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The cascading impacts of livestock grazing in upland ecosystems: a 10-year experiment

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Abstract. Livestock grazing is a major driver of land-use change, causing significant biodiversity loss globally. Although the short-term effects of livestock grazing on individual species are well studied, a mechanistic understanding of the long-term, cascading impacts is lacking. We manipulated livestock densities using a unique, replicated upland experiment over a 10-year period and found significant effects of grazing treatment on plant and arthropod biomass; the number of *Anthus pratensis* breeding bird territories; the amplitude of *Microtus agrestis* population cycles and the activity of a top predator, *Vulpes vulpes*. Lower plant biomass as a result of higher stocking densities led to cascades across trophic levels, with fewer arthropods and small mammals, the latter affecting predator activity. Breeding bird territories were a function of arthropod abundance and vegetation structure heterogeneity. Our results provide a novel food-web analysis in a grazing experiment to provide a mechanistic understanding of how food-webs in upland ecosystems respond to long-term livestock grazing pressure, with consequences for management.

Key words: agro-ecosystems; conservation; grassland; moorland; population cycles; trophic interactions.

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INTRODUCTION

Grazing by domestic livestock is a major driver of change in grassland ecosystems. Across the world, patterns of grazing are rapidly changing. Livestock grazing is intensifying and expanding in Asia and South America (Food and Agriculture Organisation 2006, Smith et al. 2007). In Brazil, for example, meat exports are expected to increase more than 50% between 2006 and 2016 (Food and Agriculture Organisation 2006) lead-

ing to a substantial increase in grazing intensity. In contrast, in the European Union (EU), after decades of increasing grazing intensification in some countries (Fuller and Gough 1999), recent changes in policy and regulations have resulted in an emergent process of abandonment of marginal grasslands at the continental scale (Tranter et al. 2007), with significant implications for species and/or habitats of conservation concern (Evans et al. 2006a, Sanderson et al. 2013). However, despite the magnitude of these

changes, our understanding of the mechanisms by which livestock grazing affects biodiversity and cascades through ecosystems is limited (Millennium Ecosystem Assessment 2005).

A wealth of studies have examined the impact of changing grazing intensities on single taxonomic groups, typically plants or birds (see Fleischner 1994, Buckingham and Peach 2005, Diaz et al. 2007, Durant et al. 2008 for reviews). A few reviews have gone further and assessed the impact of grazing on multiple groups. For instance, Vickery et al. (2001) summarized the effects of grazing on lowland grassland plants, invertebrates and birds in Great Britain, concluding that low input livestock systems (i.e., low additions of organic fertilizer and moderate levels of grazing) might minimize the detrimental effects of agricultural intensification on vegetation and invertebrate diversity, thereby improving conditions for bird nesting and feeding. Similarly, Milchunas et al. (1998) reviewed evidence on the effects of grazing on short-grass steppes of North America, concluding that while responses to grazing seemed particularly strong in both plants and birds, overall trophic structural composition (i.e., the percent composition of animal guilds) did not vary greatly in response to grazing. While reviews provide useful insights into the general consequences of livestock management on grassland ecosystems, long-term, replicated experiments on multiple trophic levels are needed to understand the mechanisms affecting multiple plant and animal groups.

To date, few grazing experiments have examined the responses to management across different trophic levels. In a semi-desert grassland, Bock et al. (1984) found that while grass cover, diversity, shrub abundance and rodent diversity increased in the absence of grazing, bird diversity declined. Moser and Witmer (2000) found that ungulate grazing in a steppe area also reduced shrub abundance and small mammal diversity, but plant and bird diversity were unaffected. Davidson et al. (2010) conducted a 3-year, small-scale replicated experiment, manipulating two grazing species, cattle and prairie dogs *Cynomys ludovicianus*, in a grassland in Mexico and found variable effects of cattle on rodents, and synergistic effects of cattle and prairie dogs on vegetation structure and invertebrates. In Nor-

way, a large-scale replicated experiment was conducted that manipulated sheep grazing and found variable short-term effects on plants (Austrheim et al. 2008), invertebrates (Mysterud et al. 2010), birds (Loe et al. 2007) and small mammals (Steen et al. 2005). With the exception of the Norwegian study, grazing experiments typically examine the effects of livestock inclusion/exclusion rather than gradients in grazing intensity. Moreover, few have sufficient spatial or temporal replication necessary to draw general conclusions and management recommendations.

In the UK, as elsewhere, there is concern over the impact of changing grazing management on high conservation value ecosystems (Fuller and Gough 1999, Evans et al. 2006a). We therefore established a novel long-term, replicated experiment to test the multi-trophic impacts of different livestock grazing intensities on upland moorland. We simultaneously quantified the impact of different sheep and cattle stocking densities that reflect current management options on plants, invertebrates, the most common insectivorous and ground-nesting passerine (Meadow Pipit, *Anthus pratensis*), the dominant herbivorous small mammal (field vole, *Microtus agrestis*) and a predator (red fox, *Vulpes vulpes*), all of which are dominant species linked in an upland food-web. Some of the short-term impacts of grazing on individual species and/or communities have been explored in this experiment (plants and arthropod communities [Dennis et al. 2008, Littlewood 2008, Littlewood et al. 2012]; Meadow Pipits [Dennis et al. 2005, Evans et al. 2006b]; field voles [Evans et al. 2006a] and red foxes [Villar et al. 2013b]), suggesting that low intensity, mixed livestock grazing was generally optimal for maximizing biodiversity across trophic levels, at least in the short-term. Here, for the first time, we examine the impact of a range of experimental grazing treatments on the food-web over a 10-year period by combining data across trophic levels and examining the functional responses of altered vegetation structure for the study animals.

Based on previous work, we predicted that livestock grazing intensity would affect: (1) vegetation structure, diversity and biomass, with more heterogeneous vegetation structure and diversity at intermediate grazing levels, but more biomass with lower stocking rates; (2) arthropod

abundance, with the highest abundance in the ungrazed treatment due to greater vegetation biomass; (3) breeding abundance of insectivorous birds, being greatest at intermediate grazing levels due to the availability, not abundance, of food (Evans et al. 2006b). In our experimental system, vole populations exhibit cycles with periodic multi-annual peaks and troughs in abundance, which are affected by grazing (Villar et al. 2013a). It is thought that both mean abundance and amplitude in rodent cycles are critical factors for sustaining populations of endangered carnivore predators in similar grassland systems at higher latitudes, leading to cyclical pulses in survival and reproduction in such predators (Sundell et al. 2004, Henden et al. 2008). Here, we predicted that livestock grazing intensity would affect: (4) density and fluctuations of vole populations, with higher densities found in ungrazed plots, and also larger fluctuations due to greater vegetation biomass; (5) fluctuations in activity of mammalian predators, with larger fluctuations in ungrazed plots due to greater vole fluctuations.

We did not expect that a single grazing treatment would result in ‘win-win’ biodiversity benefits across the food-web in terms of diversity and abundance, rather that intermediate grazing intensity treatments, reflecting traditional farming practices, would provide the best trade-off between ‘winners’ and ‘losers’ across trophic levels.

METHODS

Field methods

Study site.—A replicated, randomized block experiment consisting of six replicates of four treatments was initiated at Glen Finglas, in central Scotland (56°16′ N 4°24′ W), in 2002. Glen Finglas is a 4874-ha estate extensively grazed by sheep and cattle, consisting of semi-natural acid grassland and mire vegetation communities typical of many upland areas of Scotland. Livestock density on the estate prior to the experiment was approximately 0.7 ewes ha⁻¹. Plots were each approximately 3.3 ha in size and were clustered in three altitudinal blocks ranging from 200 to 500 m a.s.l., so that each block (separated by approximately 5 km) included two replicates of every treatment. Experimental treat-

ments were set to mimic realistic management alternatives including grazing at current commercial rates (treatment I, 2.72 ewes ha⁻¹), low intensity sheep-only grazing (treatment II, 0.91 ewes ha⁻¹), low intensity mixed-herbivore grazing with equivalent off-take to treatment II (treatment III, 0.61 ewes ha⁻¹ plus, for four weeks of each year, two cows with two unweaned calves), and no grazing (treatment IV). Treatments were randomly allocated to fenced plots within each replicate in 2003. Following management practices on the estate, livestock were removed from the plots from December to April each year, and occasionally for other husbandry practices.

Vegetation measurements.—A total of 25 sampling points per plot (600 total) were marked at the intersections of a grid composed of squares of 40 m-length sides superimposed upon a map of the experimental site, the precise coordinates were calculated using a geographical information system and located in each plot using a geographical positioning system (GPS) handset (Dennis et al. 2008). Sward height and density measurements were taken at each sampling point in June of each year (2003–2011, coinciding with the peak of the bird breeding season), using a stick marked at 5-cm intervals (Dennis et al. 2005). Three measures of maximum vegetation height were made at each sampling point (at arm’s length, to the front and either side of the observer). The visibility of white marks at 5-cm intervals on the vertically held stick was recorded to measure vegetation density. Height and density measurements were averaged for each point. For each plot, we calculated average vegetation height, density and the coefficient of variation (CV) of vegetation height for each year. Vegetation biomass was approximated as the product of vegetation height and density. In addition to the vegetation height and density measurements, we used a pin-frame method to measure plant cover and species richness at each sampling point in 2002, 2005, 2008 and 2011 (i.e., every 3 years; it was not logistically possible to do this every year. See Appendix: Table A1 for plant and animal sampling details). We estimated plant species richness for each plot in each year using sample-based rarefaction and functional extrapolation (Chao; see Gotelli and Colwell 2001) using package ‘vegan’ (Oksanen et al.

2013) in R 3.0.0 (R Core Team 2013).

Arthropod sampling.—Arthropods were collected using a ‘D-Vac’ suction sampler (Dietrich 1961) equipped with a circular nozzle of 34.3 cm diameter. At each of the 25 sampling points per plot (see *Methods: Vegetation measurements*), the D-Vac nozzle was placed on the vegetation in five separate places, each with a 45-s suction time (covering a total area of 0.462 m²). For logistical reasons, samples were collected from five randomly selected sampling points per plot (rather than 25) from 2005 onwards (Dennis et al. 2008). We were unable to sample the plots in 2006, 2009 and 2010 (Appendix: Table A1). Arthropods were processed and counted in the laboratory and totals pooled to provide abundances m⁻² within each plot. We acknowledge that different groups of arthropods may respond very differently to grazing treatments, but previous work by us showed significant treatment effects on spider, true bug and beetle abundances, the lowest being in the intensively grazed treatment (Dennis et al. 2008). Moreover, there were consistent effects of grazing treatment on total arthropod biomass across years, with higher biomass in the ungrazed treatment and lowest biomass in the intensively grazed treatment. This work also showed a statistically significant relationship between arthropod abundance and biomass within the plots (Dennis et al. 2008). In the absence of species-specific arthropod data after 2005, we used abundance as a proxy for arthropod biomass across years in the context of understanding food-web dynamics.

Bird territory mapping.—Within each plot, we mapped Meadow Pipit territories between April and July each year from 2002 to 2011, paying particular attention to bird breeding behavior, such as song flight, alarm calls, food or fecal sac carrying, mate guarding and using nest locations when available (see Dennis et al. 2005 for methods). Few other bird species used the plots to breed, so these data were excluded. We used the number of Meadow Pipit breeding territories per plot as a surrogate for breeding abundance (Evans et al. 2006b).

Vole surveys.—Within each plot, five of the vegetation sampling points were randomly selected and re-sampled each recording period. At each point, five randomly selected quadrats (25 × 25 cm) were searched for the presence or absence

of fresh vole clippings and droppings (vole sign indices VSI; Evans et al. 2006a). Surveys were conducted twice each year (April and October, 2003–2011), resulting in 600 quadrats survey⁻¹ (9,600 over the 9-year period; no survey was conducted in April 2005 or April 2010). VSI have been shown to be linearly related to actual vole densities based on snap-trapping methods (Lambin et al. 2000) and are an established method to estimate vole abundance.

Fox surveys.—Within each plot, three regularly spaced line transects were walked in October and March 2005–2008 in search of fox scats as an index of fox activity (Villar et al. 2013b). The location of line transects was kept constant, and scats found within 5 m either side of transects were removed. Hence, scats accumulated during the period October to March were indicative of fox activity during winter months. We validated equal probabilities of scat detection across treatments using distance sampling statistical techniques (Villar et al. 2013b).

Analysis

All statistical analyses were carried out using mixed-effects models (GLMMs) fitted using packages ‘nlme’ (Pinheiro and Bates 2002) and ‘lme4’ (Bates et al. 2013) in R 3.0.0 (R Core Team 2013) and the model fit of simplified versions of these were assessed using Akaike Information Criterion (AIC). We defined the spatial structure of the random effects in the models as plot nested within replicate nested within block following the experimental design. To account for inter-annual variation, year was defined as a categorical variable in the analyses. Summary outputs comparing treatment effects were calculated for vegetation and animals using the function ‘relevel’ in package ‘nlme’ (see Appendix: Table A2).

Vegetation.—We examined the effects of grazing treatment, year and their interaction as predictors of mean vegetation height, variation in height (CV), biomass and estimated species richness (Chao), as separate response variables.

Arthropod abundance.—We investigated the effects of grazing treatment, year and their interaction on arthropod abundance. In addition, we examined the mechanistic link between grazing and arthropod abundance by modelling arthropod abundance as a function of vegetation

biomass, year and their interaction.

Meadow Pipit breeding abundance.—First, we examined the effects of grazing treatment, year and their interactions on the number of breeding pipit territories. Second, we examined the relationship between the number of pipit territories, vegetation and arthropod abundance. We incorporated height CV and biomass as descriptors of vegetation characteristics relevant to pipits, as our expectation was that higher vegetation height CV and biomass would provide more favorable foraging and breeding conditions for ground-nesting pipits (Douglas et al. 2008). Hence our models examined the number of pipit territories as a function of vegetation height CV, biomass, arthropod abundance, year and their interactions.

Vole density and cycle amplitude.—First, to test for a long-term response of vole density to grazing intensity, the proportion of positive VSI was modelled as a function of treatment, with year as an additive explanatory covariate in order to account for some degree of background synchrony in peaks and troughs across treatments detected in previous analyses (Villar et al. 2013a), and season to account for seasonality in vole density. Second, to test the effect of grazing intensity on the amplitude of vole density fluctuations, we first derived cycle amplitude as the 10th to 90th inter-quantile range of time series of VSI scores (VSI inter-quantile; Cornulier et al. 2013) for each experimental plot separately. Cornulier et al. (2013) found that quantiles were more suitable than variance-based metrics in terms of biological interpretation, statistical properties, or ease of implementation with replicated or missing data. We then modelled cycle amplitude as a function of grazing treatment. Third, we hypothesized that the impact of grazing on vole cycle amplitude would be mediated by a reduction in vegetation biomass: hence we also modelled cycle amplitude as a function of (log-transformed) mean vegetation biomass per plot across years.

Fox activity amplitude.—Here we considered how the impact of grazing on vole cycle amplitude would affect fox activity amplitude. We first derived fox activity amplitude as maximum minus minimum fox activity index per plot. Then we modelled fox activity amplitude as a function of grazing treatment to see whether fox activity

amplitude changed between treatments. Second, we investigated fox activity in relation to vole cycle amplitude by modelling fox activity amplitude as a function of VSI inter-quantile. Third, as more heterogeneous vegetation structure might facilitate fox access to voles, we tested for an interaction between vegetation height CV and VSI inter-quantile as a predictor of fox activity amplitude. Block was the only random effect fitted in this set of models, as exploratory analyses showed that such was the best fit, which might be itself a consequence of the relative small scale of the experimental plots relative to fox ranging behavior (Villar et al. 2013b).

RESULTS

Vegetation.—We found a significant effect of grazing treatment ($F_{3,15} = 33.562$, $P < 0.001$) and year ($F_{7,157} = 58.305$, $P < 0.001$) on mean vegetation height, with shortest vegetation in the heavily grazed treatment (Fig. 1a). Similarly we found a significant effect of grazing treatment ($F_{3,15} = 11.874$, $P < 0.001$) and year ($F_{7,157} = 21.197$, $P < 0.001$) on vegetation height CV, with least variation in ungrazed plots (Fig. 1b). We also found a significant effect of grazing treatment ($F_{3,15} = 17.545$, $P < 0.001$), year ($F_{8,160} = 23.396$, $P < 0.001$) and treatment \times year interaction ($F_{24,160} = 2.66$, $P < 0.001$) on plant biomass, with lower values in the grazed plots (Fig. 1d). We found no statistically significant effects of grazing treatment or year on plant species richness (Fig. 1c).

Arthropods.—We found a significant effect of grazing treatment ($F_{3,15} = 10.156$, $P < 0.0001$) and year ($F_{5,102} = 32.230$, $P < 0.0001$) on arthropod abundance but no significant interactions, with mean arthropod abundance lowest in the most heavily grazed treatment I (mean over the sampling period = $6267 \text{ m}^{-2} \pm 680 \text{ SE}$) and highest in the ungrazed treatment IV (mean over the sampling period = $10,049 \text{ m}^{-2} \pm 741 \text{ SE}$; Fig. 2). Furthermore, we found that arthropod abundance responded strongly and positively to vegetation biomass ($F_{1,101} = 8.990$, $P = 0.003$) and year ($F_{5,101} = 34.298$, $P < 0.0001$).

Meadow Pipit breeding abundance.—We found a statistically significant effect of grazing treatment ($F_{3,15} = 3.397$, $P = 0.0457$) and year ($F_{8,184} = 11.145$, $P < 0.0001$) on the number of Meadow Pipit territories. Over the period, the mean

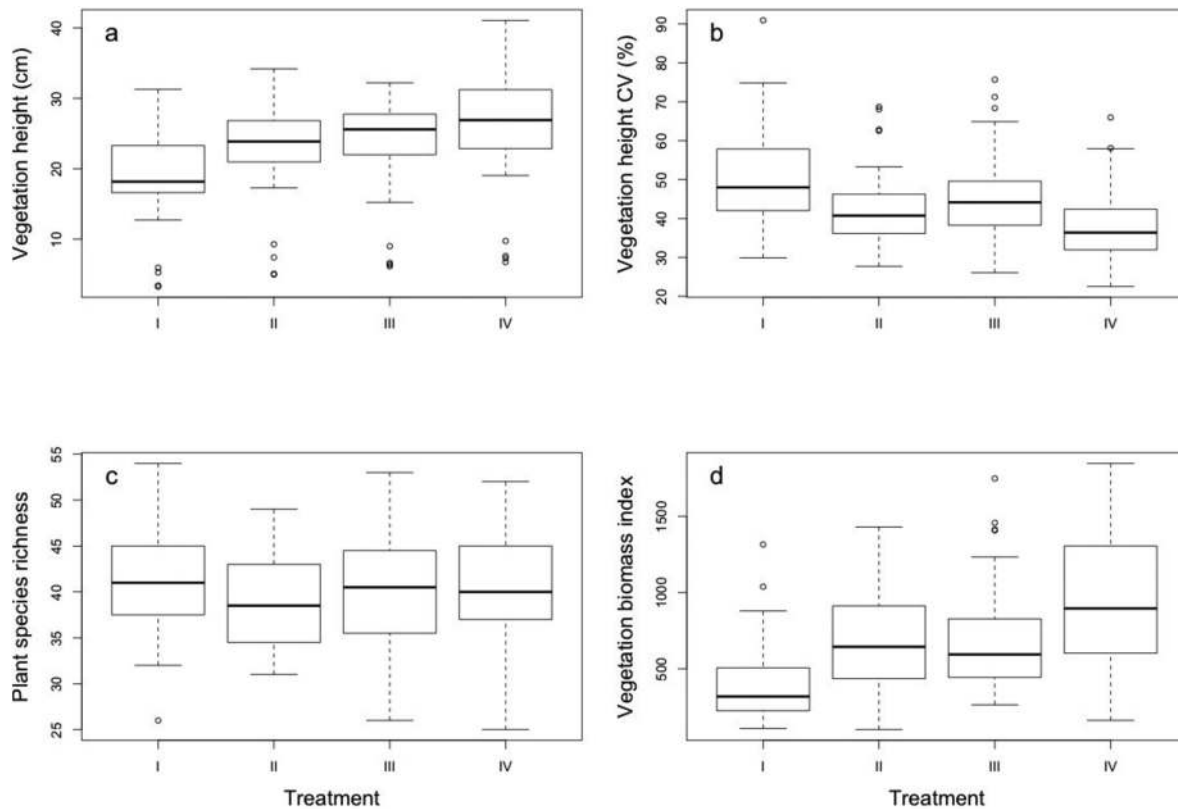


Fig. 1. The effects of grazing treatment on (a) vegetation height, (b) vegetation height CV, (c) plant species richness (raw data presented) and (d) vegetation biomass at Glen Finglas, Scotland. Data are pooled across years. Treatment I = 2.72 ewes ha⁻¹, treatment II = 0.91 ewes ha⁻¹, treatment III = mixed sheep and cattle equivalent to 0.91 ewes ha⁻¹ and treatment IV = ungrazed.

number of pipit territories was highest with intermediate stocking levels that included summer cattle (treatment III, 3.611 territories plot⁻¹) and lowest in the ungrazed treatment IV (2.963 territories plot⁻¹), although there was variation between years (Fig. 3a). Using years when pipit, vegetation and arthropod data were collected simultaneously, model simplification dropped all interactions except the vegetation biomass × year interaction, suggesting that the number of pipit territories was best explained as a function of arthropod abundance ($F_{1,90} = 3.727$, $P = 0.057$) + vegetation height CV ($F_{1,90} = 4.836$, $P = 0.030$) + vegetation biomass ($F_{1,90} = 2.704$, $P = 0.104$) + year ($F_{5,90} = 2.940$, $P = 0.017$) + vegetation biomass × year ($F_{5,90} = 3.184$, $P = 0.011$). Generally, the number of Meadow Pipit breeding territories was positively associated with arthropod abundance and plant biomass, although in

the ungrazed and intermediate grazed plots, the relationship became negative when plant biomass was high, suggesting that prey availability rather than abundance is important for this ground-feeding insectivore (Fig. 3b).

Vole density and cycle amplitude.—We found a strong negative impact of grazing on vole density ($\chi^2_{3,384} = 19.189$, $P < 0.001$; Fig. 4a), and additive effects of year ($\chi^2_{8,384} = 94.924$, $P < 0.001$) and season ($\chi^2_{1,384} = 14.993$, $P < 0.001$, lower densities in Spring). Vole cycle amplitude was also negatively affected by grazing ($F_{3,20} = 6.478$, $P = 0.036$): cycle amplitude was low in treatment I, intermediate in treatment II, but significantly higher in treatments III and IV (Fig. 4b). Vegetation biomass strongly predicted cycle amplitude ($F_{1,22} = 22.658$, $P < 0.001$), so that cycle amplitude strongly increased with increasing biomass (Fig. 4c).

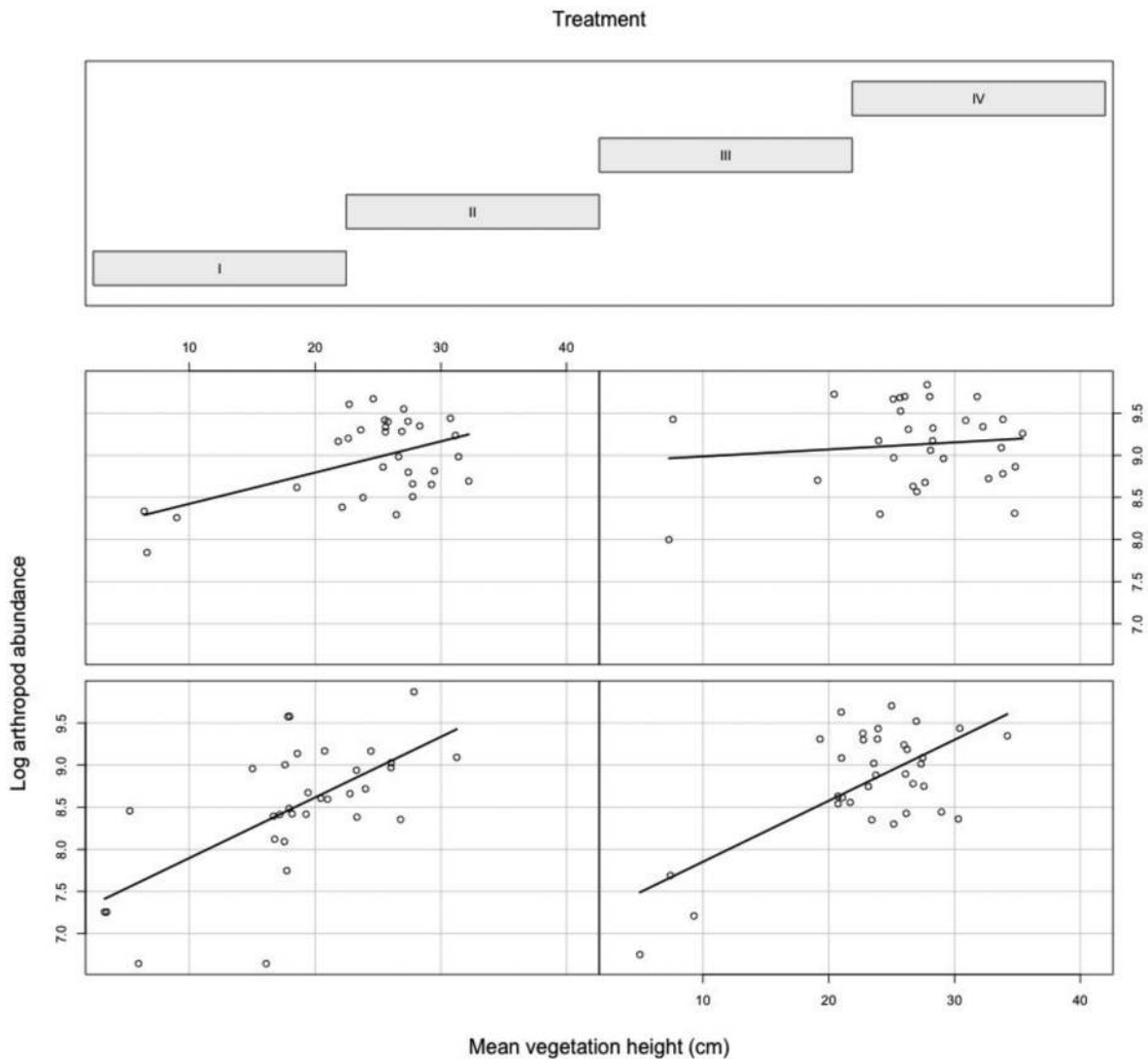


Fig. 2. Relationships between arthropod abundance and mean vegetation height at Glen Finglas, Scotland. Data are pooled across years. Treatment I (bottom, left) = 2.72 ewes ha⁻¹, treatment II (bottom, right) = 0.91 ewes ha⁻¹, treatment III (top, left) = mixed sheep and cattle equivalent to 0.91 ewes ha⁻¹ and treatment IV (top, right) = ungrazed.

Fox activity.—Fox activity amplitude also changed with grazing treatment ($\chi^2_{3,23} = 7.946$, $P = 0.047$), decreasing with increasing grazing (Fig. 5a). Furthermore: as predicted, fox activity amplitude clearly responded to vole cycle amplitude ($\chi^2_{3,23} = 5.3211$, $P = 0.021$; Fig. 5b). However, and contrary to our predictions, fox activity amplitude showed a negative response to vegetation height CV ($\chi^2_{3,23} = 4.400$, $P = 0.036$; Fig. 5c).

DISCUSSION

A grazed trophic cascade

We found significant effects of long-term ungulate grazing intensity across trophic levels in an upland grassland ecosystem. Despite year-to-year variance, our results show strong trends that are consistent with our understanding of trophic interactions in grassland ecosystems. Grazing intensity had a clear directional impact across trophic levels, though impacts were in

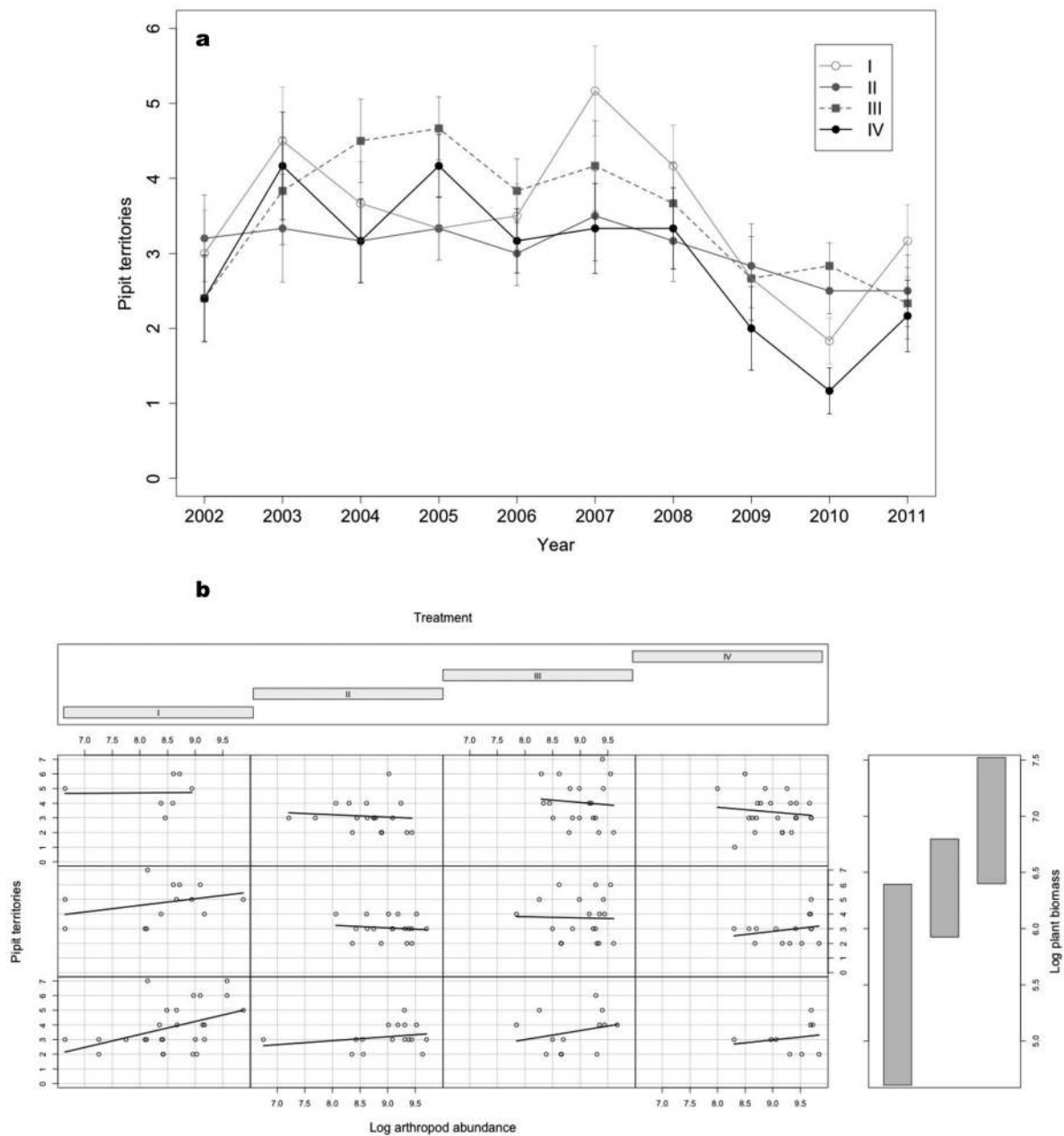


Fig. 3. The effects of grazing treatment on (a) Meadow Pipit breeding territories (mean \pm SE) at Glen Finglas, Scotland over the 10-year period and (b) relationships between the number of breeding territories and arthropod abundance and plant biomass. The coplot shows grazing treatment in columns and plant biomass bins in rows, with the relationships (fitted regression lines) between arthropod abundance and the number of pipit territories for each. Treatment I = 2.72 ewes ha^{-1} , treatment II = 0.91 ewes ha^{-1} , treatment III = mixed sheep and cattle equivalent to 0.91 ewes ha^{-1} and treatment IV = ungrazed.

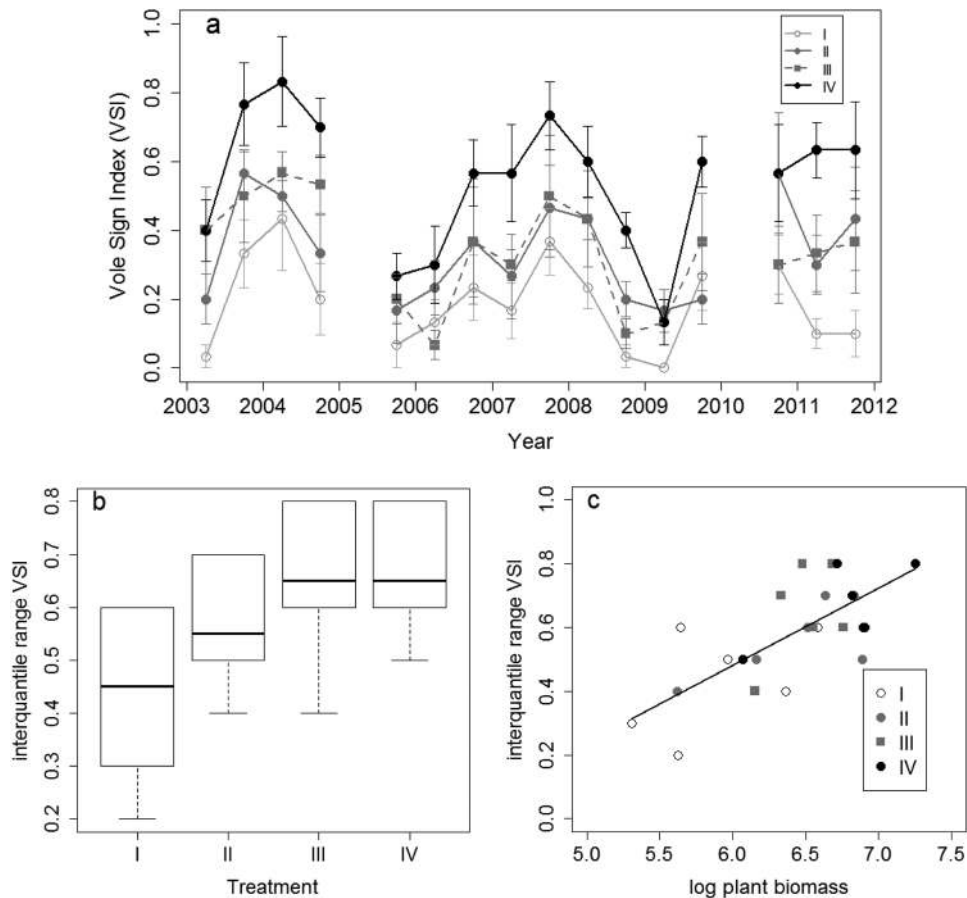


Fig. 4. The effects of grazing treatment on (a) vole density (VSI), (b) vole cycle amplitude (10th to 90th interquartile range of time series of VSI scores), (c) the relationship between vole cycle amplitude and vegetation biomass at Glen Finglas, Scotland. Two spring surveys were missed on years 2005 and 2010 due to logistical reasons. Treatment I = 2.72 ewes ha^{-1} , treatment II = 0.91 ewes ha^{-1} , treatment III = mixed sheep and cattle equivalent to 0.91 ewes ha^{-1} and treatment IV = ungrazed.

some cases not linearly related to grazing intensity.

In our ten-year experiment, vegetation structure was significantly affected by livestock grazing, but not plant diversity. It has been argued that changes in composition and functional diversity in plant communities might take a long time to appear, while changes in vegetation structure are immediate due to the removal of plant biomass by grazers (Pakeman 2004, Diaz et al. 2007). While some degree of positive feedback between ungulate grazing and grazing tolerant plant communities exists (Augustine and McNaughton 1998, Pakeman 2004, Diaz et al. 2007), our results suggest that the net removal of plant biomass by livestock exceeds this positive

feedback, permanently affecting vegetation structure in a way consistent with grazing intensities.

The net removal of vegetation biomass by livestock significantly affected both arthropod abundance and vole cycle amplitude. Clearly, increasing grazing intensity led to lower plant biomass which resulted in lower arthropod abundance and lower vole densities and periodic fluctuations. For arthropods, previous results suggest that increasing grazing intensity leads to a consistent reduction in foliar arthropod abundance and biomass across taxonomic groups (Dennis et al. 2008, Littlewood 2008, Littlewood et al. 2012). Thus, grazing negatively impacts on herbivorous arthropods and also leads to a concomitant reduction of arthropod

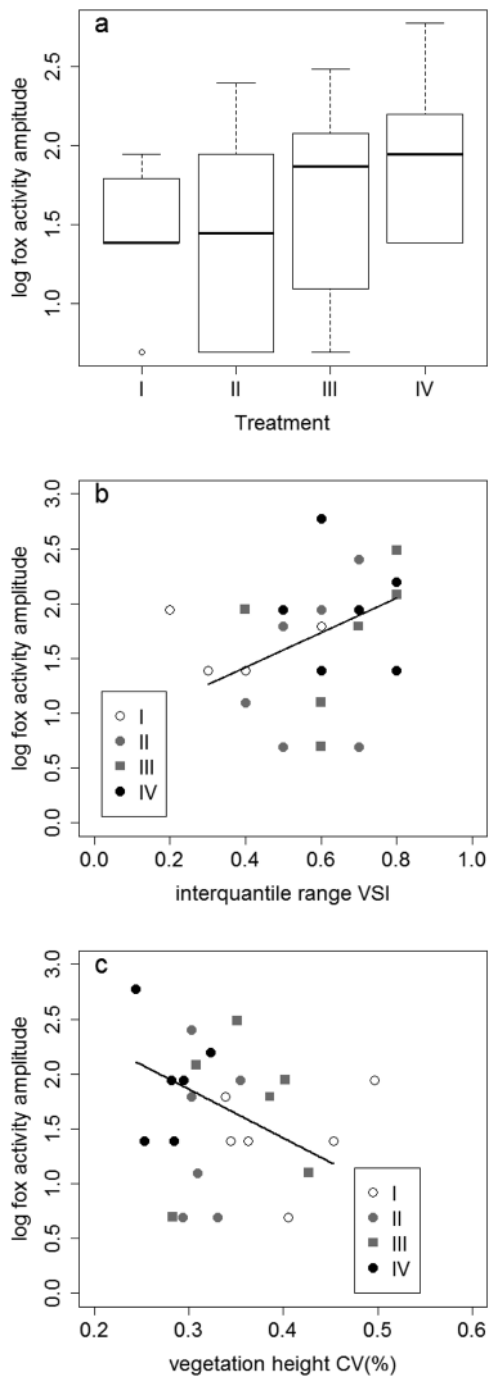


Fig. 5. The effects of grazing treatment on (a) fox activity amplitude; (b) the relationship between fox activity amplitude (logarithmic scale) and vole cycle amplitude; (c) the relationship between fox activity amplitude and vegetation height CV. The outlier in (a), treatment I was the same single influential observation as the leftmost outlier in (b) and rightmost in (c), hence it was removed from the analyses. Treatment I = 2.72

predators. It was not logistically possible for us to study the impacts of livestock grazing on individual arthropod groups, but this warrants further research as it is likely that not all groups will be negatively affected by grazing (such as soil-dwelling insects and/or larvae). For small mammals, the link between rodent cycles and vegetation biomass has been hypothesized previously by several authors (Oksanen et al. 1981, Jedrzejewski and Jedrzejewska 1996), but here ungulate removal of plant biomass allowed us to validate this link experimentally for the first time. Our results indeed suggest that proximal mechanisms responsible for cycle amplitude are strongly correlated with vegetation biomass. We predicted that prey availability to vertebrate predators, represented by foxes and pipits in our experiment, would be greater at intermediate grazing levels due to a combination of heterogeneous vegetation structure and prey abundance. The rationale is that ungulate grazers will open the sward and increase the accessibility of prey. Our results for Meadow Pipits support this prediction, as both invertebrate abundance and vegetation height CV increased the number of breeding territories. In addition, craneflies (*Tipulidae*), a key food resource for some grassland birds of conservation concern including pipits, also peaked at moderate livestock intensities (Dennis et al. 2008), which probably reinforced pipits' preference for this treatment. Earlier work suggested that Meadow Pipits allocate more resources to egg production at intermediate grazing levels (Dennis et al. 2005). Additionally, increased vegetation biomass might increase favorable ground-nesting conditions due to decreased nest exposure to predators (Vickery et al. 2001), which could also explain why breeding pipits select areas with higher vegetation biomass amongst those with sufficient food availability (see Douglas et al. 2008). Furthermore, the number of breeding pipits was also explained by an interaction between plant biomass and year, highlighting the importance of weather. In contrast, red foxes did not show

(continuation of Fig. 5 legend)

ewes ha^{-1} , treatment II = 0.91 ewes ha^{-1} , treatment III = mixed sheep and cattle equivalent to 0.91 ewes ha^{-1} and treatment IV = ungrazed.

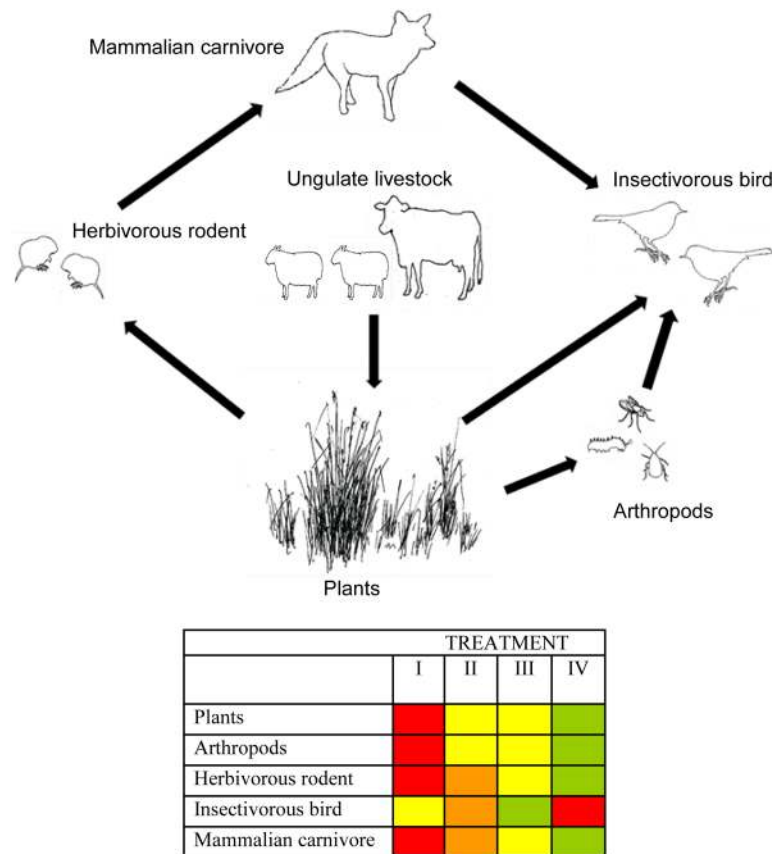


Fig. 6. Diagrammatic representation of the upland system studied in this experiment. For the four grazing treatments, we measured the response in vegetation biomass, arthropod abundance, the number of Meadow Pipit breeding territories, field vole density and red fox activity. For each trophic level we ranked the effects of treatment based on our results from red (highest) to green (lowest). Treatment I = 2.72 ewes ha^{-1} , treatment II = 0.91 ewes ha^{-1} , treatment III = mixed sheep and cattle equivalent to 0.91 ewes ha^{-1} and treatment IV = ungrazed.

the same pattern as pipits, as the amplitude in their activity decreased with vegetation structural heterogeneity and increased with vole cycle amplitude. Hence, our results suggest a strong bottom-up cascading impact of ungulate grazing on foxes (Villar et al. 2013b).

Added value of mixed low-stocked grazing?

Over ten years, our experimental results suggest that decreasing grazing would increase species abundance and overall biomass across trophic levels. However, Meadow Pipits benefited most from low-intensity, mixed livestock grazing. Hence, the question is whether we can reconcile the conservation of biodiversity in upland ecosystems to maintain food-web integrity while allowing for domestic ungulate graz-

ing. Based on our results, we argue that mixed, low-stocking intensity ungulate grazing would provide the best trade-off between 'winners' and 'losers' across trophic levels in this particular type of grassland (Fig. 6). On one hand, our results suggest that the plant-arthropod-insectivorous bird trophic pathway benefits from mixed low-stocking densities, as revealed by the higher number of breeding pipits. On the other hand, both vole cycle amplitude and fox activity amplitude at mixed low-stocking densities were similar to those in the absence of grazing. Given the critical importance of rodent densities and cycle amplitude on populations of endangered carnivore predators (Cornulier et al. 2013), low-intensity, mixed livestock grazing offers substantial benefits compared to moderate homogeneous

grazing for both the preservation of vole cycles of large amplitude and the conservation of associated predators. Furthermore, a large number of other vole predators dependent on small mammal density fluctuations at regular periods in grassland systems, such as diurnal raptors, owls and mustelids (Hanski et al. 1991, Sundell et al. 2004, Millon et al. 2014), could also benefit from this grazed management option, including those that might actively select for a combination of structural heterogeneity and sufficient prey abundance (Aschwanden et al. 2005). Indeed, with small mammal cycles collapsing at continental scales in similar grassland types (Cornulier et al. 2013), a general reduction of livestock in intensively grazed areas could help to mitigate the ecosystem level consequences of such dampening.

It is also important to consider the side-effects of increased predation on alternative prey in these habitats. Several studies had suggested negative effects of generalist predation on ground-nesting birds in grassland systems (Vickery et al. 2001), and there is also evidence of indirect effects of small mammal cycling dynamics on nest predation mediated by generalist predators (Ims et al. 2013), so that increased activity of, e.g., foxes as a result of reduced livestock grazing and high amplitude small mammal cycles could result in increased predation on ground-nesting birds, although nest predation in our study was low (<20%; Dennis et al. 2005). Here we also argue that mixed, low-intensity grazing is a good option for benefitting biodiversity conservation, as it optimizes the compromise of simultaneously preserving large numbers of small mammals, ground-nesting birds and carnivore predators, as suggested by our results. Furthermore, as recent experimental results suggest, low-intensity grazing enhances plant and soil carbon sequestration compared with high intensity grazing (Smith et al. 2014), and mixed livestock grazing systems that include cattle improve livestock productivity and reduce methane emissions compared to equivalent sheep only alternatives (Fraser et al. 2014), which increases the value of this management option.

The broader context

It is now generally recognized that the impacts of livestock grazing on a particular grassland

ecosystem are likely to depend on its historical association with native ungulate grazers (Milchunas et al. 1988) and that the ecology of plants and animals cannot be understood in isolation. For example, the traits of plants and animals under historic grazing pressure in the Serengeti ecosystem suggest coevolution among trophic web members, which affects the functional dynamics (McNaughton 1985). Thus the mechanisms operating at our temperate grassland study site (which historically would have been forest) are likely to be different than in other ecosystems. To better understand food-web dynamics and co-evolutionary interactions, we recommend phylogenetic trait-based analyses of ecological networks (Rafferty and Ives 2013) and how these respond to livestock grazing.

Future directions

Our experiment sheds light on the implications of alternative domestic ungulate management options for grassland food webs and biodiversity. We now need to understand the impacts of grazing at larger spatial scales and on the wider food-web (Villar et al. 2013b). Indeed ungulate foraging in grassland ecosystems and patterns of biodiversity and trophic interactions are density and scale-dependent (Hanski et al. 2013). In addition, there is an urgent need for experiments that account for landscape mosaics with a variable degree of heterogeneity in agricultural management options, reflecting more realistic scenarios closer to real-world landscapes. In the context of meeting global food demands, experiments similar to this are urgently needed to maximize the conservation of biodiversity in grazed systems.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. A chart showing the years in which plant and animal measurements were taken at Glen Finglas, Scotland, 2002–2011. An asterisk represents years in which sampling was undertaken; ‘p’ represents years where at least one sampling period was missed; ellipses indicate years when no measurements were taken.

Sampling	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
Plant height	...	*	*	*	*	*	*	*	*	*
Plant density	...	*	*	*	*	*	*	*	*	*
Plant diversity	*	*	*	*
Arthropod abundance	...	*	*	*	...	*	*	*
Meadow Pipit territories	*	*	*	*	*	*	*	*	*	*
Vole sign index	...	*	*	p	*	*	*	*	p	*
Fox activity	*	*	*	*

Table A2. Model outputs (P values) from all pairwise treatment comparisons and taxa analyzed. See *Methods* for information on models. Values in boldface represent statistically significant differences.

Sampling	I	II	III	IV
Vegetation height				
I	...	0.0085	0.0021	0.0001
II	0.5091	0.0290
III	0.1028
IV
Vegetation height CV				
I	...	0.0016	0.0423	<0.0001
II	0.1263	0.0645
III	0.0025
III
Vegetation biomass				
I	...	<0.0001	<0.0001	<0.0001
II	0.9463	0.0021
III	0.0018
IV
Arthropod abundance				
I	...	0.1424	0.0418	0.0018
II	0.4919	0.0373
III	0.1406
IV
Meadow Pipit territories				
I	...	0.0602	0.8305	0.0346
II	0.0399	0.7755
III	0.0226
IV
Vole cycle amplitude				
I	...	0.1160	0.0147	0.0093
II	0.3167	0.2321
III	0.8393
IV
Fox activity amplitude				
I	...	0.3427	0.0856	0.0101
II	0.4007	0.0724
III	0.3304
IV