and Fraser 2015), neutral (Söderström et al. 2001, Cole et al. 2006, Batáry et al. 2007, Pétillon et al. 2007) or unimodal (hump-shaped; Kaltsas et al. 2013) relationships to increased ungulate grazing intensity. The direction of the response has generally been explained by habitat heterogeneity (Davidson and Lightfoot 2007), vegetation height (Kruess and Tscharntke 2002), plant diversity (Joern 2005) as well as vegetation structural complexity (Morris 2000, Brose 2003, Dennis 2003, Pöyry et al. 2006). Contrary to our prediction, species richness of Carabidae did not change in response to the exclusion treatments in our study. However, our results revealed that mammalian herbivores strongly affected the richness of carabids with certain functional traits by altering plant biomass. The neutral response of the overall richness of carabids could either be related to the fact that the exclusions had significant but opposing effects on the richness of different groups of carabid species with specific traits, or that our exclusion treatments did not result in a significant change in plant diversity and vegetation structural heterogeneity (Supplementary material Appendix 3 Fig. A3). In addition,

at certain study scales, the overall species richness might not be a sensitive (Vanbergen et al. 2010) or suitable (Gobbi et al. 2015) measure for assessing the influences of environmental heterogeneity on carabid beetles.

Increases in plant biomass are likely responsible for the increased richness of herbivorous carabids that we found when excluding large and medium mammals. Similarly, the richness of small-eyed species was higher on fenced plots with higher plant biomass, likely for the same reasons as highlighted above for the differences in the activity density of species with these traits. As a transient evolutionary form, wing-dimorphic carabid species likely have an advantage in surviving in a changing or deteriorating environment (Kotze and O'Hara 2003). Interestingly, we found that the richness of wing-dimorphic species was significantly lower when large ungulates or all mammalian herbivores were excluded, suggesting that less disturbed habitats would harbor fewer wing-dimorphic species.

Investigations into how mammalian herbivores impact other animals within a system often use 'coarse' metrics, such as total abundance, species richness and diversity indices (Foster et al. 2014, Gobbi et al. 2015). While these measures are convenient for comparisons between studies, generally, not much ecological information such as life-history characteristics is retained when using this approach (Kotze and O'Hara 2003, Cole et al. 2006). Our results show that indices describing specific traits (i.e. individuals and number of species per category of traits such as dispersal ability and feeding guild) can retain such information. Moreover, for the assessment of the influences of habitat quality on biodiversity, our results support that the changes in species composition may be used as better indicators compared to the overall richness of the species assemblage (Taboada et al. 2010). Specifically, our study suggests that large mammalian herbivores are key factors in shaping the composition of the local carabid community in the short-grass vegetation, and the impacts were driven by the variation in plant biomass. This result is generally consistent with studies reporting that the carabid species composition can be significantly altered along the gradient of grazing intensity in grasslands (Dennis et al. 1997, Gardner et al. 1997), associated with aboveground plant biomass, height, and architectural structure of dominant plant species (Gardner et al. 1997), or the vegetation structure and botanical diversity (Dennis et al. 1997).

Conclusions

Our results demonstrate that mammalian herbivores can strongly affect total biomass, species composition and functional group traits of carabid beetles in grassland ecosystems, most likely by influencing plant biomass, following the resource concentration hypothesis (Root 1973). Thus, our findings support our hypothesis that the responses of these beetles to mammalian grazing are driven by bottom–up forces. The generally negative effects of mammalian grazing on carabids that we found are consistent with the conclusions of recent reviews (van Klink et al. 2015a, Daskin and Pringle 2016). Further, our study highlights the importance of smaller mammals for the assessments of the effects of grazing on insect assemblages, as only the joint effect of large and smaller mammals significantly affected some of the carabid variables. Carabid beetles that belong to different species trait groups strongly differed in their responses to mammalian grazing, and some trait groups (i.e. the herbivorous, short-winged or small-eyed beetles) are more sensitive than their counterparts. The changes in total biomass, community composition, and the functional group traits of carabids may affect other species within the system, thus the ecosystems functioning such as energy turnover (Thiele 1977) and food web dynamics (Koivula 2011).

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Supplementary material (available online as Appendix oik-05198 at <www.oikosjournal.org/appendix/oik-05198>). Appendix 1–3.