

# The short-term effect of sheep grazing on selected invertebrates (Diptera and Hemiptera) relative to other environmental factors in an alpine ecosystem

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## Abstract

Grazing by large herbivores is well-known to influence plant communities, while much fewer studies have been carried out on grazing effects on invertebrates. In Norway, some 2.2 million sheep graze on outlying pastures during summer, most of them in the alpine zone, but no study has reported the relative impact of sheep grazing on invertebrate communities relative to other environmental factors such as the plant community and altitude. A fully replicated landscape-scale experiment (2.7 km<sup>2</sup>) was performed with no, low (25 per km<sup>2</sup>) and high (80 per km<sup>2</sup>) sheep densities in an alpine habitat of Norway (1050–1300 m a.s.l.). *The increased vulnerability hypothesis* (H<sub>1</sub>) predicts that the more folivorous invertebrates, the higher the grazing pressure by sheep, as large herbivore grazing may stress the plants so they are more vulnerable to insect herbivory. *The increased defence hypothesis* (H<sub>2</sub>) predicts increased levels of general anti-herbivore defences, and thus a lower abundance of invertebrates with increasing sheep densities. Contrary to both predictions, no evidence was found that sheep grazing affected invertebrate richness, or abundance of folivorous, predatory or detritivore invertebrates – in a community dominated by Diptera and Hemiptera. Demonstrating an effect will always be a function of sample size, but at least our study shows that other environmental variables (such as plant species richness and functional plant richness) are more important determinants than sheep grazing for the selected invertebrate groups. Our study was short-term (first year of grazing) mainly designed to test specific hypotheses related to induced plant defences; long-term effects are probably owing to the impact sheep may have on vegetation composition, primary production, litter cover and soil properties.

**Key words:** sheep, grazing, Diptera, Hemiptera, alpine ecosystem

## INTRODUCTION

Large herbivores have an impact on ecosystems through processes such as grazing, browsing, trampling, defecation and urination. Compared to the enormous amount of work that has been done to document the effects of grazing by wild and domestic herbivores on plants and soil processes (reviews in Jefferies, Klein & Shaver, 1994; Hobbs, 1996; Augustine & McNaughton, 1998), little has been done to document the impact of large herbivores on invertebrates. The effects of grazing on plants and on insect diversity may be different (Kruess & Tscharntke, 2002), so grazing effects cannot simply be deduced from knowing the effects on plants. One review reported large responses by invertebrates despite small changes in plants

(Milchunas, Lauenroth & Burke, 1998), and more studies of grazing effects on invertebrates are clearly needed (e.g. Stewart, 2001).

That grazing can affect invertebrates comes from a heterogeneous collection of studies including widely different ecosystems and species of large herbivores and targeting different taxonomic groups of invertebrates. In forest ecosystems, elk *Cervus elaphus* browsing on trees affected arthropods in Arizona, U.S.A. (Bailey & Whitham, 2002), and arthropods were more abundant and diverse in (ungulate) grazed than in ungrazed plots in Spain (Gonzalez-Megias, Gomez & Sanches-Pinero, 2004). In Britain, butterfly populations were either positively or negatively affected by cervid grazing, mainly through hindering tree regeneration and hence succession (Feber *et al.*, 2001). Insect species richness was not different between grazed and ungrazed habitats, although insect abundance increased four- to 10-fold in ungrazed vegetation in ponderosa pine-grassland

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in Arizona, U.S.A. (Rambo & Faeth, 1999). Effects may also be apparent in alpine habitats. Intense cattle grazing on a montane grassland in Central Argentina reduced abundance, richness, diversity and biomass of the insect assemblages (family level) (Cagnolo, Molina & Valladares, 2002). Cattle and sheep grazing in Scotland affected the abundance of up to 24 out of 32 Coleoptera species (Dennis, Young, Howard *et al.*, 1997). Carabid beetles, as a family, were more common in plots grazed by reindeer *Rangifer tarandus* in all sites in Finland, while curculionid beetles were more common in ungrazed plots in the birch dominated sites (Suominen *et al.*, 2003).

In Norway, domestic sheep are by far the most common large herbivore during summer, with c. 2.2 million sheep grazing freely (i.e. unherded) in forest and alpine ecosystems (Drabløs, 1997), most of them in the alpine zone. Alpine habitats constitute about 50% of the area of Norway and have been used for grazing since the Bronze age (Kvamme, 1988; Moe, Indrelid & Fasteland, 1988). This habitat thus has a long grazing history, which is known as a key variable when assessing the ecological effects of grazing (Milchunas & Lauenroth, 1993; Milchunas *et al.*, 1998).

Apart from some studies of the grazing effects on plants (Wielgolaski, 1975a,b, 1976; review in Austrheim & Eriksson, 2001), there is limited knowledge about the effect of sheep grazing on other aspects of the alpine ecosystem (review in Mysterud & Mysterud, 1999).

In this study, as part of a fully replicated, landscape-scale experiment in an alpine habitat in Norway, the short-term impact (first year of grazing) of sheep grazing on the invertebrate fauna (mainly Diptera and Hemiptera) is presented. Invertebrates are a wide taxonomic grouping, and there is still limited theory to predict effects on different functional groups. Several different mechanisms are likely to be involved, which can be either positive or negative depending on the particular group or the habitat in which it lives (Suominen *et al.*, 2003), as well as depending on interactions with other factors such as fire (Bailey & Whitham, 2002). In addition, short-term effects may differ from long-term effects of grazing. Based on a review of the literature, the following hypotheses for short-term effects were derived and tested:

H<sub>1</sub>: *the increased vulnerability hypothesis* (Danell & Huss-Danell, 1985). Grazing by large herbivores may make plants more vulnerable to insect herbivory, and thus a positive association between grazing and abundance of folivorous insects has been reported (e.g. Danell & Huss-Danell, 1985). This may in turn increase the presence of both predatory and detritivore insect species. The prediction is thus an increasing abundance of invertebrates with increasing levels of sheep grazing. Long-term grazing of reindeer had a positive effect on galling and mining insects on *Salix lanata* (Olofsson & Strengbom, 2000).

H<sub>2</sub>: *the increased defence hypothesis* (Karban & Baldwin, 1997). Grazing by large herbivores may increase the overall defence levels in plants, decreasing the abundance of folivorous insects, which may again also decrease the abundance of predatory and detritivore species. Our

study is particularly suited for testing this hypothesis, as the experiment was conducted in an area that had been previously lightly grazed, and therefore the effects of long-term changes in vegetation can be ruled out (Hartley, Gardner & Mitchell, 2003). The prediction is thus a decreasing abundance of invertebrates with increasing sheep grazing.

Other factors, such as plant species richness (Hartley *et al.*, 2003) and altitude (Fielding *et al.*, 1999; Hodkinson *et al.*, 1999), are also important for predicting patterns of invertebrate species richness and abundance in alpine habitats. The aim, therefore, was to scale sheep grazing effects relative to these other environmental variables. That grazing effects were indeed present in our area was evidenced both by population growth responses of voles (lower at high than low sheep density), and a lower cover of vascular plants in highly grazed areas (Steen, Mysterud & Austrheim, 2005). This study only assessed short-term effects, but litter removal or changes in vegetation composition may be important in the longer term.

## MATERIAL AND METHODS

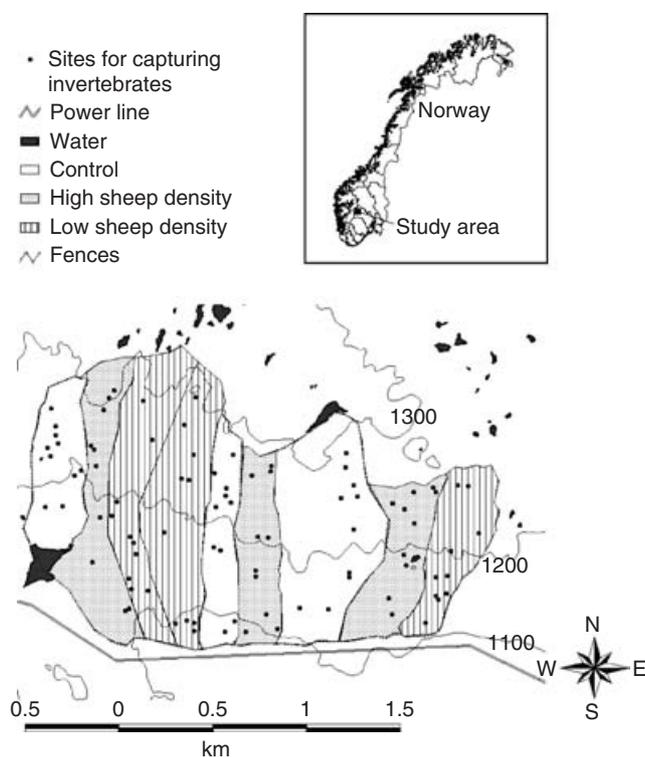
### Study area

A large enclosure covering 2.7 km<sup>2</sup> was established in summer 2001 in Hol municipality, Buskerud county in the southern part of Norway (between 7°55'–8°00' and 60°40'–60°45'). The enclosure consisted of a total of 17.3 km standard sheep fencing (110 cm high). Hol has a sub-continental alpine climate with moderate to low annual precipitation (7–800 mm; Førland, 1993). The soil is moderately base-rich especially in landscape depressions with seepage water (Austrheim, Evju & Mysterud, 2005). The enclosure is situated in an alpine habitat typical of southern Norway, from 1050 to 1300 m a.s.l. (Fig. 1). The lower border is close to the forest line mainly in the lower alpine zone and goes up to the middle alpine zone, and there are only a few scattered birch *Betula* sp. trees in the lowest areas. Vegetation is dominated by low shrubs interspersed with grass-dominated meadows (Rekdal, 2001).

Before fencing, there was very low grazing pressure by domestic sheep (< 10 sheep per km<sup>2</sup>) in the area, and only occasional visits by single individuals or small herds of wild reindeer *Rangifer tarandus* in spring. Moose *Alces alces* occasionally use part of the area for foraging during summer, but large herbivores other than sheep probably have a negligible effect on the system.

### Experimental design

The large enclosure was split into 9 treatment enclosures, hereafter referred to as sub-enclosures, so that 3 full replicates could be run. Altitude is a main determinant of habitat in the mountains, so each sub-enclosure was made so that all had about the same altitudinal range (Fig. 1).



**Fig. 1.** The location of the study area in Hol, Norway, showing also the experimental design and the 90 sites at which invertebrates were sampled.

Average size of the sub-enclosures was 0.3 km<sup>2</sup>, but there was some size variation owing to practical problems in putting up fencing in areas with bare surface rock.

A block-wise randomization design was used. The treatments 'control' (no sheep), low and high density of sheep were randomly assigned for each of 3 adjacent sub-enclosures. In 2001, a professional grazing ecologist (Y. Rekdal, NIJOS) mapped the vegetation of the area and assessed its value for grazing by sheep (Rekdal, 2001). Based on this, 25 sheep per km<sup>2</sup> as low density and 80 sheep per km<sup>2</sup> as high density were used, which covers most of the variation in densities of sheep grazing on mountain pastures in Norway (Mysterud & Mysterud, 1999; Mysterud, Langvatn *et al.*, 2002). Habitats with little or no forage were excluded when calculating densities (such as water bodies and areas dominated by mosses, rocks, lichens and bogs). Density was thus calculated relative to the area of grazeable habitat, so the gross densities were consequently slightly lower. The distribution of main habitat types used by sheep was similar between the sub-enclosures (Rekdal, 2001). Sheep were of the 'Kvit norsk sau' breed (often called 'Dala' breed), which is the most common breed in Norway (Drabløs, 1997). Data reported are from 2002, which was the first year of grazing. The grazing season lasted from the last week of June (green upwell started at the lower altitudes in the enclosure) to the first week of September (plants often dying owing to first frost), which is the same as is used for most mountain regions in southern Norway (e.g. Mysterud, 2000; Mysterud, Stenseth *et al.*, 2001).

A review of studies from North America concludes that low grazing pressure was 32% degree of use of forage plants, moderate grazing pressure was 43%, and heavy grazing pressure was 57% degree of use of the most important forage plants (Holechek *et al.*, 1999). The degree of use of herbs was assessed based on data from 2003 and 2004 for our area (M. Evju, A. Mysterud, G. Austrheim & R. Økland, pers. obs.). The most heavily used herbs were *Solidago virgaurea* (low density 39.0%, high density 59.6%), *Omalotheca norvegica* (low density 25.9%, high density 38.5%), *Rumex acetosa* (low density 6.0%, high density 22.7%), *Saussurea alpine* (low density 5.9%, high density 33.8%), and *Geranium sylvaticum* (low density 4.3%, high density 9.1%), which on average for low sheep density was 16.2% and for high sheep density 32.5%. However, this may be an underestimate of the grazing pressure, as herbs made up only c. 20–30% of sheep diet, while graminoids made up 50–60% (Kausrud, 2004), but it is difficult to assess grazing pressure on graminoids (since they are often removed altogether in the grazing process). Compared to other ranges in Norway, a grazing ecologist described our grazing levels as low and moderate, respectively (Rekdal, 2001).

Total standing crop for dwarf shrubs and grassland communities was 207.6 ( $n = 54$ , year 2002) and 100.2 g/m<sup>2</sup> ( $n = 54$ , year 2001) dry weight. Dwarf shrub communities are dominated by woody species (85%) such as *Vaccinium myrtillus*, *Empetrum hermaphroditum* and *Phyllodoce caerulea*, while graminoids (6%), bryophytes and lichens (8%) and herbs (1%) are rarer. Annual production of graminoids and herbs is 13.1 and 1.3 g/m<sup>2</sup>, respectively. Grasslands are dominated by graminoids (47%) such as *Carex bigelowii* and *Deschampsia flexuosa*, woody species (31%), herbs (12%) and bryophytes and lichens (9%). Annual production of graminoids and herbs is 47.3 and 12.1 g/m<sup>2</sup>, respectively. Neither 2001 nor 2002 had extreme climatic conditions, and the annual production was considered to be comparable among years (G. Austrheim, pers. comm.).

### Invertebrate data

Invertebrate data were collected at 10 randomly selected sites where the plant communities had been described in detail (Austrheim *et al.*, 2005 and below). Sweep-netting was chosen as a method, as we aimed to collect dominating groups of invertebrates in Norwegian mountains such as Diptera and Hemiptera sitting in the vegetation (Totland, 1993; Skartveit & Solhøy, 1997). The netting procedure was standardized using 10 strokes (equals 1 sample) in straight lines back and forth on c. 1 m<sup>2</sup>. One person (CP) did all this work to ensure that there was no between-operator variability. Sampling was carried out from 4 July to 2 August 2002, which is the period with most insect activity in the region. Netting was carried out 3 times at each site, at c. 10-day intervals. Sampling usually took 1 day for each of the 9 sub-enclosures. The order in which the 90 sites were visited was therefore made random at

the block level (3 adjacent sub-enclosures, 1 with each treatment) and then within block.

The invertebrates were identified (by LOH) down to family level. Family identification keys were mainly derived from Borror, Triplehorn & Johnson (1989), while we relied on more detailed sources for Hemiptera (Dolling, 1991) and Diptera (Unwin, 1981). Information about the functional role of the different families was derived from several sources (Ossiannilsson, 1983; Dolling, 1991; Papp & Darvas, 1997, 1998, 2000*a,b*). Although several functional groups may be found within the same family, this was not considered to be a major problem as families were often dominated by a few species with a similar functional role.

### Plant data: community description and functional species diversity

Data on the vascular plant community, coverage and plant height were collected within the same 90 plots (10 in each of the 9 sub-enclosures) each measuring 0.25 m<sup>2</sup> in 2001 (Austrheim *et al.*, 2005). The plots were randomly chosen with a balanced stratified distribution among habitats and altitudinal levels. Quadrats with more than 10% cover of bedrock and stones were excluded. Plant species abundance in each plot is based on presence–absence within 16 subplots (0.0156 m<sup>2</sup>), i.e. frequency data. The following aspects of the plant community were considered:

- (1) *PCA1 and PCA2*. Principal component analysis (PCA) was used to extract information on the plant community (data as percentage and therefore arcsin (square root) transformed before analysis) from the vegetation sites. The first (PCA1) and second (PCA2) axis of the principal component explained, respectively, 30.1% and 20.7% of the variation in the abundance of the 15 most common plant species. PCA1 and PCA2 were used in further analyses as a gross representation of the vegetation community.
- (2) *DCA1 and DCA2*. Detrended correspondence analysis (DCA) was also used for the same purpose with detrending by segments and non-linear rescaling of ordination axes (Hill & Gauch, 1980).
- (3) *Plant species richness*. The number of vascular plant species recorded at a site/plot (ln-transformed).
- (4) *Functional plant richness*. Plant functional groups are usually defined by suites of correlated traits or by species groupings (Lavorel, McIntyre, Landsberg *et al.*, 1997). It has been demonstrated that taxonomic groups differed in most characteristics and were the best way of describing plant functional groups (Dyer *et al.*, 2001). The taxonomic distinctness index (Warwick & Clarke, 1995, 1998; Clarke & Warwick, 1998, 1999) was used to calculate an index of biodiversity that incorporates taxonomic differences. Hereafter data on occurrence of species is referred to as taxonomic richness. Taxonomic levels considered were family,

order, superorder, subclass, class, subphylum and phylum following a recent phylogenetic based taxonomy (Judd *et al.*, 1999). In the calculations, equal weights were given to all taxonomic levels (Warwick & Clarke, 1998). Such a method will give a higher value to a point in which species are from a different taxonomic level, in contrast to species richness that only counts species per se disregarding relatedness.

The correlation between plant species richness and functional richness was so high ( $r_{\text{Pearson}} = 0.9875$ ), that they were not entered in the same model.

Data on (5) *vascular plant cover (%)* and (6) *plant height (cm)* were also used to characterize the vegetation. Vascular plant cover was estimated by visually assessing the coverage (carried by the same person for all sites). Plant height was measured as height of the dominating strata within 5 cm intervals, as there was a marked height structure of the vegetation in this alpine habitat (Steen *et al.*, 2005), and because plant height is important, especially to folivorous invertebrates (Morris, 2000).

### Statistical analyses

As the sites were sampled 3 times during the summer, linear mixed models (LME) were used with ‘site’ as a random effect to account for the non-independency of observations (Lindsey, 1999; Crawley, 2003). As the response variables were counts, they were ln-transformed to avoid heteroscedasticity (i.e. similar to using a Poisson error distribution). Akaike information criterion (AIC) were used for guiding model selection (Burnham & Anderson, 1998; Johnson & Omland, 2004). Model selection was carried out with linear models (LM), since AIC cannot be used based on REML (as in LME). The model with the lowest AIC value is considered to be the most parsimonious model, i.e. the best compromise between explaining most of the variation and simultaneously using as few parameters as possible. A manual procedure was used for finding the best model. Analyses were done in S-Plus versions 6.1 and 6.2 (Venables & Ripley, 1994; Crawley, 2003), except for DCA, which was calculated in CANOCO version 4.5 (Ter Braak & Smilauer, 2002).

### RESULTS

A total of 673 individuals from 44 families and nine orders of invertebrates was recorded. Of these, six families were Hemiptera (Hemiptera Lygaeidae, Hemiptera Miridae, Hemiptera Delphacidae, Hemiptera Cicadellidae, Hemiptera Triozidae, Hemiptera Psyllidae) and 14 families were Diptera (Diptera Limoniidae, Diptera Culicidae, Diptera Ceratopogonidae, Diptera Cecidomyiidae, Diptera Mycetophilidae, Diptera Sciaridae, Diptera Chironomidae, Diptera Empidae, Diptera Dolichopodidae, Diptera Therevidae, Diptera Phoridae,

**Table 1.** Overall mean (and SE) for the treatment effects control (no sheep), low sheep density (25 sheep per km<sup>2</sup>) and high sheep density (80 sheep per km<sup>2</sup>) in Hol, Norway, summer 2002 (first year of grazing)

Response variable/treatment	Control		Low sheep density		High sheep density	
	Mean	SE	Mean	SE	Mean	SE
ln (Invertebrate richness)	0.254	0.092	0.192	0.093	0.246	0.089
ln (Abundance of predatory invertebrates)	0.314	0.050	0.255	0.046	0.253	0.045
ln (Abundance of folivorous invertebrates)	0.502	0.073	0.629	0.094	0.581	0.075
ln (Abundance of detritivore invertebrates)	0.202	0.042	0.170	0.037	0.175	0.040
ln (Abundance of Hemiptera Cicadellidae)	-0.252	0.088	-0.027	0.118	-0.025	0.096
ln (Abundance of Diptera Empidae)	-0.401	0.058	-0.457	0.053	-0.454	0.054

Diptera Chloropidae, Diptera Agromyzidae, Diptera Anthomyiidae).

Individuals from the Hemiptera constituted 57.4% and Diptera constituted 29.9% of the total material, i.e. 87.3%.

Mean values (and SE) for (ln) abundance and family invertebrate richness were similar among treatments (Table 1). Further, sheep grazing was not included in any of the most parsimonious models, increasing the AIC of the model for invertebrate richness (from 659.282 to 662.774), abundance of predatory (from 308.369 to 309.663), folivorous (from 604.506 to 608.386) and detritivore invertebrates (from 231.106 to 234.277) and abundance of Hemiptera Cicadellidae (from 717.363 to 720.106) and Diptera Empidae (from 394.952 to 397.261). Grazing was not estimated to have a significant impact on either invertebrate family-level richness or abundance of the three functional groups (predatory, folivorous and detritivore invertebrates) or the two most common taxonomic groups, Hemiptera Cicadellidae and Diptera Empidae when added to the model with the lowest AIC (Table 2). Therefore we rejected both hypotheses.

Invertebrate family-level richness increased positively with plant species richness, and was also related to the abundance of dominating plants; both the first and second axes of the PCA describing the plant community were significant (Table 2). Abundance of predatory invertebrates peaked in the middle of July (second order term for date) and increased with plant species richness, while abundance of folivorous invertebrates were negatively related to altitude and increased in abundance over the summer. Abundance of detritivore species was only related to plant species richness and positively so.

The most common folivorous insect group was Hemiptera Cicadellidae, and the most parsimonious model explaining its abundance included only date (positive) and altitude (negative) (Table 2).

The most common predatory insect group was Diptera Empidae, and the most parsimonious model explaining its abundance included date up to second order (i.e. peaking mid-season) and functional plant species richness (positive).

## DISCUSSION

In a fully replicated, landscape-scale experiment, we failed to find evidence that low (25 per km<sup>2</sup>) or high (80 per km<sup>2</sup>)

levels of summer sheep grazing affected invertebrate richness, abundance of important functional groups (detritivore, phytophage and predatory invertebrates) or the abundance of the most common folivorous (Hemiptera Cicadellidae) and predatory (Diptera Empidae) insect groups in an alpine habitat in Norway over a short timescale (first year of grazing). Finding an absence of an effect is always difficult in ecology, as this will be a function of sample size. Within the same experiment, it was found that high levels of grazing by sheep lowered summer population growth rates of field voles *Microtus agrestis* (Steen *et al.*, 2005). Vascular plant cover was also significantly lower in the high sheep density sub-enclosures compared to the controls, while cover in low sheep density and control was similar (Steen *et al.*, 2005). Therefore, grazing effects were certainly present in the area. Corroborative evidence that the insect communities were not much affected by sheep grazing was the lack of difference in populations of insectivorous shrews between the different sub-enclosures (H. Steen & A. Mysterud, pers. obs.). The main conclusion from our study is therefore that other factors, such as plant community composition and diversity as well as altitude (Ottesen, 1996) are more important for determining richness and abundance at the family level of these specific insect groups than short-term effects of sheep grazing. There is increasing attention paid to plant functional groups (Lavelle *et al.*, 1997; Dyer *et al.*, 2001; McIntyre & Lavelle, 2001). Plant species richness and functional richness were highly correlated in our area, and the use of functional plant richness did not improve the predictive ability for patterns of invertebrate richness.

Grazing as a process has both short- and long-term effects (e.g. Jefferies *et al.*, 1994). At the shortest time-scales, induced plant defences towards herbivory have received considerable attention (e.g. Karban & Baldwin, 1997). For insects, lowering of flowering plant abundances (Augustine & Jordan, 1998), total standing biomass or height (Anderson, 1994; Clary & Leininger, 2000) or structure of vegetation (Dennis, Young & Gordon, 1998; Morris, 2000) can also be important factors for invertebrates after just 1 year of grazing. Our study was conducted in the first year of grazing in a previously lightly grazed area and, therefore, our conclusion only holds for short-term effects. Grazing over the long-term is also known to affect plant diversity and succession patterns in northern, arctic and alpine ecosystems (reviews

**Table 2.** Parameter estimates from the linear mixed models (site as random effect) for the most parsimonious (linear) models, but with sheep grazing added to test the hypotheses (see Appendix)

Parameter	l.s. estimate	SE	d.f.	<i>t</i>	<i>P</i>
ln (Invertebrate richness)					
Intercept	-0.4120	0.2674	179	-1.541	0.125
Plant community: PCA1	-0.0610	0.0309	85	-1.972	0.052
Plant community: PCA2	0.1183	0.0343	85	3.451	0.001
ln (Plant species richness)	0.3062	0.1099	179	2.786	0.006
Sheep density (low vs control)	-0.0635	0.1373	85	-0.463	0.645
Sheep density (high vs control)	-0.0826	0.1387	85	-0.596	0.553
ln (Abundance of predatory invertebrates)					
Intercept	-53.6782	12.8651	177	-4.172	<0.001
ln (Plant species richness)	0.1506	0.0433	177	3.480	0.001
Date	0.5348	0.1282	177	4.171	<0.001
(Date) <sup>2</sup>	-0.0013	0.0003	177	-4.168	<0.001
Sheep density (low vs control)	-0.0558	0.0661	87	-0.844	0.401
Sheep density (high vs control)	-0.1038	0.0669	87	-1.553	0.124
ln (Abundance of folivorous invertebrates)					
Intercept	2.7883	1.3916	179	2.004	0.047
Altitude	-0.0040	0.0009	86	-4.282	<0.001
Date	0.0131	0.0040	179	3.271	0.001
Sheep density (low vs control)	0.0082	0.1346	86	0.061	0.951
Sheep density (high vs control)	0.0178	0.1323	86	0.135	0.893
ln (Abundance of detritivore invertebrates)					
Intercept	-0.0487	0.0882	179	-0.552	0.582
ln (Plant species richness)	0.1141	0.0360	179	3.170	0.002
Sheep density (low vs control)	-0.0299	0.0551	87	-0.543	0.589
Sheep density (high vs control)	-0.0498	0.0555	87	-0.897	0.372
ln (Abundance of Hemiptera Cicadellidae)					
Intercept	0.3467	1.7320	179	0.200	0.842
Date	0.0239	0.0050	179	4.836	<0.001
Altitude	-0.0044	0.0012	86	-3.759	0.000
Sheep density (low vs control)	0.0939	0.1682	86	0.559	0.578
Sheep density (high vs control)	0.1467	0.1653	86	0.887	0.377
ln (Abundance of Diptera Empididae)					
Intercept	-74.6116	15.0330	178	-4.963	<0.001
ln (Functional plant richness)	0.1425	0.0509	86	2.797	0.006
Date	0.7359	0.1498	178	4.913	<0.001
(Date) <sup>2</sup>	-0.0018	0.0004	178	-4.916	<0.001
Sheep density (low vs control)	-0.0516	0.0788	86	-0.655	0.514
Sheep density (high vs control)	-0.0964	0.0796	86	-1.211	0.229

in Jefferies *et al.*, 1994; Austrheim & Eriksson, 2001). The Hemiptera is also a major group of herbivorous insects on moorlands in Scotland, where a reduction in grazing altered vegetation structure and hence the composition of the hemipteran community (Hartley *et al.*, 2003). As plant richness was the main determinant for invertebrate richness (dominated by families of Diptera and Hemiptera) in our study, it may therefore be that grazing mainly affects these invertebrates through long-term effects on the pattern of plant distribution.

Spatial scale is also of profound importance in ecology (e.g. Wiens, 1989; Bissonette, 1997). Our study was fully experimental at a landscape scale, while most studies of grazing effects are conducted within small enclosures. In a survey of grazing studies, 86% of small refuge studies reported positive effects on plant diversity compared to 50% for large refuges (Milchunas & Noy-Meir, 2002). Similarly, comparing a wide variety of grazing studies

in North America, it was concluded that grazing mainly impacted plant communities at local scales, and that climate was more important at coarse scales (Stohlgren, Schell & Heudel, 1999). The kind of grazing system may also be important, with rotational grazing systems regarded as more beneficial than continuous grazing for diversity of both plants and insects (Gebeyehu & Samways, 2003). At present, we are unfortunately quite far from having a good theoretical understanding that would enable us to predict effects on different functional invertebrate groups subject to different types of grazing in different systems.

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