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PLANT-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

# Grazing-induced effects on soil properties modify plant competitive interactions in semi-natural mountain grasslands

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**Abstract** Plant–soil feedbacks are widely recognized as playing a significant role in structuring plant communities through their effects on plant–plant interactions. However, the question of whether plant–soil feedbacks can be indirectly driven by other ecological agents, such as large herbivores, which are known to strongly modify plant community structure and soil properties, remains poorly explored. We tested in a glasshouse experiment how changes in soil properties resulting from long-term sheep grazing affect competitive interactions (intra- and inter-specific) of two graminoid species: *Nardus stricta*, which is typically abundant under high sheep grazing pressure in British mountain grasslands; and *Eriophorum vaginatum*, whose abundance is typically diminished under grazing. Both species were grown in monocultures and mixtures at different densities in soils taken from adjacent grazed and ungrazed mountain grassland in the Yorkshire Dales, northern England. *Nardus stricta* performed better (shoot and root biomass) when grown in grazing-conditioned soil, independent of whether or not it grew under inter-specific competition. *Eriophorum vaginatum* also grew better when planted in soil from the grazed site, but this occurred only when it did not experience inter-specific competition with *N. stricta*. This indicates that plant–soil feedback for *E. vaginatum* is dependent on the presence of an inter-specific competitor. A yield density model showed that indirect effects of grazing increased the intensity of intra-specific competition in both species in comparison with ungrazed-conditioned soil. However, indirect effects of grazing on the intensity of inter-specific competition were species-specific favouring *N. stricta.* We explain these asymmetric grazing-induced effects on competition on the basis of traits of the superior competitor and grazing effects on soil nutrients. Finally, we discuss the relevance of our findings for plant community dynamics in grazed, semi-natural grasslands.

**Keywords** Plant community dynamics · Upland grasslands · *Nardus stricta* · *Eriophorum vaginatum* · Plant–soil interactions

## Introduction

The study of factors that modify plant competitive interactions is key to understanding plant community dynamics and species coexistence. A number of mechanisms and ecological factors that can modify plant competition have been identified (Aarssen 1983, 1989; Bengtsson et al. 1994; Pacala and Tilman 1994; Chesson 2000; Barot 2004). These include those that promote heterogeneity across spatial and temporal scales (Pacala and Tilman 1994; Chesson 2000; Barot 2004), and others where species-specific plant responses to environmental heterogeneity (morphological, physiological or phenological) can reduce niche overlap (Casper and Jackson 1997; Grime 2001; McKane et al. 2002). In another line of enquiry, Bever et al. (1997) highlighted the importance of plant–soil feedbacks in regulating plant competition. These feedbacks

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are defined as the positive or negative effects that a soil, in which a certain plant species has grown, has on the performance of that or another plant species. As interest in aboveground–belowground linkages has risen in recent years (Bardgett and Wardle 2010), numerous studies have shown the importance of plant–soil feedbacks in structuring plant communities (Blomqvist et al. 2000; Van der Putten et al. 2001; Klironomos 2002; Bezemer et al. 2006; Casper and Castelli 2007; Harrison and Bardgett 2010).

It is also well known that grazing by large herbivores directly modifies plant competition by reducing dominance of some plant species through consumption (Anderson and Briske 1995; Hartley and Amos 1999) or through changes in disturbance regimes (Coffin and Lauenroth 1988; Bardgett and Wardle 2010). However, despite widespread recognition that grazing can also strongly modify soil microbial communities and rates of nutrient mineralization (Bardgett et al. 1999a; Hamilton and Frank 2001; Frank et al. 2003), little is understood about the indirect effects of grazing on plant competitive interactions via its effects on soil properties. In temperate grasslands in particular, previous studies have shown that grazing can cause shifts in the composition of soil microbial communities leading to increases in rates of nitrogen (N) mineralization, and hence N availability to plants (Bardgett et al. 1997, 2001; Frank et al. 2000). Such changes in soil communities and nutrient availability are likely to affect plant–plant interactions through plant–soil feedbacks, thereby modifying vegetation dynamics. However, as far as we know, the potential for grazing to indirectly affect plant–plant interactions via this route has not been explored.

The aim of this study was to test how grazing-induced changes on soil properties affect intra- and inter-specific competitive interactions between *Nardus stricta* L and *Eriophorum vaginatum* L, two dominant graminoids, which are known to vary in dominance in grazed and ungrazed semi-natural mountain grasslands (Grant et al. 1985; Marrs et al. 1988). Specifically, we tested the hypothesis that plant competitive interactions would be modified by grazing-induced changes in soil conditions, and consequently that each species would perform better relative to its neighbour in the soil in which it is most dominant. This was tested by growing naturally occurring populations of both plant species in a glasshouse competition experiment using soils taken from a grazed *N. stricta*-dominated acidic-grassland and from an adjacent ungrazed area where *E. vaginatum* was more dominant. These areas formed part of a landscape-scale re-wilding experiment established in 2000 in the Yorkshire Dales, northern England. Previous work at this site by Medina-Roldán et al. 2012 showed that cessation of sheep grazing leads to significant changes in aboveground and belowground properties, including a shift in the dominant graminoid from *N. stricta* to *E. vaginatum*, and an associated decrease in soil microbial activity and soil N availability.

## Materials and methods

### Experimental design

We tested how effects of grazing on soil properties affected *N. stricta–E. vaginatum* interactions using a plant competition experiment combined with a plant–soil feedback approach. Whereas the 'ideal' plant–soil feedback experiment involves cultivating soil with targeted plant species, the use of soil from habitats with known plant occurrences is common practice (Kulmatiski and Kardol 2008). We sampled soil in December 2008 from two areas in the Ingleborough National Natural Reserve in the Yorkshire Dales National Park, northern England (54.18°N, 2.36°E). One area is an acidic upland grassland dominated by *N. stricta* (Rodwell 1992) and subjected to continuous grazing by sheep, whereas the other is an ungrazed adjacent site that was fenced-off in 2000 in order to exclude domestic herbivores (see Medina-Roldán et al. 2012 for more information about the site characteristics). Soils are formed from carboniferous sandstones in the Yoredale group (Waltham 2008), and characterised by a low pH (4.5) and an organic surface horizon of 20–30 cm depth (Medina-Roldán et al. 2012).

Exclusion of herbivores has resulted in an increase in the abundance of *E. vaginatum* and ericaceous shrubs, decreases in soil microbial activity and soil N availability, and an increases in soil moisture content (Medina-Roldán et al. 2012). Using a spade, we sampled soil from the first 30 cm within the peaty topsoil layer at five randomly chosen points in each of the grazed and ungrazed areas in order to collect sufficient material for the experiment. Soil samples from each plot were merged into a composite soil sample. Soils were passed through a 2-mm mesh to remove roots and plant residues and stored at 4°C. Since our aim was to test how plant–plant interactions can be affected by grazing-induced effects on soil biological properties, we eliminated confounding effects caused by differences in initial soil nutrient contents between grazed and ungrazed soils by mixing each soil with sand in a 1:5 ratio. This practice is common in plant–soil feedback experiments (Bever 1994; Frank et al. 2003), and has the advantage that differences in soil properties at the end of the experiment can be assigned purely to experimental factors. Most soil properties including extractable inorganic N did not differ significantly in the soil–sand mixtures between the soils taken from the grazed and ungrazed areas at the beginning of the experiment (Table 1), except for a higher net potential $NH_4^+$ mineralisation rate in the grazed compared

**Table 1** Summary of soil properties of soil–sand mixtures in continuously-grazed acidic grassland (G+) and a contiguous grazing-excluded moorland (G−) in the Yorkshire Dales, northern England

| Variable | G+ | G− | *t* value (*P*) |
|---|---|---|---|
| $C_{mic}$ | 127 (13) | 159 (26) | 1 |
| $N_{mic}$ | 49 (2.5) | 48 (1.4) | −0.1 |
| $NH_4^+$av | 16.0 (0.4) | 14.5 (0.3) | −2.0* |
| $NO_3^-$av | 2.1 (0.25) | 1.6 (0.17) | 1.5 |
| $NH_4^+$min | 1.19 (0.07) | 0.26 (0.09) | −8.0*** |
| $NO_3^-$min | −0.15 (0.01) | −0.11 (0.01) | 1.5 |
| $C_{soil}$ | 6.0 (0.15) | 7.3 (0.30) | 4.5** |
| $N_{soil}$ | 0.27 (0.005) | 0.26 (0.006) | 1.3 |

Values are means (SEM) and *t* test for pairwise comparisons ($df = 6$)

$C_{mic}$ and $N_{mic}$: soil C and N in microbial biomass (mg kg dry soil$^{-1}$), respectively; $NH_4^+av$, $NH_4^+min$, $NO_3^-av$, $NO_3^-min$: *av*, soil extractable concentration (mg kg dry soil$^{-1}$) and *min*, net potential mineralization rates (mg kg dry soil$^{-1}$ day$^{-1}$) for $NH_4^+$ and $NO_3^-$, respectively; $C_{soil}$ and $N_{soil}$: total soil C and N (%), respectively

Significant differences between sites: * $0.1 < P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

with the ungrazed soil, and a slightly higher total C content in the ungrazed than the grazed soil (Table 1). The mixture was used to fill 1-L experimental pots (10 × 12 cm) where plant species were planted, as described next.

Competitive interactions between *N. stricta* and *E. vaginatum* were assessed with a full-factorial design with four combined densities of each plant species in order to separate intra- and inter-specific components of competition. This design is commonly used to study plant–plant competitive interactions because it overcomes many of the disadvantages present in the additive or substitution series (Snaydon 1991; Watkinson and Freckleton 1997; Inouye 2001). Intact soil turves taken from the grazed and ungrazed areas, with plants of *N. stricta* and *E. vaginatum*, respectively, were sampled on the same date as soil, and taken to Lancaster University where they were placed in a glasshouse for 6 weeks. Once the plants had grown fully-green tissues, they were split into individual tillers with 2 fully developed leaves and roots. We removed all soil from tiller roots and disinfected them superficially with a 10% bleach solution before planting them in the experimental pots. After soil removal and disinfection, tillers of each species were randomly assigned to 1 out of 32 combinations of the full-factorial arrangement of soil source (grazed vs. ungrazed) and four tiller densities for each plant species (4 densities for *N. stricta* and 4 densities for *E. vaginatum*), with five replicates per treatment ($2 \times 4 \times 4 \times 5 = 160$). We used the following plant densities for each plant species: no plants; low density = 2 tillers; medium density = 4 tillers; and high density = 6 tillers. Tillers were planted equidistantly, and in the case of both species mixtures, tiller position was assigned randomly. After planting, tillers were allowed to establish for another 6 weeks. During this period, unsuccessful tillers were replaced until full establishment was achieved. At this time, the experiment was allowed to run for 7 months with a 12/12 h light–dark cycle, a mean irradiance of 430 W m$^{-2}$ (SD 190 W m$^{-2}$), mean average temperature of 20°C, and mean atmospheric humidity of 55%. Experimental pots were watered every day with deionized water to reach approximately 60% of the water holding capacity (65% gravimetric soil content).

## Plant measures

In late September 2009, experimental pots were harvested by cutting the shoot material. Crowns (defined as the transitional tissue between shoots and roots) and roots were separated from the soil manually and sorted by species, except for a root fraction (0.36 ± 0.03 g per pot) which could not be assigned with certainty to any of the species, and which was not included in the analyses. All plant material was oven-dried at 70°C for 48 h and weighed per species to determine individual tiller weight, total shoot, crown, and root biomass, and to partition of total biomass among these three plant components.

## Soil measures

The soil collected after plants were harvested was passed through a 2-mm sieve and stored at 4°C until laboratory analysis took place. Soil was analysed for concentrations of extractable ammonium ($NH_4^+$) and nitrate ($NO_3^-$), for soil microbial biomass carbon (C) and N, and basal respiration, as a measure of microbial activity. Soil $NH_4^+$ content was measured by extracting 10 g of fresh soil in 1 M KCl, stirring the extracts during 1 h in an orbital shaker, filtering them in Whatman paper No.1, and determining $NH_4^+$ concentration by continuous-flow colorimetry using the sodium nitroprusside reaction in a Bran and Luebbe AutoAnalyzer 3. Nitrate was measured as for $NH_4^+$, but through the sulfanilamide method. Microbial biomass C and N were assayed by the chloroform ($CHCl_3$) fumigation extraction technique. Microbial biomass was estimated according to Vance et al. (1987) by extracting 5 g of both non-fumigated and 24-h $CHCl_3$-fumigated fresh soil in 0.5 M $K_2SO_4$, shaking the soil extract for 30 min in an orbital shaker, and filtering the soil extract in Whatman paper No.1. Microbial biomass C was calculated as the difference between fumigated and non-fumigated samples after analysing the extracts for C content in a Shimadzu 5000A TOC analyser (Shimadzu Inc., Japan), and using an extraction efficiency of 0.45 (Sparling et al. 1990). Microbial biomass N was assayed by digesting the soil extracts with potassium persulfate (Cabrera and Beare 1993) and determining N contents with flow colorimetry as described above. Microbial biomass N was calculated as the N difference between fumigated and non-fumigated soils using an extraction efficiency of 0.54 (Brookes et al. 1985). Soil basal respiration was determined following Bardgett et al. (1999b) as the production of $CO_2$ by incubated soils (24-h incubated at 25°C, 1 g dry mass equivalent soil within sealed McCartney bottles). The $CO_2$ production after the incubation period was measured by injecting 1 mL of sample from the bottles' head-space into an ADC 225 MK3 IRGA (ADC Bioscientific, Hoddesdon, UK), and using respective blanks and $CO_2$ standards. Soil moisture content was standardised in all samples at 30% for the basal respiration determinations.

## Data analysis

### *Plant biomass responses*

Plant responses to soil source and plant competition were analysed following two approaches. First, soil source (grazed vs. ungrazed) and type of competition (intra-specific = monocultures vs. inter-specific = both plant mixtures) effects on plant response variables per plant species were tested with ANOVA. Plant response variables included: total shoot biomass, crown biomass, root biomass, shoot to belowground (crown + roots) ratio, and the proportion of total biomass partitioned to shoots, roots or crowns. For brevity, in the description of the results, we use grazed and ungrazed to make reference to the soils from the two areas with contrasting grazing regimes, and competition effect for the difference between inter-specific and intra-specific competition. In the second approach, we used a plant competition model, as described below.

### *Intra- and inter-specific competition*

Shoot biomass per individual tiller for each species was analysed by the hyperbolic competition model (Mead 1970). This model has the form:

$$w_i = w_{mi} \cdot \left[1 + \alpha_i \cdot \left[x_i + \varepsilon_j \cdot x_j\right]\right]^{-1} \tag{1}$$

which, on a natural logarithms basis, can be expressed as:

$$\log[w_i] = \log[w_{mi}] - \log\left[1 + \alpha_i \times x_i + \alpha_{ij} \times x_j\right] \tag{2}$$

where $w_i$ is the weight of an individual of species i which is modelled as a function of the density of conspecifics ($x_i$) (i.e., intra-specific competition) and heterospecifics ($x_j$) (i.e., inter-specific competition). Parameter $w_{mi}$ is the mean weight of an individual of plant species i experiencing no competition, $\alpha_i$, $\alpha_{ii}$ are parameters which measured the strength of intra- and inter-specific competition, respectively, and $\varepsilon_j$ can be considered as a plant species equivalence term (how many individuals of the species j are necessary to have a completive effect equivalent to a conspecific individual) (Freckleton and Watkinson 1997). Parameter estimates for the model were obtained by using the non-linear least squares estimation routine in *R*. Effects of soil source on intra- and inter-specific competition for each species were determined by comparing the values of the parameters in the model for plants which were grown in grazed versus ungrazed soil (4 models).

### *Soil responses*

Differences in soil extractable $NH_4^+$ and $NO_3^-$, microbial biomass C and N, and basal soil respiration between grazed and ungrazed soil at the end of the experiment were analysed with ANOVA using soil source (grazed and ungrazed) as a factor. We were interested in testing how the presence of a plant species affected soil nutrient cycling, including N availability, since this is a trait involved in plant competition (e.g. Tilman and Wedin 1991). The fact that most properties between grazed and ungrazed soil did not differ at the beginning of the experiment (Table 1), and that we had a non-planted treatment (density of both species = 0), allowed us to test such "plant species" effects on soil (using plant species presence or absence). To do this, we included in the ANOVA a factor that we called type of pot, based on the presence or absence of our plant species (four levels: non-planted, monocultures of *E. vaginatum* and *N. stricta*, and both species mixtures). Note that testing species effects at the end of the experiment is different from the main objective of testing grazing-induced effects on plant competition. Although we added a fixed water volume to the pots during the experiment duration, there was pot-to-pot variation in soil water content at the end of the experiment. Thus, final soil water content was used as a covariate for most of the analyses, except for basal respiration, as moisture was standardised for this measure (see "Soil measures"). All variables were transformed to meet the criteria of normality and variance homogeneity when necessary, but results are presented for untransformed values (mean ± SE), except in the case of the competition model. All analyses were carried out with the statistical package R for Linux (R Development Core Team 2010), using a significance level of $P = 0.05$.

## Results

### Plant biomass responses

Shoot biomass of *E. vaginatum* in monocultures was approximately two-fold greater in plants grown in grazed than in ungrazed soil, but it was similar in both soils when plants experienced inter-specific competition (soil source × competition interaction, $F_{1,108} = 45.0, P < 0.001$; compare C− and C+ in Fig. 1a). Likewise, *E. vaginatum* crown biomass was reduced by inter-specific competition only in the grazed soil (Fig. 1b; soil source × competition interaction, $F_{1,107} = 8.5$, $P < 0.01$). Negative effects of inter-specific on *E. vaginatum* root biomass were marginally greater in grazed than in ungrazed soil (Fig. 1c; soil source × competition interaction, $F_{1,107} = 2.0$, $P = 0.06$).

In contrast to *E. vaginatum*, the negative effect of inter-specific competition on *N. stricta* shoot biomass (Fig. 1a; competition effect, $F_{1,111} = 25.0$, $P < 0.001$) was independent from soil source (soil source × competition interaction, $F_{1,111} = 0.5$, $P = 0.4$). Shoot biomass of *N. stricta* was 92% larger in grazed than in ungrazed soil (soil source $F_{1,111} = 73.6$, $P < 0.001$). Likewise, inter-specific competition reduced *N. stricta* crown biomass (Fig. 1b; competition effect, $F_{1,108} = 24.4$, $P < 0.001$), but this response was independent from soil source (soil source × competition interaction, $F_{1,108} = 0.3$, $P = 0.5$). *Nardus stricta* crown biomass was on average 25% greater when grown in grazed than in ungrazed soil (Fig. 1b; soil source effect, $F_{1,108} = 2.6$, $P < 0.01$). Averaged across soils, inter-specific competition decreased *N. stricta* root biomass by 40% (competition effect, $F_{1,107} = 30.8$, $P < 0.001$), and this reduction was independent from soil source again (Fig. 1c; soil source × competition interaction $F_{3,107} = 2.6$, $P = 0.1$). Root biomass of *N. stricta* was 51% larger in grazed than in ungrazed soil (Fig. 1c; soil source $F_{1,107} = 40.2$, $P < 0.001$).

### Biomass partitioning

For *E. vaginatum*, 15% lower (competition effect, $F_{1,106} = 7.1$, $P < 0.01$) and 22% greater (competition effect, $F_{1,106} = 5.9$, $P < 0.05$) biomass was allocated to shoots and crowns; respectively; when plants experienced intersspecific in comparison to intra-specific competition (Fig. 2a). Inter-specific competition did not affect biomass allocated to roots by *E. vaginatum* (competition effect, $F_{1,106} = 0.03$, $P = 0.8$), but the above:below (crowns + roots) ratio of this sedge species was reduced under inter-specific competition with *N. stricta* (Fig. 1d; competition effect, $F_{1,106} = 6.5$, $P < 0.05$). *Eriophorum vaginatum* biomass partitioning did not vary between grazed and ungrazed soils in any case (soil source effect for proportion in: shoots, $F_{1,106} = 1.9$, $P = 0.1$; crowns, $F_{1,106} = 0.7$, $P = 0.3$; roots, $F_{1,106} = 0.06$, $P = 0.8$; and above:below ratio $F_{1,106} = 2.1$, $P = 0.1$).

On the other hand, for *N. stricta*, biomass allocated to shoots and crowns was 13% greater (soil effect, $F_{1,105} = 13.6$, $P < 0.001$) and 20% lower (soil source effect, $F_{1,105} = 26.9$, $P < 0.001$), respectively, when grown on grazed compared to ungrazed soil (Fig. 2b). There was no effect of soil source on biomass allocation to roots (soil effect, $F_{1,105} = 0.8, P = 0.3$), but the above: below ratio of *N. stricta* was greater in grazed than in ungrazed soil (Fig. 1d; soil effect, $F_{1,105} = 13.2$, $P < 0.001$). Inter-specific competition did not modify *N. stricta* biomass partitioning in any case (competition effect for proportion in: shoots, $F_{1,105} = 1.2$, $P = 0.2$; crowns, $F_{1,105} = 0.3$, $P = 0.5$; roots $F_{1,105} = 1.3$, $P = 0.3$; and above: below ratio $F_{1,105} = 1.1$, $P = 0.2$).

### Intra- and inter-specific competition parameters

Biomass of an individual plant experiencing no intra- nor inter-specific competition (represented by the parameter $w_{mi}$) was larger in the grazed than in the ungrazed soil for both species (Table 2; a ratio for $\log[w_{mi}]$ between grazed and ungrazed soils >1). Also, the strength of intra-specific competition ($\alpha_i$) increased in grazed in comparison with ungrazed soil for both species (Table 2; ratio for $\alpha_i$ between grazed and ungrazed soils >1). Whereas intra-specific competition was higher in grazed soils for both plant species, the effect of soil source on inter-specific competition was different for each plant species. Thus, the competitive effect that *N. stricta* exerted on *E. vaginatum* increased two-fold in grazed compared to ungrazed soil (Table 2; a ratio of 2.05 for $\varepsilon$*E.vaginatum* between grazed and ungrazed soils). On the other hand, the effect that *E. vaginatum* had on *N. stricta* decreased by almost a half in grazed compared to ungrazed soil (Table 2, a ratio <1 for $\varepsilon$*N.stricta* between grazed and ungrazed soils).

### Soil responses

We tested whether the presence of a particular plant species affected soil properties at the end of the experiment by comparing non-planted pots (density of both species = 0) against each species monocultures and pots where both species grew in mixtures (pot treatment effect hereafter).

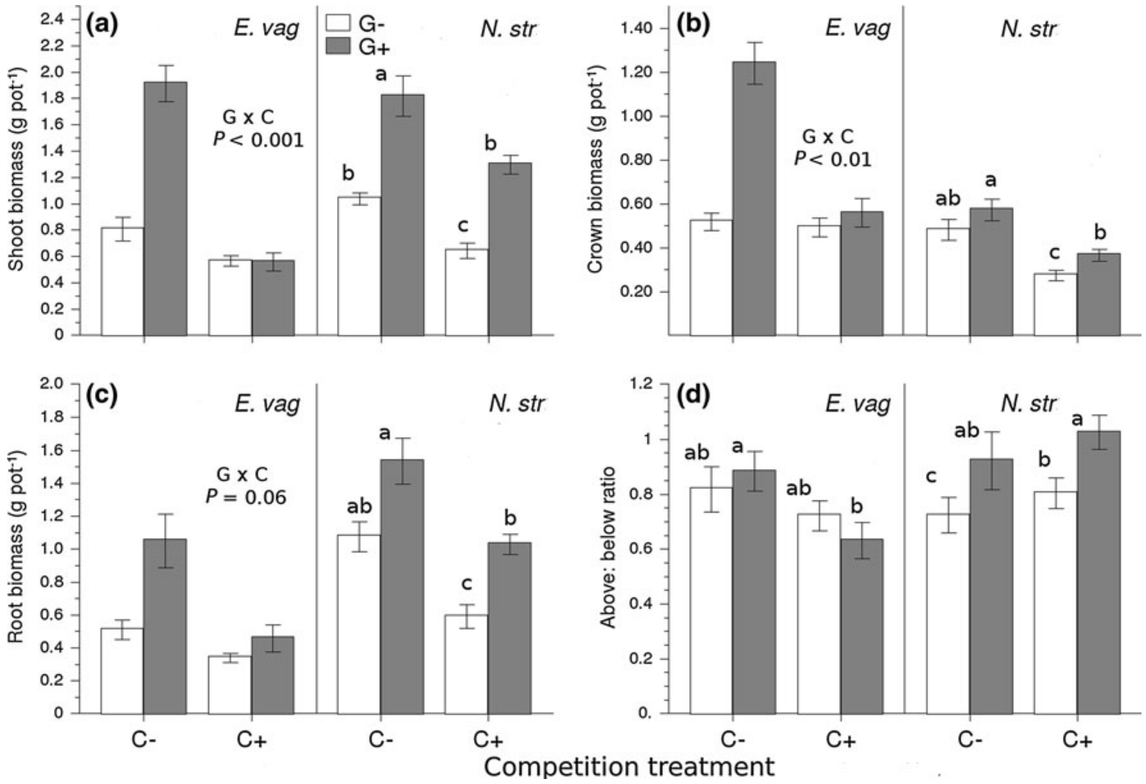

**Fig. 1** Effects of soil source (*G*) and competition (*C*) on: **a** total shoot biomass, **b** crown biomass, **c** root biomass, **d** above:below (crown + -root) ratio of *Eriophorum vaginatum* (*E. vag*) and *Nardus stricta* (*N. str*). Soil source effect represents differences in plant response to soil coming from a continuously-grazed acidic grassland (*G*+) or a contiguous grazing-excluded moorland (*G*−) in the Yorkshire Dales, England. Plants were grown in monocoltures (*C*−) or inter-specific competition (*C*+). *Bars* mean ± SE. *Different letters* within a species indicate significant differences at $P \leq 0.05$ after Tukey honest significant differences test. Significant and marginal interactions ($G \times C$) are also indicated. Statistical tests were carried out with transformed values, but non-transformed values are depicted for clarity

There was a significant interaction between soil source and pot treatment for microbial biomass C ($F_{3,110} = 2.6$, $P < 0.05$) as a result of the large difference between ungrazed and grazed soils in the non-planted pot treatments (Fig. 3a). Despite the significant interaction, there was no evidence that microbial biomass C differed between the pot treatments (Fig. 3a; $F_{3,110} = 1.8$, $P > 0.05$). On the other hand, microbial biomass N was 12% greater in ungrazed than grazed soil (Fig. 3c; $F_{1,134} = 4.0$, $P < 0.05$), but only as a result of the difference between soil sources in the non-planted pot treatments. There was no effect of soil source (Fig. 3b; $F_{1,110} = 1.5$, $P > 0.05$) nor pot treatment ($F_{3,110} = 1.0$, $P > 0.05$) on microbial biomass C:N ratio. Soil basal respiration was 13% greater in grazed than ungrazed soil (Fig. 3d; soil source effect, $F_{1,142} = 5.0$, $P < 0.05$), and differed among pot treatments ($F_{3,142} = 5.0$, $P < 0.01$). Post hoc contrasts showed that basal respiration was almost 50% lower in non-planted than in planted pot treatments, but this measure did not vary across planted pot treatments.

At the end of the experiment, soil $NH_4^+$ concentration was twice as high in grazed than in ungrazed soil (Fig. 3e; $F_{1,141} = 60.0$; $P < 0.001$). Ammonium concentration was lower in *N. stricta* and in species mixture, in comparison to *E. vaginatum* and non-planted pot treatments (pot type effect, $F_{3,141} = 28.0$; $P < 0.001$). Soil $NH_4^+$ concentration was also significantly lower on *E. vaginatum* than on non-planted pot treatments. Despite a marginally significant interaction between soil source and pot treatment ($F_{1,139} = 2.5$, $P < 0.10$), soil $NO_3^-$ showed the same response to plant species as $NH_4^+$; i.e. lower concentrations when *N. stricta* was present in comparison with *E. vaginatum*, and lower concentrations when plants were present in comparison with non-planted pot treatments (Fig. 3f).

## Discussion

Our main objective was to evaluate the indirect effects of grazing on plant–plant interactions of dominant graminoids of semi-natural mountain grassland via grazing-induced modifications of soil properties. We observed that both intra- and inter-specific competition between *N. stricta*, a grass species abundant in grazed environments (Welch

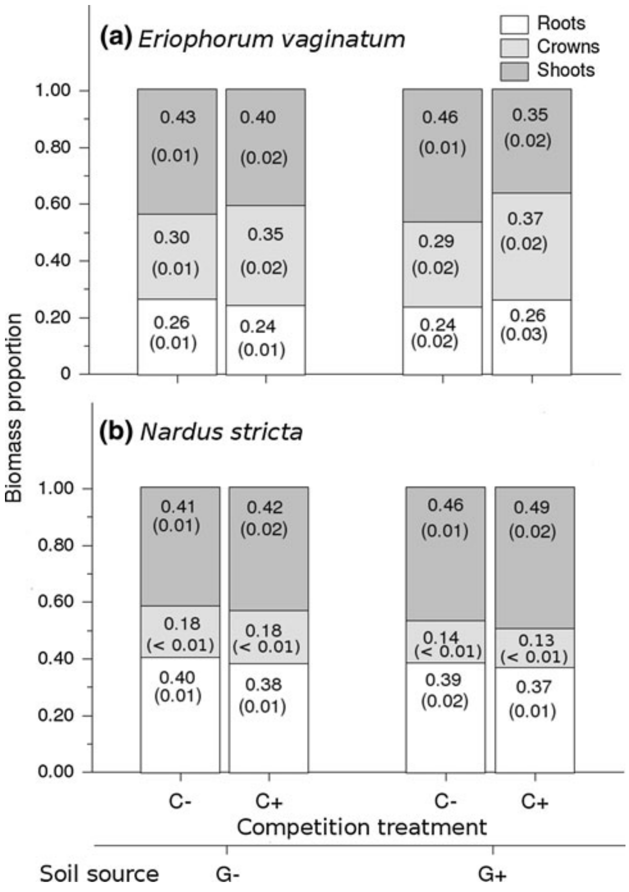

**Fig. 2** Effects of soil source and competition on biomass partitioning in *roots*, *crowns* and *shoots* of **a** *Eriophorum vaginatum* and **b** *Nardus stricta*. Abbreviations for soil source and competition as in Fig. 1. Data for each component are given as means and SE

1986), and *E. vaginatum*, a sedge species found in long-term ungrazed upland grasslands (Edgell 1971), was modified as a result of changes in soil resulting from grazing by large herbivores. Specifically, we found that the intensity of intra-specific competition for both species was greater in soils from the grazed grassland. However, the effects of grazing on inter-specific competition were species-specific: grazing increased the competitive effects of *N. stricta* on *E. vaginatum* but not vice versa (Table 2).

Unlike intra-specific competition, indirect effects of soil conditioning by grazing on inter-specific competition were species-specific, increasing the competitive ability of *N. stricta* at the expense of *E. vaginatum*. In this way, the negative influence that *N. stricta* exerted on *E. vaginatum* increased two-fold, but that of *E. vaginatum* on *N. stricta* decreased by half when they were grown on grazing-conditioned soil (Table 2). This grazing-induced asymmetric effect on interspecific competition, benefiting only the plant species that is most abundant under grazing, might be explained by: (1) differences in plant species traits related to competition for soil resources and the plant–soil feedbacks effects on them; and (2) plant–soil feedback effects on soil properties. First, in terms of plant traits, *N. stricta* displayed traits positively related to competition for resources, such as increased allocation to shoots and roots in comparison to crowns (Casper and Jackson 1997), and allocation to these traits was enhanced in grazed soils. Hartley and Amos (1999) attributed the higher competitive ability of *N. stricta* versus *Calluna vulgaris* to its higher root length and percentage of mycorrhizae infection, which allowed *N. stricta* to exploit soil N more efficiently. Thus the enhanced expression of competitive traits might have contributed to the greater negative effect of *N. stricta* on *E. vaginatum* in these soils. The idea that *N. stricta* was more efficient at exploiting soil resources is additionally supported by the finding that N concentration at the end of the experiment was lower in microcosms where *N. stricta*

**Table 2** Parameter estimates, standard errors (natural log) for the hyperbolic competition model for *Eriophorum vaginatum* and *Nardus stricta* grown in a glasshouse competition experiment with soil from a continuously grazed acidic grassland (*G*+) and a contiguous grazing-excluded moorland (*G*−) in the Yorkshire Dales, England

| Species ($w_i$) | Parameter estimates | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | log($w_{mi}$) (mg) | | | $\alpha_i$ | | | $\alpha_{ij}$ | | $\varepsilon_j$ | | |
| | G+ | G− | G+/G− | G+ | G− | G+/G− | G+ | G− | G+ | G− | G+/G− |
| *E. vaginatum* | 7.20 | 6.40 | 1.13 | 0.12 | 0.08 | 1.50 | 0.25 | 0.08 | 2.08 | 1.02 | 2.05 |
| Standard error | 0.21 | 0.19 | | 0.04 | 0.03 | | 0.03 | 0.02 | | | |
| *t* value | 33.57 | 32.80 | | 3.14 | 2.17 | | 9.32 | 3.27 | | | |
| *P* | *** | *** | | ** | * | | *** | ** | | | |
| *N. stricta* | 7.91 | 6.80 | 1.16 | 0.25 | 0.15 | 1.67 | 0.06 | 0.06 | 0.24 | 0.40 | 0.60 |
| Standard error | 0.18 | 0.19 | | 0.03 | 0.03 | | 0.02 | 0.02 | | | |
| *t* value | 41.72 | 34.42 | | 6.87 | 4.07 | | 2.64 | 2.47 | | | |
| *P* | *** | *** | | *** | *** | | ** | * | | | |

G+/G− estimates' ratio between both soils

Significant differences in parameter estimates between sites: * $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$

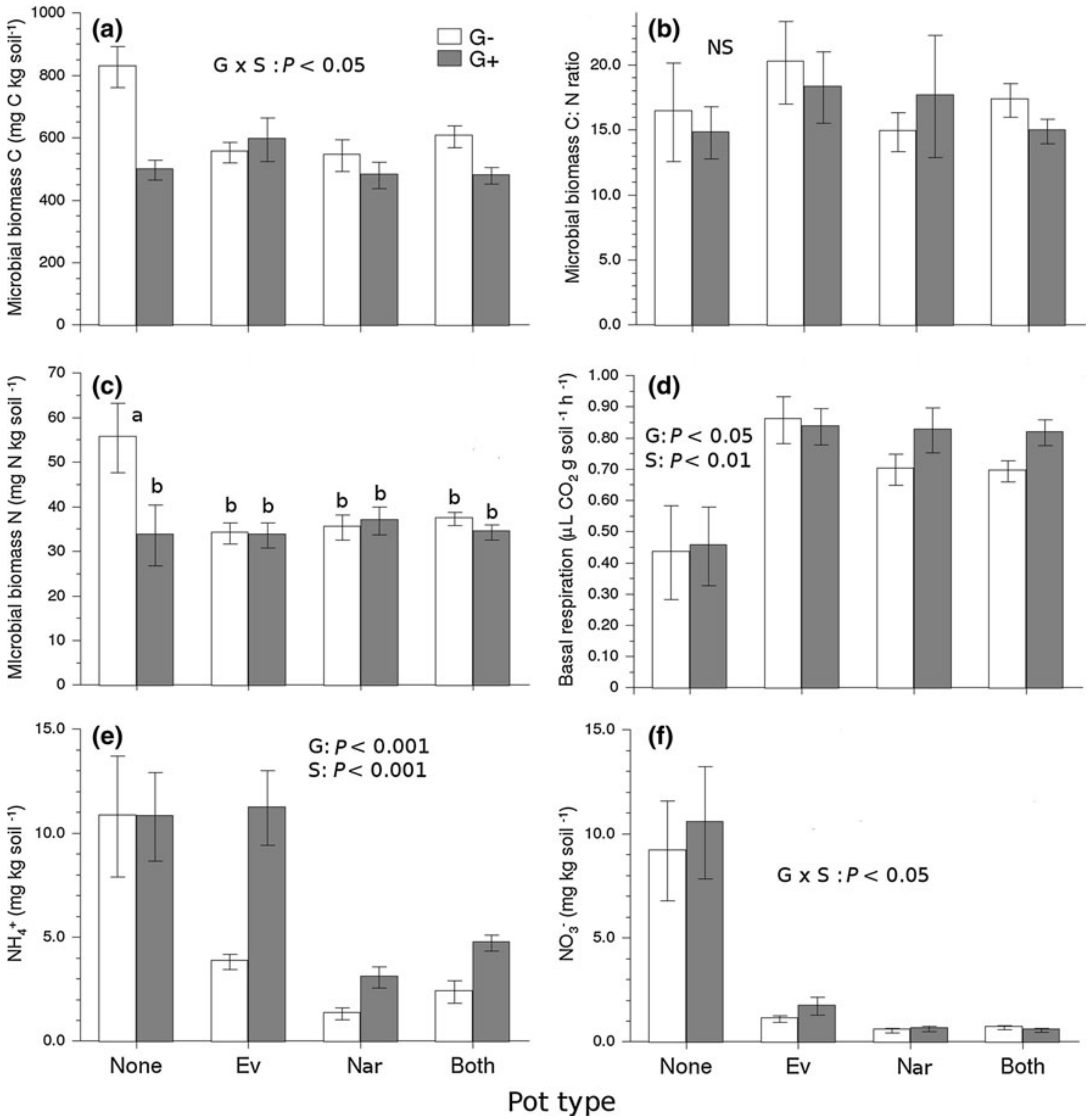

**Fig. 3** Effects of soil source (*G*) and pot type (*S*, a proxy for plant species) on: **a** soil microbial biomass C, **b** microbial biomass C:N ratio, **c** soil microbial biomass N, **d** soil basal respiration, **e** soil $NH_4^+$ concentration, **f** soil $NO_3^-$ concentration at the end of the experiment. Pot type effect includes pots planted with *E. vaginatum* in monocoltures (*Ev*), *N. stricta* in monocoltures (*Nar*), both plant species in mixtures (*Both*), and soil without plants (*None*). *Different letters* for a soil property indicate significant differences at $P \leq 0.05$ after Tukey honest significant differences test. Significance of the treatments and interactions ($G \times S$) after ANOVA are given. *NS* Non-significant effects from ANOVA. *Bars* mean ± SE. Statistical tests were carried out with transformed values but non-transformed values are depicted for clarity. See Fig. 1 for key to soil treatments

was present (both in monocultures and mixtures) in comparison with microcosms where it was absent (i.e. *E. vaginatum* or unplanted soil). An ability to reduce soil nutrients is considered an important trait in plant competition (Wedin and Tilman 1993).

Second, grazing-induced effects on inter-specific competition which benefited *N. stricta* might have resulted from higher soil N availability in grazed soils. Grazing-induced changes on soil nutrient cycling and the activity of soil organisms are mediated directly by herbivore effects on nutrient transfers, and indirectly by changes in vegetation productivity and composition (quality and quantity of organic matter entering soil) (Frank et al. 2003; Bardgett and Wardle 2003; Mikola et al. 2009; Medina-Roldán and Bardgett 2011). Direct effects of grazing through defoliation and excreta return, as well as differences in initial N concentration between both soils, were eliminated with our experimental approach. Therefore, we propose that higher nutrient availability in grazed soils resulted from greater organic matter quality, which led to higher soil microbial activity and rates N mineralisation. The idea that grazing-induced effects on inter-specific competition that benefited *N. stricta* were due to higher soil N availability in grazed soils is supported by our measures of plant performance, soil N availability, and soil microbial activity, which were all greater in grazed than in ungrazed soils at the end of the experiment. Greater soil N availability and microbial activity were also observed in the field in grazed soils, which was attributed to the return of animal faeces, which short-cuts the litter decomposition pathway, and the promotion of grasses, which produce higher quality plant litter, over other dwarf-shrubs by grazing (Medina-Roldán et al. 2012). Overall, the grazing-induced effect on inter-specific competition, which asymmetrically benefited *N. stricta,* was most likely due to traits of this species that confer a greater ability to exploit soil resources in comparison to *E. vaginatum* (Havill et al. 1974; Hartley and Amos 1999), together with greater N availability in grazed soils. Higher soil N concentration in grazed soil was also likely the cause of increased intensity of intra-specific competition in both plant species (Weiner 1990; Schwinning and Weiner 1998), resulting from larger individual plants as shown in our competition model.

Rather few empirical studies have looked at the effects of plant–soil-feedback on plant competition and its components (intra- and inter-specific). In a serpentine grassland in Pennsylvania, Casper and Castelli (2007) showed how a negative plant–soil feedback translated into larger biomass of grass species when they grew in soil conditioned by heterospecific plants, but this plant–soil feedback effect was cancelled when plants experienced inter-specific competition. Since negative effects of intra- and inter-specific competition on biomass were the same, independently of soil conditioning, Casper and Castelli (2007) suggested that plant species show no niche differentiation in plant–soil feedbacks and competition interactions. We observed that the larger biomass of *E. vaginatum* in grazing-conditioned soil was cancelled out when this species grew in competition with *N. stricta.* However, unlike Casper and Castelli (2007), we interpret this finding as a result of a greater ability of *N. stricta* to exploit the increased soil N availability attributed to grazing. This interpretation is supported by the fact that competition with *E. vaginatum* did not influence soil effects on *N. stricta*. As far as we are aware, this differential effect on inter-specific competition induced by grazing is an aspect of plant–soil feedbacks that has not previously been described.

Do changes in competitive interactions between these species driven indirectly by grazing effects on soil have any significance for the dynamics of plant communities in temperate semi-natural mountain grasslands? Although artificial (Damgaard 1998), we can use our experimental results, together with observed species abundance in the field, to make some conjectures on coexistence between our plant species. The heuristic approach in Bever et al. (1997) and Bever (2003) suggests that, for plants that show strong competitive interactions to coexist, a strong negative plant soil feedback should operate (scenario 1). Conversely, strong competition and the occurrence of a positive feedback should lead to competitive exclusion in pair-wise competitive arenas (scenario 2). The microcosm experiment showed that *N. stricta* has improved performance in grazed soils, and that this was associated with a stronger detrimental effect on *E. vaginatum* as a result of competition. This is equivalent to a positive plant–soil feedback (since *N. stricta* dominates grazing-induced soils), and a high competitive interaction (scenario 2). This scenario implies that, under equilibrium conditions, *E. vaginatum* should be competitively excluded by *N. stricta* in areas where soils have been conditioned by grazing. However, *E. vaginatum* typically occurs in low densities in grazed grasslands of the type used in our study, and also at our field site where it co-exists with *N. stricta*. This observation, therefore, suggests that a non-equilibrium process, such as gap creation by herbivore disturbance or heterogeneity in soil conditions, promotes *N. stricta*–*E. vaginatum* co-existence in these semi-natural grazed grassland. This hypothesis of maintenance of *E. vaginatum* in *N. stricta*-dominated grasslands agrees with results by Ejankowski (2008), who observed that experimental gap creation increased *E. vaginatum* seedling recruitment in an open bog habitat in Poland.

On the other hand, our study showed that *E. vaginatum* performed worse in ungrazed soil, and *N. stricta* was the strongest competitor when also grown on this soil. This is equivalent to a negative plant–soil feedback (since *E. vaginatum* dominates ungrazed soils in our field area), together with a strong competitive interaction dominated by *N. stricta* (scenario 1). This scenario implies that, under equilibrium conditions, *N. stricta* should be able to invade areas where grazing has been excluded, co-existing with *E. vaginatum*. However, *N. stricta* abundance was negligible in our ungrazed field site. This observation therefore suggests that *N. stricta* is unable to invade ungrazed areas due to detrimental effects of other environmental variables, such as higher soil moisture and increased surface organic matter accumulation, on its performance. Consistent with this, in our study site, the cessation of grazing caused an increase in soil moisture content and a build-up of plant litter on the soil surface (Medina-Roldán et al. 2012), which commonly occurs as a result of the removal of grazing in these grasslands (Bardgett et al. 2001). Our model parameters of competition are analogous to those used in the Lotka–Volterra model (Damgaard 1998). Apart from competition coefficients, key parameters that determine equilibrium plant species densities in the Lotka–

Volterra model are the intrinsic rate of growth ($r$) and the carrying capacity of a particular habitat ($K$). It seems likely that the changes in soil conditions caused by grazing exclusion on soil properties are beyond the optimal area of the *N. stricta* ecological response curve (i.e. a habitat in which *N. stricta* $r$ and $K$ are low). Our view that sub-optimal soil conditions might exclude *N. stricta* from ungrazed areas agrees with other experimental results which have shown that *N. stricta* was out-competed by *C. vulgaris* only when *N. stricta* roots were not exposed to soil mineral layers (i.e. exposed to sub-optimal conditions; Genney et al. 2002).

We suggest that changes in *E. vaginatum–N. stricta* intra- and inter-specific competition observed in our pot experiment resulted from indirect effects of herbivores on soil properties, which led to a higher soil nutrient availability where grazing occurs (see above). However, it is worth noting that we could not isolate herbivore legacies on soil microbes, and other elements of the soil food web that affect soil nutrient cycling, from those on plant species composition that also affect soil microbes and nutrient cycling (e.g. through changes in quality of soil organic matter). Nevertheless, since grazing is ultimately responsible for changes in plant species composition in semi-natural mountain grasslands, we conclude that grazing was the main ecological factor indirectly affecting *E. vaginatum–N. stricta* competitive interactions. Such grazing-induced changes on soil properties are one of the main routes by which large herbivores indirectly influence the functioning of terrestrial ecosystems, and are coined under the term herbivore–plant–soil feedbacks (Frank et al. 2003; Bardgett and Wardle 2003). Additionally, although we sterilised plant roots superficially, our experiment did not isolate potential effects on plant performance and competition due to soil symbionts, such as arbuscular mycorrhizae and dark septate endopyhtes. Higher competitive ability in comparison to other plant species (Hartley and Amos 1999), as well as observations of positive plant–soil feedbacks (Kardol et al. 2006), have been attributed to the presence of mycorrhizae in *N. stricta*. Thus, higher competitive ability of *N. stricta* in comparison to the non-mycorrhizal *E. vaginatum* observed here could have resulted from *N. stricta* mycorrhizal status, although we are not sure of this fact since we did not measure mycorrhizal colonisation.

In summary, our results showed that grazing indirectly alters competitive interactions of *E. vaginatum* and *N. stricta* by affecting soil N availability and the activity of soil microbes. It is well established that grazers directly influence plant competitive interactions via selective grazing, and our results point to an additional indirect mechanism by which grazers might alter plant–plant interactions via plant–soil feedbacks. Moreover, our results are the first, as far as we know, to document a differential plant–soil feedback effect induced by grazing on intra- and inter-specific plant competition. Further studies are needed in more realistic situations to test the significance of such plant–soil feedback mechanisms as regulators of plant community dynamics in grazed ecosystems, including semi-natural mountain grasslands where *E. vaginatum* and *N. stricta* occur.

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