

Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands

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Abstract Studies addressing the role of large herbivores on nitrogen cycling in grasslands have suggested that the direction of effects depends on soil fertility. Via selection for high quality plant species and input of dung and urine, large herbivores have been shown to speed up nitrogen cycling in fertile grassland soils while slowing down nitrogen cycling in unfertile soils. However, recent studies show that large herbivores can reduce nitrogen mineralization in some temperate fertile soils, but not in others. To explain this, we hypothesize that large herbivores can reduce nitrogen mineralization in loamy or clay soils through soil compaction, but not in sandy soils. Especially under wet conditions, strong compaction in clay soils can

lead to periods of soil anoxia, which reduces decomposition of soil organic matter and, hence, N mineralization. In this study, we use a long-term (37-year) field experiment on a salt marsh to investigate the hypothesis that the effect of large herbivores on nitrogen mineralization depends on soil texture. Our results confirm that the presence of large herbivores decreased nitrogen mineralization rate in a clay soil, but not in a sandy soil. By comparing a hand-mown treatment with a herbivore-grazed treatment, we show that these differences can be attributed to herbivore-induced changes in soil physical properties rather than to above-ground biomass removal. On clay soil, we find that large herbivores increase the soil water-filled porosity, induce more negative soil redox potentials, reduce soil macrofauna abundance, and reduce decomposition activity. On sandy soil, we observe no changes in these variables in response to grazing. We conclude that effects of large herbivores on nitrogen mineralization cannot be understood without taking soil texture, soil moisture, and feedbacks through soil macrofauna into account.

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Soil moisture

Introduction

Large vertebrate herbivores play a key role in determining the community structure and functioning of grassland ecosystems. They act on plant diversity (Oloff and Ritchie 1998) and vegetation heterogeneity (Frank et al. 2000; McNaughton 1984), and can have a major influence on the local food web, both aboveground (de Visser et al. 2011; Samways and Kreuzinger 2001) and belowground

(Bardgett and Wardle 2003; King and Hutchinson 1976). Two main mechanisms have been proposed via which large herbivores affect the vegetation composition. Firstly, grazers alter the light competition balance for plants by removing plant biomass and selective foraging (Huisman and Olff 1998; e.g., Pastor et al. 2006). Secondly, grazers promote nutrient cycling by production of dung and urine, which stimulates soil microbial activity (e.g., McNaughton et al. 1997a), leading to dominance of fast-growing grazing-tolerant plants (Olff and Ritchie 1998). Both mechanisms may stimulate high quality plant regrowth resulting in high quality litter production, higher rates of litter decomposition, and rapid cycling of nutrients, thus creating a positive feedback loop on large herbivore densities (Fryxell 1991; McNaughton et al. 1997a; Pastor et al. 2006). Evidence for this mechanism has been found in several grassland ecosystems, where it leads to the formation of grazing lawns (Frank and McNaughton 1993; Knapp et al. 1999; McNaughton 1984). Soil fertility, however, seems a key aspect (Hobbs 1996). While grazing on fertile soils results in dominance of palatable plant species and high nitrogen mineralization, grazing on infertile soils promotes dominance of plant species with low palatability (and low N concentration in tissue and litter), resulting in lower decomposition and lower nitrogen mineralization rates (Hobbs 1996; Pastor et al. 1993, 2006).

However, on some fertile soils, large herbivores reduce rates of nitrogen mineralization instead of promoting it, while vegetation quality is not reduced. For instance, in coastal salt marshes and river flood plains, herbivores have been found to reduce nitrogen mineralization rates (Bakker et al. 2004; van Wijnen et al. 1999), despite the dominance of highly palatable plant species. Also, a recent large cross-site study questions the generality of the idea that large herbivores promote nutrient cycling on fertile soils. At some sites, the nitrogen mineralization rate increased in response to grazing, while at other sites the nitrogen mineralization rate did not change or decreased in response to grazing (Bakker et al. 2006, 2009). Apparently, other factors than soil fertility may also change the effect that grazers have on the nitrogen mineralization rate.

One aspect that has received little attention in this controversy, and which may explain the contrasting results outlined above, is the effect of large herbivores on soil physical properties (Hamza and Anderson 2005). In temperate agricultural grasslands, soil compaction via trampling of large herbivores is frequently reported to have a negative effect on nitrogen mineralization (Hamza and Anderson 2005, and references therein), where the strength and direction of the effect largely depend on soil texture and soil moisture (Hamza and Anderson 2005; Rasiah and Kay 1998). On fine-textured clay soils, herbivore trampling has been found to strongly reduce soil porosity, which

negatively affects diffusion of water, nutrients and oxygen content (Rasiah and Kay 1998). This negatively affects the nitrogen mineralization rate in two different ways. Firstly, the reduction in soil porosity can lead to a lower soil fauna activity which results in a reduction in the rate of nitrogen mineralization (Breland and Hansen 1996). Secondly, the decrease in oxygen diffusion can result in a higher denitrification, resulting in a lower amount of available nitrogen to plants (Le Roux et al. 2003; Menneer et al. 2005). On coarse-textured, sandier soils, where soil particles are on average 100–1,000 times larger, herbivore trampling is not likely to decrease soil porosity to the extent that nutrient mineralization is affected. In fact, herbivore trampling on sandy soils may lead to a higher nutrient diffusion rate (Rasiah and Kay 1998; Voorhees et al. 1985) and better water retention (Xu et al. 2008). Although these are well-described effects in many agricultural systems (Hamza and Anderson 2005; Mikola et al. 2009), few studies have addressed the potential impact of trampling-induced soil bio-physical effects in natural ecosystems, but with some notable exceptions (Gass and Binkley 2011; Kiehl et al. 2001). Nevertheless, in none of these studies were the effects of large herbivores assessed on different soil types, nor were effects on the decomposer community taken into account.

In the present study, we have investigated the effects of large herbivore trampling on soil nitrogen mineralization in two types of soils, a clay soil and an adjacent sandy soil. Following the literature discussed above, we expected that herbivore trampling affects nitrogen mineralization differently in the two soils. On the fine-textured clay soil, we expected herbivore trampling to result in an array of strong effects: (1) a decrease in soil porosity; (2) an increase in soil moisture level; (3) a decrease in soil aeration; (4) a decrease in decomposition activity; and (5) a decrease in nitrogen mineralization rate. Moreover, we expected a change in the soil macrofauna community composition towards smaller and fewer species. On the sandy, coarse-textured soil, we expected a much smaller effect of large herbivores on soil physical properties, fauna composition, and nitrogen mineralization rate.

Materials and methods

Study area

A long-term (37-year, starting in 1973) grazing experiment on the salt marsh was used for this study. The salt marsh on the coastal barrier island of Schiermonnikoog, The Netherlands (53°48'N, 6°22'E) has developed on a sandy beach plain with small dunes. Clay-rich sediment [clay + silt fraction (<0.74 µm) ~47 %, hereafter clay soil] is deposited on the lower parts of the salt marsh on top of the

underlying sand layers (De Groot 2009). The higher parts have not been covered by sediment, so soils have remained sandy (clay + silt fraction <3 %, hereafter sandy soil; De Groot 2009). The grazed part of the study area received a long-term stable grazing management since 1973, with a relatively constant stocking density of 0.5 cows ha⁻¹ (Bakker et al. 2002), parts of the area were left ungrazed on both the clay and sandy soil. Since grazing by cattle was installed, vegetation in the grazed and ungrazed parts of the marsh has developed quite differently (see Bos et al. 2002).

Study design

We selected 11 locations on clay soil and 6 locations on sandy soil. All locations were spaced at least 30 m apart. For a detailed map of the locations, see Electronic Appendix, Fig. 1a. All locations had a 3 × 3 m grazed plot and a similar-sized ungrazed plot which were separated by a grazing fence and 2 m of unused surface on either side of the fence (Electronic Appendix, Fig. 1b). Additionally, a 3 × 3 m mown plot was present at 8 of the locations on clay soil only. It was laid out on the ungrazed part of the locations, at least 2 m from the other treatments and has been hand-mown with a bush-cutter twice yearly (in June/July and August/September) since 1973. Details on abiotic soil parameters can be found in the Electronic Appendix, Table 1.

Soil physical parameters

Measurements on the degree of soil compaction, soil macro-porosity, water content, organic matter content, nitrogen mineralization, decomposer activity, sediment (clay) layer thickness, and soil fauna composition were done in all 3 × 3 m plots for all treatments on both sandy and clay soil in July 2010.

Bulk density, soil moisture, and organic matter content were determined by taking the average of three soil samples. Soil samples were taken 2 m from each other using a soil corer (Ø 10 cm, 10 cm height) which was also used to take soil micro-arthropod samples (Van Straalen and Rijninks 1982). Care was taken to avoid compaction of the sample. Prior to sampling, above-ground vegetation was carefully cut (1 cm above the soil surface) using a pair of scissors and removed from the sample. The cores were weighed, dried (at 70 °C, for 48 h), and weighed again to calculate bulk density and to determine water content (% of initial fresh weight). After removal of living roots, organic matter content (OM) was determined as loss on ignition at 550 °C for 3 h.

Bulk density is a commonly used measure to assess the effects of large herbivores on soil structure (Bakker et al. 2009). However, it does not explicitly take into account differences in specific weight of the different soil components. In other words, the bulk density of soil samples with a much

higher organic matter content (a very low specific weight) but equal or slightly lower mineral content (a high specific weight) will be equal or differ slightly from other soils. However, the effect on soil porosity could potentially be large, which may result in a very different soil functioning. Therefore, we also compared total soil porosity, air-filled porosity, and water-filled porosity between the treatments and soil types. In order to calculate these parameters, we used the specific weights of sand and clay (2.65 g cm⁻³) and organic matter (1.47 g cm⁻³) and the water content of the soil samples (LNV 1970).

As a proxy for the saturation of oxygen in the soil and the microbial processes that happen therein, we measured the soil redox potential. We chose a set up in which five electrodes with a platinum tip and one Ag/AgCl calomel reference electrode (Cole-Palmer[®]) were connected to a Graphtec GL200 Datalogger (Graphtec GB). All redox measurements were taken on 13 November 2010. In order to obtain a depth profile of the soil redox potential, all electrodes were first placed into the soil at 2 cm, and subsequently at 5 and 10 cm depth. Measurements were read out exactly 2 min after the electrodes were placed at a particular depth. Averages of these five electrodes were used for graphs and statistics, after correction for reference electrode (+192 mV), temperature, and soil pH. Quick measurements on redox may not necessarily reflect absolute values but are suitable for making comparisons between treatments (van Bochove et al. 2002), and are an important predictor for plant species distribution on salt marshes (Davy et al. 2011).

Soil fauna

Soil fauna was extracted from soil cores taken with a soil corer (see above) from the top 5 cm of the soil in all treatments using the Tullgren method (Van Straalen and Rijninks 1982). Above-ground plant biomass was removed prior to sampling. All invertebrate species were identified to the species level for Collembola, the important detritivorous amphipod *Orchestia gammarellus*, and to morphospecies for other taxa. In order to check whether differences in soil fauna composition were larger between treatments at deeper soil layers, we also took samples from 5–10 cm deep at locations 4, 5, 6, 8, and 9 on clay soil, but not from locations on sandy soil. At these locations, the clay layer was thicker than 10 cm. In the analyses, we distinguished between meso- (<4 mm) and macrofauna (≥4 mm) as we expected stronger effects of a decrease in pore volume on macrofauna than on mesofauna.

Decomposer activity

We measured decomposer activity using one bait lamina strip per plot (Kratz 1998). This method is widely used as a

proxy for decomposer activity, especially to allow comparisons between treatments (see Rozen et al. 2010). Bait lamina sticks (8 cm long, 0.5 cm wide) contained 16 holes spaced 5 mm apart, filled with a standard mixture of cellulose, bran flakes, and active coal in a ratio of 70:27:3. Sticks were put into the soil with the top most hole 0.5 cm below soil surface on 28 August 2010 and were taken out on 4 October 2010. Afterwards, sticks were carefully rinsed and holes subsequently checked on activity of decomposers. Holes that were empty or almost empty and let the light of a lamp (60 W) shine through were recorded as signs of ‘active decomposers’, while holes that did not let light come through were recorded as ‘inactive decomposers’.

Nitrogen mineralization

The net nitrogen mineralization rate was measured in situ during a 5-week period using the incubation method described by Berendse et al. (1989). On 16 June 2010, a pair of intact soil cores was taken at every plot using a PVC tube (Ø 4.3 cm, 10 cm height). Of each pair, one sample was transported to the laboratory in a cooling box, after which extractable nitrogen (NH_4^+ and NO_3^-) was extracted within 24 h. The second tube was incubated in situ, of which the bottom was sealed off with a nitrogen-free Philitron[®] filter to prevent root ingrowth and to facilitate in and outflow of water and air. A plastic lid was placed on top to prevent plant growth and leaching. After 5 weeks, the incubated soil tube was brought to the laboratory for analysis. From both samples, NH_4^+ and NO_3^- were extracted from 12.5 g of field-moist soil, which was mixed with 30 ml 1 M KCl for 8 h and centrifugated afterwards. The extract was analyzed using a Skalar 5100 autoanalyzer (Skalar, The Netherlands). Net nitrogen mineralization, expressed as mg of extractable NH_4^+ and NO_3^- produced per month, was calculated by taking the difference between the nitrogen content in the incubated soil cores and the first paired sample. Samples that were disturbed by cows were excluded from the analysis.

Temporal replication of N mineralization

Rates of N mineralization can be highly variable over time. We therefore included another dataset on N mineralization rate, which was collected during the field season 1995–1996, 23 years after the grazing and mowing experiments were started. Measurements were done at one of the sites from the 2010 study (site near 5 in Fig. 1a of the Electronic Appendix). Mineralization rate was measured six times between March 1995 and March 1996. The in situ methods of measuring mineralization rates were equal to the 2010 measurements. Incubating vials were put at least 3 m from each other. At each of the incubation

points, bulk density was determined once and gravimetric soil moisture was determined at each of the sampling moments, using the same methods as in the 2010 measurements.

Statistics

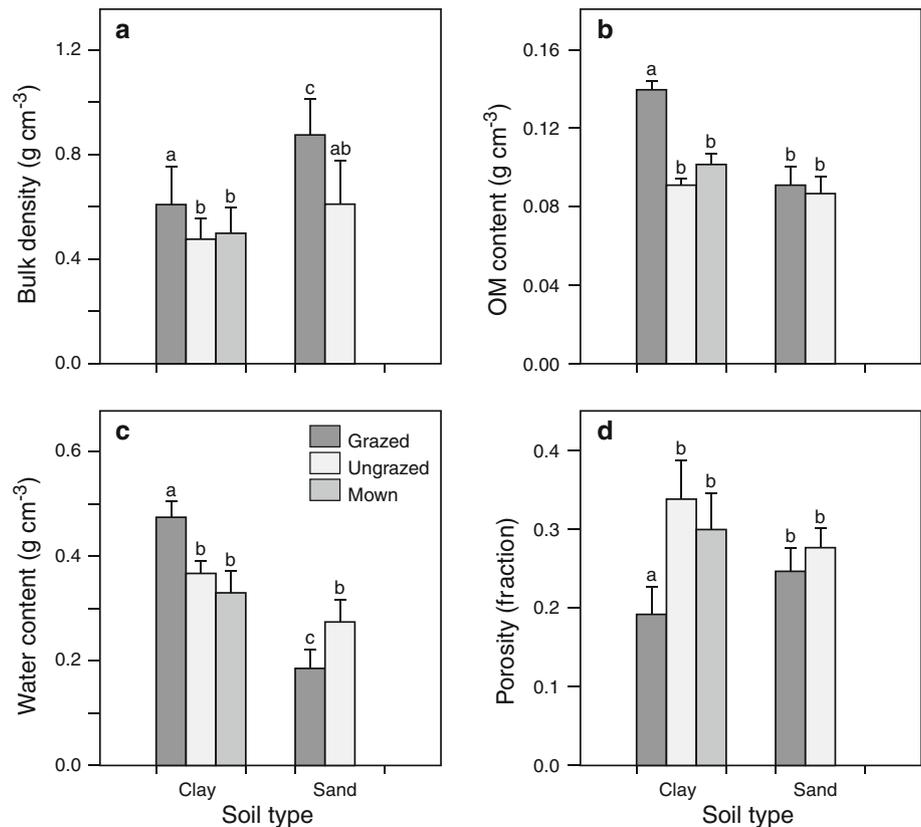
Statistical testing on soil fauna species and specimen numbers was done using a non-parametric Kruskal–Wallis test as data were not Poisson or normally distributed. Decomposer activity data from the bait lamina sticks was analyzed using a logistic regression with log-link function, because the data follow a binomial distribution (0 = inactive, 1 = active), where treatments were categorical predictors and depth was a continuous predictor. A general linear model was calculated on all soil variables to test for treatment effects. A multiple regression analysis with backwards stepwise removal was used to investigate the variables explaining the differences in macro-porosity of the soil types, with macro-porosity as a dependent variable and organic matter content, water content, and treatment as independent variables. We used a general regression model to test for independent effects of treatment and soil type on nitrogen mineralization rate, and we took the interaction effect between these to test whether the treatment showed differences between soil types. Additionally, we used water-filled porosity, total porosity, bulk density, and organic matter content into account as covariates. A general linear model with a post hoc Tukey test was used to test for differences in the mineralization rate in the 1995–1996-season. To test the assumptions of homoscedasticity, we used the Levene’s test. To meet the assumption of homogeneity of variance, a Levene’s test was used; to meet the assumption of normality of residuals, we inspected the standardized residuals and tested those on normality using a KS test. All statistics were done using Statistica 9.0.

Results

Soil physical parameters

In accordance with our expectations, soil bulk density was significantly higher in the grazed plots, both on clay and sandy soil (Fig. 1a). On clay soil, grazing resulted in a 30 % higher bulk density. No significant differences were found between the bulk density of mown and ungrazed plots on clay soil. On sandy soil, bulk density was 41 % higher in the grazed treatment than in the ungrazed treatment. Bulk density was 32 % higher in the grazed sandy soil compared to the grazed clay soil. On clay soil, SOM content was 31 % higher in the grazed plots than in the

Fig. 1 Soil physical properties in the grazed (black bars), ungrazed (light gray bar) and mown (dark gray bar) treatments. Different letters indicate significant differences at α 0.05. **a** Bulk density, **b** organic matter (OM) content as fraction of total weight, **c** water content as fraction of total wet weight, **d** macro-porosity as a fraction of the total volume



ungrazed plots, and 27 % higher than in the mown plots (Fig. 1b). SOM content was not different between treatments on sandy soil. On clay soil, the grazed plots had 31 % higher water content than the ungrazed plots and 43 % higher water content than in mown plots. We found the opposite for sandy soil, where water content was 31 % lower in the grazed plots than in the ungrazed plots (Fig. 1c). Grazing on clay soil resulted in 8–10 % lower total soil porosity compared to mown and ungrazed treatment (Fig. 1d). For sandy soil, grazing resulted in a 12 % lower total porosity (Fig. 1d). On grazed clay soil, water-filled porosity was on average more than 20 % higher than in the mown and ungrazed treatment, and well above 60 % (Fig. 2a). On sandy soil, no differences between the percentages of water-filled porosity were found (Fig. 2b).

Factors influencing air-filled soil porosity

On clay soil, differences in air-filled porosity were explained by four factors: grazing treatment, SOM content, water content, and soil water content (Table 1). This indicates that the decrease in porosity on clay soil was clearly influenced by the grazing treatment. On sandy soil, variation in air-filled soil porosity was best explained by variation in bulk density and organic matter fraction (Table 1), but not by grazing treatment and water content.

Redox potential

Soil redox potentials on sandy soil were on average between 120–160 mV higher than on clay soil ($F = 115.6_{1,88}$; $P < 0.001$). On clay soil, we found a strong effect of grazing treatment ($F_{2,50} = 22.2$; $P < 0.001$) and of depth ($F_{2,44} = 13.6$; $P < 0.001$). On sandy soil, no effect of grazing treatment ($F_{1,33} = 0.0$; $P > 0.9$) and depth ($F_{1,28} = 1.3$; $P > 0.6$) were found. In clay soil we found the redox potential at 2 cm depth to be 83 mV lower in the grazed treatment compared to the ungrazed and mown treatment, but this difference was not significant (Fig. 3a). This difference increased to 140 mV at 5 cm depth ($n = 7.7$; $t = 3.0$; $P = 0.02$) and 205 mV at 10 cm depth ($n = 7.7$; $t = 5.0$; $P = 0.002$).

Soil fauna

Overall, we found 21.7 (\pm SD 4.2) species and 207.5 (\pm SD 88.4) specimens in the upper 5 cm of clay soil and 27.1 (\pm SD 5.7) species and 221.6 (\pm SD 94.3) specimens in sandy plots (see Electronic Appendix, Fig. 4). If we subdivide the soil fauna compartment into mesofauna (<4 mm) and macrofauna (≥ 4 mm), we found no differences between treatments on sandy soil, but strong differences between treatments on clay soil. Abundances of

Fig. 2 Air-filled porosity (dark gray bars) and water-filled porosity (light gray bars) in grazed, ungrazed, and mown treatments. **a** Grazed, ungrazed, and mown treatments on clay soil, **b** grazed and ungrazed treatments on sandy soil. Different letters indicate significant differences at α 0.05

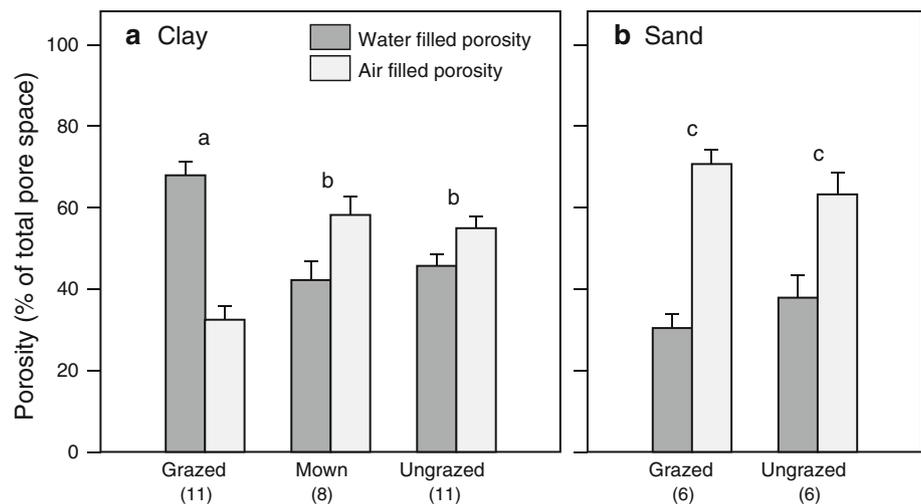


Table 1 Factors explaining air-filled porosity

Factors	Clay ($F_{(2,24)} = 144.5$; R^2 0.96)			Sand ($F_{(2,9)} = 19.8$; R^2 0.78)		
	<i>F</i>	<i>P</i>	Estimates (β)	<i>F</i>	<i>P</i>	Estimates (β)
Intercept	1.77	NS		129.33	<0.001	
Bulk density	4.75	0.039	-0.22 ± 0.10	38.92	<0.001	-1.39 ± 0.22
OM content	8.66	0.007	0.40 ± 0.13	18.36	0.002	-0.95 ± 0.22
Water content	76.76	<0.001	0.73 ± 0.08		NS	
Treatment	12.66	<0.001			NS	

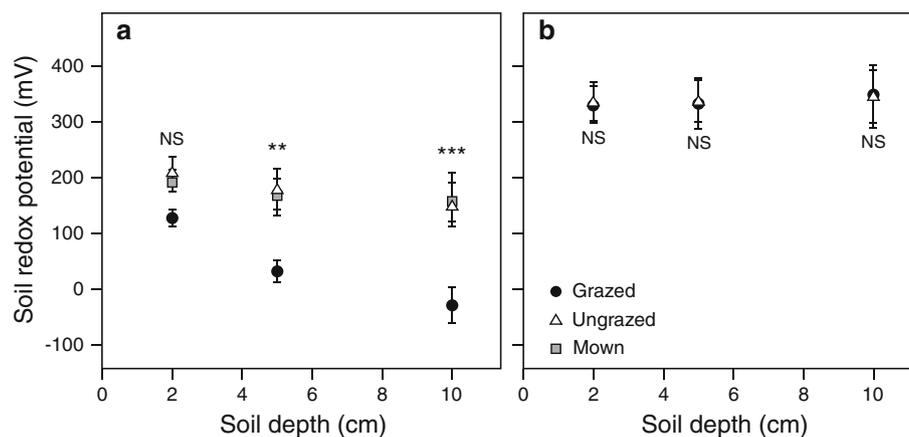


Fig. 3 Redox potentials in grazed (closed circles), ungrazed (open triangles), and mown (gray squares) treatment. **a** Grazed treatment on clay soil is significantly different from other treatments at 5 and

10 cm depth. **b** Treatments on sandy soil are not significantly different. Bars standard errors. ** $P < 0.01$; *** $P < 0.005$; NS not significant

macrofauna in the top 5 cm in ungrazed clay soil were 91 % higher than in the grazed treatment ($n = 11$; $Z = 2.53$; $P = 0.033$). We did not observe differences between numbers of individuals of mesofauna between grazed and ungrazed clay soil ($n = 30$; $H = 1.81$; $P = 0.412$; Electronic Appendix Fig. 2). Community composition of the mown treatments was intermediate,

both for macro- and mesofauna and not statistically different from either of the other treatments.

In the soil layer of 5–10 cm deep, differences between soil fauna compartments were much more pronounced. We found significantly more specimens of mesofauna in the ungrazed treatment ($n = 5$; $Z = 2.02$; $P = 0.04$), and three times more specimens of macrofauna in the ungrazed

treatment ($n = 5$; $Z = 2.02$; $P = 0.04$). Mown plots were intermediate, and did not differ significantly from both the grazed and the ungrazed plots. The detritus-feeding crustacean *Orchestia gammarellus*, which exhibits digging behavior, was only observed in the ungrazed plots ($3.4 \pm \text{SE } 1.0$ individuals per sample) and in the mown plots on clay soil ($0.6 \pm \text{SE } 0.4$ individuals per sample), but was not found in the grazed plots on clay soil nor in any of the sandy plots.

Decomposer activity

Overall, decomposer activity was found to be highest in ungrazed treatments on both clay and sandy soil which also have the highest soil porosity (Fig. 4). In clay soil, we found a steep decrease in decomposer activity with depth in all treatments ($n = 29$; Wald Stat = 64.55, $P < 0.001$; Fig. 4a). Grazed clay soil showed a strong decrease in decomposer activity, where we found only 10 % decomposer activity at 8 cm depth, versus a 45–51 % decomposer

activity at 8 cm depth in ungrazed and mown treatments. In sandy soil, we only found a minor decrease in decomposition with depth in the grazed sandy treatment ($n = 6$; Wald Stat = 4.8; $P = 0.027$; Fig. 4b), but no effect of depth in the ungrazed treatment ($n = 6$; Wald Stat = 2.16; $P = 0.14$). Furthermore, decomposition activity in the grazed clay soil was lower than in grazed sandy soil ($n = 11.6$; Wald Stat = 8.3; $P = 0.004$).

Nitrogen mineralization

Paired t tests within soil type showed a lower total N mineralization rate in the grazed plots on clay soil compared to the mown plots ($n = 11.7$; $t = 2.6$; $P = 0.04$) and ungrazed plots ($n = 11.11$; $t = 4.1$; $P = 0.004$) (Fig. 5a). On sandy soil, no difference was found between grazed and ungrazed treatments (Fig. 5b). The multiple regression analysis showed that both grazing treatment ($F_{1,26} 8.77$; $P = 0.006$) and the interaction between treatment and soil type ($F_{1,26} 10.02$; $P = 0.004$) had a significant effect on

Fig. 4 Logistic regression of decomposer activity as measured with bait lamina sticks with depth in grazed (closed circles), ungrazed (open triangles), and mown (gray squares) treatments. **a** Clay soil, **b** sandy soil. Symbols indicate the average fraction of empty (active) holes at each depth. Letters indicate significantly different slopes. Statistics and regressions are mentioned in the text

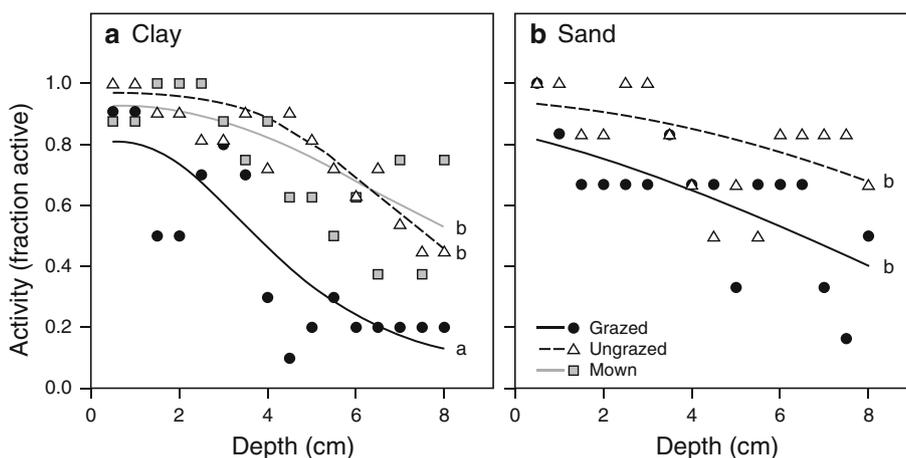
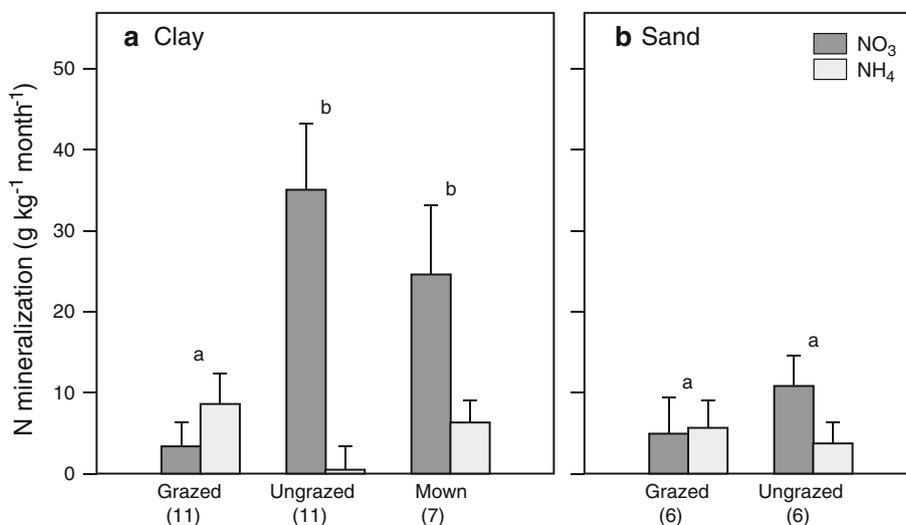


Fig. 5 N-mineralization (in mg kg^{-1}) in grazed, ungrazed and mown plots on clay (a) and sand (b). Black bars NO_3^- nitrification. Gray bars NH_4^+ mineralization. Numbers in parentheses sample size. Statistical testing was done on total nitrogen mineralized. Different letters indicate significant differences at $\alpha 0.05$



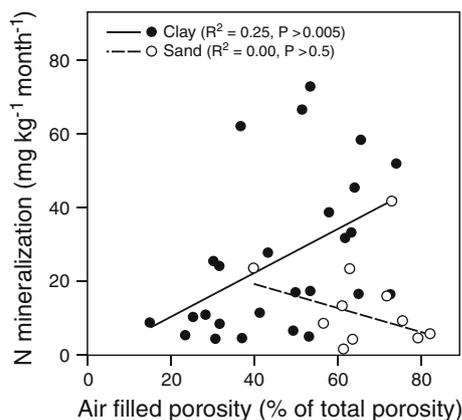


Fig. 6 Air-filled porosity versus the total nitrogen mineralization between 18 June and 26 July 2010. Closed circles samples from clay soil (R^2 0.25; $P < 0.005$), open circles results for sandy soil (NS)

total N mineralization rate. Of all covariates that were taken in the analysis, only air-filled porosity explained additional variation ($F_{1,26}$ 4.71; $P = 0.04$). N mineralization was positively correlated to air-filled porosity on clay

soils, but we found no relationship on sandy soil (Fig. 6). In turn, air-filled porosity on clay soil was positively correlated to redox potential ($n = 29$; R^2 0.44; $P < 0.001$) and negatively correlated to OM content ($n = 29$; R^2 0.15; $P = 0.01$).

We also found a remarkable difference in the ratio of $\text{NH}_4:\text{NO}_3$ between the treatments. On grazed clay soil, 73 % of the mineralized nitrogen was available as NH_4 , while in the mown treatment only 20 % was available as NH_4 , and in the ungrazed treatment only 2 % was available as NH_4 . On sandy soil, we found no differences in the ratio $\text{NH}_4:\text{NO}_3$ between the grazing treatments (Fig. 5b). Neither absolute values for the amount of mineralized N and the difference between the proportions were significantly different.

The year-round measurements on N mineralization, soil moisture, and bulk density between March 1995 and March 1996 yielded very similar results. We found an on average 83 % lower total N mineralization rate in the grazed treatments than in the mown and ungrazed treatments ($F_{2,27} = 86.2$; $P < 0.001$; Fig. 7a) on clay. Only during the

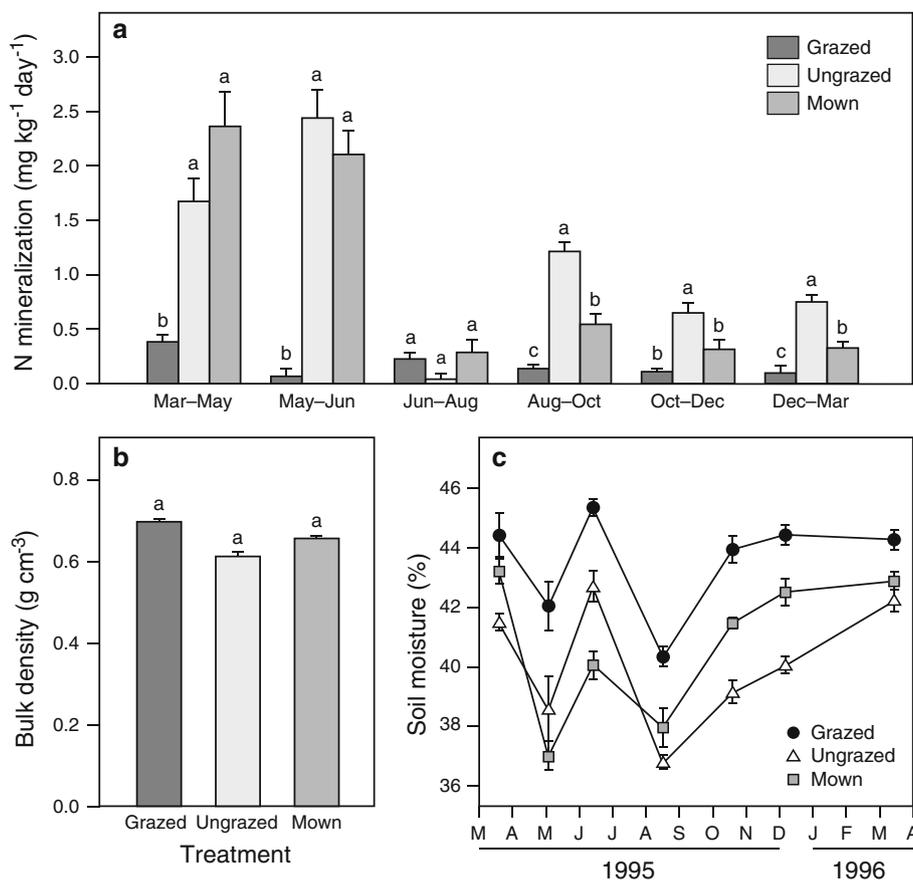


Fig. 7 Year-round dynamics in **a** total N-mineralization (in mg kg^{-1}), **b** bulk density, and **c** soil moisture dynamics, in grazed, ungrazed, and mown plots on clay soil. Measurements were taken between March 1995 and March 1996. **a**, **b** Dark gray bars grazed

treatments, white bars ungrazed treatments, light gray bars mown treatments; **c** black circles grazed treatments, open triangles ungrazed treatments, gray squares mown treatment. Bars standard errors. Different letters indicate significant differences at α 0.05

August sampling, was no significant difference found between the treatments (Fig. 7a). Values for bulk density were 7–14 % higher in the grazed treatments ($F_{2,27} = 30.06$; $P < 0.001$), and values for soil moisture were 4–8 % higher in the grazed treatment ($F_{2,27} = 30.06$; $P < 0.001$). This indicates that during these year-round measurements, air-filled porosity was also substantially lower in the grazed treatments than in the ungrazed and mown treatments.

Discussion

Long-term effects of grazing on soils with different texture

The results of the present study show that herbivore trampling and the associated effects on soil functioning may provide an important third route via which herbivores can create long-standing effects on nitrogen mineralization and soil macrofauna (Fig. 8). This figure shows the paradox of how increased soil hypoxia through compaction can in turn promote the palatability of the vegetation (Pathway 3). This is only possible when direct effects of stress on vegetation composition (with dominance of species with high palatability; see Bakker 1989) are more important than the negative effect of hypoxia on nitrogen mineralization.

Our findings, therefore, may also shed light on some of the conflicting results from earlier studies on the impact of large herbivores on N cycling, which were also done in

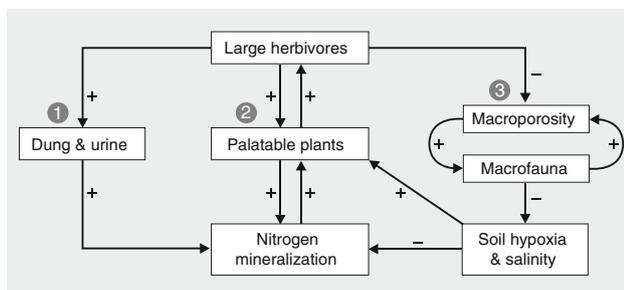


Fig. 8 Conceptual model illustrating the three pathways via which large herbivores can influence nitrogen mineralization in fertile soils. Pathway (1) reflects the input from dung and urine from large grazers which can increase nitrogen mineralization (McNaughton et al. 1997b; Mikola et al. 2009). Pathway (2) reflects the effect of herbivores on vegetation palatability and hereby on quality of litter inputs, which in effect stimulates nitrogen mineralization (Frank et al. 2000; McNaughton 1983). Pathway (3) illustrates the effect of large herbivores on nitrogen mineralization via their negative effect on macro-porosity and macrofauna abundance and increased soil anoxia. The resulting positive effect of soil anoxia on plant quality is only possible when direct effects of stress on vegetation composition is more important than the negative effect of hypoxia on nitrogen mineralization

study areas with fine textured soils (Bakker et al. 2006, 2009; Kiehl et al. 2001; van Wijnen et al. 1999).

An essential element of this conceptual diagram is that herbivores affect nitrogen mineralization via compaction in some soils, but not in others (Pathway 3, Fig. 8). Both our results of the 2010 and those of the year-round study in 1995–1996 indicate that large herbivores reduce nitrogen mineralization and associated reduction in soil fauna through soil compaction on a clay soil. We found no indications that herbivores had a similar effect on sandy soil. The general idea that trampling leads to soil compaction on both sand and clay is confirmed by several other studies on cattle (Menneer et al. 2005; Mwendera and Saleem 1997), savannah herbivore communities (Belsky 1986), sheep (Kiehl et al. 2001), and for human trampling (Hsu et al. 2009). However, the consequences of soil compaction for porosity are much larger on clay than on sand, which we attribute to the physical structure of clay soils that makes them more compactable, a finding that is also supported by other studies (Di et al. 2001; see also electronic appendix, Fig. 2 for an X-ray picture of a compacted and a non-compacted clay soil; Hsu et al. 2009; Rasiah and Kay 1998). We suggest the observed negative effects on nitrogen mineralization in grazed clay soils operated both via adverse effects on soil fauna and via increased gaseous losses of nitrogen. When pores get smaller, organic matter may be physically protected against microbial attack, and microorganisms may be inaccessible to predating soil fauna (Bouwman and Arts 2000). We found considerable reductions in larger soil fauna in grazed clay soil, especially in deeper soil layers, which may have retarded decomposition due to lower grazing on microbial biomass and lower degrees of litter fragmentation (Bouwman and Arts 2000; Osler and Sommerkorn 2007). The observed shift in soil fauna community composition may partly be attributed to the differences in plant community composition, as plants are known to affect the soil fauna community (Patra et al. 2005; Veen et al. 2010). However, the strong reduction of larger soil fauna implies that the effects of herbivores on soil fauna composition mainly operates via a reduction in soil porosity. The high water-filled porosity (WFP) in the grazed clay (67 %) compared to the ungrazed clay soil (45 % WFP) indicated that denitrification may also have played a role in losses of inorganic nitrogen. Also, the dataset from 1995–1996 reports a strong increase in soil moisture, as well as a considerable increase in soil bulk density, which both indicate a similarly strong decrease in air-filled porosity. Reported threshold values of WFP causing denitrification differ according to soil type, but for sandy and clay soils, threshold WFP ranging from 50 to 74 % have been reported (e.g., Menneer et al. 2005; Nelson and Terry 1996; Sexstone et al. 1988). The observed differences in soil

redox potential also indicate a much higher potential for denitrification in grazed clay soil (Laanbroek 1990). Both results therefore strongly suggest that, in grazed clay soil, denitrification has contributed to the lower amounts of inorganic N, while we found little indication that denitrification may have played a role in the ungrazed and mown treatments on clay soil and the treatments on sandy soil. Thus, we conclude that grazing by large herbivores on clay soils may have a stronger effect on nitrogen mineralization rate than grazing on sandy soils, due to their difference in susceptibility to compaction and the resulting changes in soil porosity and WFP. In other words, the magnitude of the arrow from ‘Grazers’ to ‘Macroporosity’ in Fig. 8 is modified by soil type.

Alternative explanations for explaining differences in N mineralization

Differences in root mass have previously been suggested to explain differences in N mineralization. Fornara et al. (2011) showed that higher root mass lead to higher N mineralization. However, our results show the opposite: clay soils with grazing cattle contained a higher root mass and showed a lower N mineralization rate (Electronic Appendix, Table 1). So, we suggest that differences in root mass do not satisfactorily explain the observed differences in N mineralization rate. Differences in grazing intensity have also been argued to explain differences in N mineralization rate. In general, higher grazing intensity results in a larger effect on N mineralization (e.g., Le Roux et al. 2003). Grazing intensities have not been monitored during the 37 years of the experiment, but our measurements on canopy height show that grazing on clay may have been more intensive than on sand (data in Electronic appendix, Table 1). Firstly, the vegetation in grazed plots on sand had a higher canopy than the grazed plots on clay (6.8 vs. 3.1 cm; $n = 11.6$; $t = 3.3$; $P < 0.01$). Secondly, within-plot variation in vegetation height is also higher at the sandy grazed plots than at the grazed clay plots (29.1 vs. 19.5 %). However, though a lower grazing intensity on sandy soil may partly explain the small observed effect of grazing on N mineralization, it does not provide an explanation for the strong adverse effects of grazing on N mineralization on grazed clay soil. Our plots, especially those on clay soil, were spatially clustered. Hence, (unknown) underlying spatial gradients may be an alternative explanation for our findings. In order to test this hypothesis, we compared N mineralization in a number of clay plots and adjacent sandy plots [plots 3–4–9–14 on clay and 10–11–12–17 on sand, (Fig. 1, Electronic Appendix)] with the overall results. These plots on clay soil had a mineralization of 5.9 mg N kg^{-1} for the grazed treatment and a mineralization of $48.7 \text{ mg N kg}^{-1}$ in the ungrazed

treatment, while on sand we found $12.8 \text{ mg N kg}^{-1}$ for the grazed treatment versus $12.14 \text{ mg N kg}^{-1}$ for the ungrazed treatment. These figures were very similar to the overall results in Fig. 5, indicating that the differences between soil types are also clear on a small scale. Although other factors may cause differences in N mineralization, we believe that these results suggest that there are no large-scale spatial gradients that explain our results on N mineralization.

How large grazers slow down net nitrogen mineralization rate on clay soil in our study is in marked contrast to the effect of moose browsing in boreal forests (Pastor et al. 2006) and grazing of deer in oak savannah (Ritchie 1998), with very different consequences for the vegetation composition. Moose browsing and deer grazing in these systems shifts the vegetation to species of higher litter C:N ratio, resulting in lower decomposition and N mineralization (Pathway 2, Fig. 8). In our salt marsh study site, we find that, despite the slowing down of nitrogen mineralization on clay soil, plant quality for herbivores is strongly enhanced by grazing. Crude protein ratios in a grazed community range between 12.5 % (*Festuca rubra* dominated) and 20 % (*Puccinellia maritima* dominated), while in the ungrazed community, crude protein is between 9.25 % (*Juncus maritimus*-dominated) and 10.5 % (*Elytrigia atherica*-dominated). Also, cell wall content of the ungrazed plant community is 10–30 % lower than in the grazed communities (data from Bakker 1989). We suggest that this may reflect plant responses to increased abiotic stress (Pathway 3, Fig. 8). Our results are comparable to other studies reporting an increase in vegetation quality and a decrease in N mineralization rate (e.g., Bakker et al. 2004; Chaneton and Lavado 1996; van Wijnen et al. 1999). In our case, large grazers promote plant species that are tolerant to both herbivory and soil abiotic stress and have high tissue N concentrations. The soil abiotic stress results from the earlier mentioned hypoxia, but may also arise as a result of increased salinity on compacted soils due to lower leaching of salt and higher evapotranspiration of grazed vegetation (Olf and Ritchie 1998; Srivastava and Jefferies 1996). However, the increase in litter quality resulting from a shift to high quality plants does not enhance mineralization in our study system precisely because of the same unfavorable abiotic conditions for mineralization. A similar mechanism may be causing the decoupling between litter quality dynamics and N mineralization reported by Chaneton and Lavado (1996), van Wijnen et al. (1999), and Bakker et al. (2004). However, other mechanisms such as patchy nutrient return could also explain this decoupling (Mikola et al. 2009). Yet, the enhanced plant quality as a result of grazing leads to the formation of grazing lawns and, therefore, creates a positive feedback of large herbivores on their own presence (Bos et al. 2002).

Contrast and consistency with previous studies

The strong difference between nitrogen mineralization in the mown and grazed treatments on clay soil indicates that the breakdown of litter is the limiting step for nitrogen mineralization in our study system, not its inputs. We argue that this mechanism works via the herbivore-induced abiotic stresses on nitrogen mineralization as a result of soil compaction (Pathway 3, Fig. 8). Both the build-up of organic matter and the low decomposition activity in the grazed plots on clay soil also indicate a long-term decrease in nitrogen mineralization in the grazed plots on clay soil. This provides an explanation for the contrast between our results and results from studies in which an increased nitrogen mineralization rate was found in response to grazing (Frank and Groffman 1998; McNaughton et al. 1997a; Ruess and Seagle 1994). In dry savannah and steppe ecosystems, where these studies were done, grazers do not restrict decomposition by means of strongly increased soil water content and, thus, no organic matter accumulation occurs (Sankaran and Augustine 2004). Hence, nutrient mineralization can be speeded up according to Pathways 1 and 2 (Fig. 8). Moreover, in these systems, herbivores interact strongly with fire frequency, which plays an additional major role in the nutrient dynamics in these systems (Bond and Keeley 2005), while wildfires do not occur in the temperate salt marshes of north western Europe. In our study system, herbivores do restrict decomposition on clay soil, resulting in a dominant effect of Pathway 3 (Fig. 8), and a decrease in nitrogen mineralization. In hindsight, this may also explain the previously inexplicable results by Bakker et al. (2004) in a floodplain grassland. Here, cow grazing decreased nitrogen mineralization, but rabbits and vole grazing increased nitrogen mineralization, while in all treatments vegetation quality was enhanced. By taking the soil compaction effects of cows (which rabbits and voles do not have; Pathway 3) on this fine-textured soil into account, this seems a classic example of how Pathway 3 and Pathways 1 and 2 separate out in the same study system.

In order to track the effects of herbivores on soil porosity, bulk density is a less appropriate measure than water-filled porosity. The reason for this is that the measure of bulk density is greatly influenced by differences in specific weight between mineral substances (clay, sand) and organic matter content (leaf litter); organic matter is light but fills many pores and has a high water-holding capacity (White 2006). Because grazing by herbivores on clay soil results in a higher organic matter accumulation than in the ungrazed treatments and the grazed sandy soil treatment, the results of bulk density comparisons between these treatments show an underestimation of the compactive

effect on clay soils, something which is captured by a measure of the porosity.

As an ultimate consequence of our findings, we argue that effects of large herbivores on coarse textured soils may operate predominantly through the classic Pathways 1 and 2 in Fig. 8 by increasing or decreasing N mineralization, either through the promotion or reduction of litter quality inputs. In contrast, on fine-textured soils, large herbivores may have a strong effect via soil compaction (Pathway 3 in Fig. 8), and the observed negative effects on the abundance of bioturbating soil macrofauna could result in a long-term lack of ‘decompaction’. In wet, saline soils these effects are expected to be the most extreme. As a result, the apparent presence of grazing lawns on the clay soils on salt marshes shows that grazing lawns can develop despite the negative effect of large grazers on the soil nitrogen mineralization rate.

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