Reindeer grazing and soil microbial processes in two suboceanic and two subcontinental tundra heaths

Sari Stark, Rauni Strömmer and Juha Tuomi

In oceanic, nutrient-rich Fennoscandian arctic-alpine tundra heaths, grazing by reindeer has been found to increase herbs and graminoids in relation to dwarf shrubs. In continental lichen heaths in the inland with nutrient-poor conditions, however, slowly decomposable dwarf shrubs are favoured by grazing. According to a hypothesis, by favouring easily decomposing plants in nutrient-rich conditions and slowly decomposing plants in nutrient-poor conditions, herbivory enhances soil nutrient cycling in nutrient-rich and retards it in nutrient-poor areas. We tested this hypothesis by comparing the impact of reindeer grazing on soil C and N mineralization between two oceanic and two continental arctic-alpine tundra heaths. Although soil respiration and microbial metabolic activity were enhanced by grazing in the suboceanic but not in the subcontinental tundra heaths, gross N mineralization rates were higher in the grazed areas in soils from all study sites, indicating that reindeer grazing leads to increased rates of nutrient cycling in both nutrient-poor and nutrient-rich tundra heaths. Thus, in the subcontinental tundra heaths, the increase in soil N concentrations due to mammalian waste products enhances N mineralization rates, even though the organic C quality is not improved by reindeer grazing. There was some site-specific variation in the strength of the reindeer effects on various microbial processes and soil properties, which can be related to spatial variation in grazing intensity and timing, as these factors in turn affect the nutrient sink strength of the vegetation.

Grazing by reindeer (Rangifer tarandus L.) significantly influences the plant community structure on northernmost Fennoscandian arctic-alpine tundra heaths (Oksanen 1978, Oksanen and Virtanen 1995, Oksanen et al. 1995, Olofsson et al. 2001). Reindeer is the only large mammalian herbivore species in the area, and has been present throughout the post-glacial period (Oksanen et al. 1995). Mammalian herbivores frequently have many effects on soil nutrient cycling and organic matter decomposition. Firstly, herbivores alter the quality of organic matter and litter by changing the composition of plant communities and via their urine and faecal N input, which has an impact on the mineralization rates (McKendrick et al. 1980, Pastor and Naiman 1992, Pastor et al. 1993, Augustine and McNaughton 1998, Frank and Groffman 1998). Secondly, soil microbial processes are affected by an impact of herbivores on the soil microclimate (Zimov et al. 1995, Insam et al. 1996). As productivity in arctic ecosystems is strongly limited by soil nutrient availability (Chapin and Shaver 1996, Jonasson et al. 1999a), any herbivore-mediated change in nutrient mineralization rates...
has a potential to have a major feed-back effect on the ecosystem productivity. According to a hypothesis by Bryant et al. (1983), Oksanen (1990) and Chapin (1991), herbivory often selects for fast-growing and easily decomposing plants – such as graminoids – in nutrient-rich ecosystems, and slowly decomposing dwarf shrubs with high levels of defensive chemicals in nutrient-poor systems. Consequently, herbivory may enhance soil nutrient cycling in fertile soils and retard it in infertile soils (Chapin 1991). In northernmost Fennoscandia, the climatic differences between the Atlantic coast and the inland create a natural gradient where the continental and oceanic sections differ in plant productivity and soil nutrient availability (Ahti et al. 1968, Haapasaaari 1988, Oksanen and Virtanen 1995). Reindeer annually migrate between these areas. In the oceanic nutrient-rich coastline, summer pastures of reindeer, vegetation consists of dwarf shrubs and graminoids which are preferred in their summer diet, and grazing has been found to increase herbs and graminoids in relation to dwarf shrubs (Olofsson et al. 2001). Covered by lichens, the most important food resource for the reindeer during the winter, the continental uplands with nutrient-poor conditions are used as winter ranges (Warenberg et al. 1997). Lichen biomass is considerably reduced by grazing, and grazing favours dwarf shrubs with high levels of defensive chemicals (Oksanen and Virtanen 1995, Olofsson et al. 2001). Therefore, the reindeer-mediated changes in the decomposability of vegetation in the arctic-alpine ecosystems would appear to support the hypothesis of Chapin (1991).

We tested the hypothesis of differential responses of microbial processes to herbivory in nutrient-rich and nutrient-poor ecosystems, and compared the long-term impact of reindeer grazing on mineralization processes between oceanic and continental arctic-alpine tundra heaths. Our first-hand prediction was that reindeer grazing enhances C and N mineralization in oceanic, and either enhances or retards them in continental arctic-alpine tundra heaths. Mineralization in oceanic, and either enhances or retard it in infertile soils (Chapin 1991). Consequently, soil C and N mineralization in marine, and either enhances or retards them in continental arctic-alpine tundra heaths.

**Methods**

**Study sites**

Two subcontinental arctic-alpine tundra heaths in northern Finland (Jesnalvaara and Nuorttitunturi) and one suboceanic tundra heath in northernmost Norway (Lagisduoddar) were chosen for study. Soil data from another suboceanic tundra heath (Raisduoddar), collected one year previously and reported by Olofsson et al. (2001), were included. The study sites were established just above the forest line to the low oroarctic zone (Ahti et al. 1968, Haapasaaari 1988, Oksanen and Virtanen 1995).

The suboceanic tundra heaths, Lagisduoddar (70°30’N, 27°30’E) and Raisduoddar (69°30’N, 27°30’E), in northernmost Norway are both divided into a section of ungrazed and grazed parts by a fence built in the 1960’s to reduce the risk of reindeer illegally entering the winter ranges during the summer. The winter range side of the fence will here be referred to as ungrazed control, because the area has deep snow cover during reindeer spring migration, and the animals pass through the area within a short time during their autumn migration (Olofsson et al. 2001). In Lagisduoddar, the vegetation consists of dwarf shrubs (Betula nana, Vaccinium uliginosum, V. myrtillus, V. vitis-idaea), graminoids (Deschampsia flexuosa, Juncus trifidus, Carex sp.). Grazing by reindeer has somewhat increased not only the proportion of graminoids in the vegetation, but also the bare ground area (Olofsson et al. 2001). In Raisduoddar, the vegetation on the ungrazed part consists of the same species as in Lagisduoddar, but on the grazed part the abundance of graminoids (e.g. Carex sp., J. trifidus, D. flexuosa) and herbs have dramatically increased (Olofsson et al. 2001).

In Jesnalvaara (69°46’N, 26°57’E) and Nuorttitunturi (67°48’N, 29°40’E) in northern Finland, the lichen grounds are grazed by reindeer during the winter. Jesnalvaara is situated in the hemiarctic zone where the forests mainly consist of birch woodland (Ahti et al. 1968, Haapasaaari 1988, Oksanen and Virtanen 1995). There are a few bush-like *Betula pubescens* ssp. czerepanovii on the summit of Jesnalvaara, but the dominant higher plants are Empetrum nigrum, *V. uliginosum*, *Arctostaphylos alpina* and *Loiseleuria procumbens* (Kyötöviita 1988). A reindeer enclosure (size of 4000 m²) was built on the summit in 1968. The exclosed area is dominated by *Cladonia stellaris* and *Cetraria nivalis*, but in the grazed area their abundance and the amount of lichen biomass in general are significantly smaller (Kyötöviita 1988, Broll 2000). *E. hermaphroditum* is decreased by grazing, while *J. trifidus* is increased. Nuorttitunturi is a treeless hill situated in the eastern border of Finland in the northern boreal zone in the Saariselkä uplands, where the forests are mainly dominated by...
Norway spruce (Picea abies). Nuorttitunturi is divided into grazed and ungrazed sections by the fence built close to the borderline to Russia to prevent the Finnish reindeer from entering there. The ungrazed part of Nuorttitunturi has not been grazed for approximately 80 years, because there are hardly any reindeer on that Russian territory. The ground layer is dominated by several species of Cladonia and dwarf shrubs (V. uliginosum, V. vitis-idaea, B. nana), and the effect of grazing on the species composition and biomass is similar to that in Jesnalvaara (S. Stark, pers. obs.).

Soil sampling and analysis

Eight sampling plots were chosen along the reindeer fence on both the grazed and ungrazed sides, the plots being situated 12 m from the fence and 24 m from the nearest replicate on the same side of the fence. The distances in Jesnalvaara were 6 m and 12 m, respectively. Composite soil samples consisting of 3 soil cores of 10 cm diameter and reaching through the whole organic layer (> 5 cm in thickness) were taken from each sampling plot. The samples were kept cool during transportation to the laboratory, and then frozen until analysis.

Live plant material and roots were removed and the samples were carefully homogenized. Bulk density, gravimetric moisture (105°C, 12 h) and organic matter content (475°C, 4 h) were determined. A subsample of ca 6 g was extracted with 50 ml of 0.5M K₂SO₄ for a PO₄-P with automated 0.5M K₂SO₄ after chloroform fumigation (18 h) (Brookes et al. 1985), and the effect of grazing on the species composition and biomass is similar to that in Jesnalvaara (S. Stark, pers. obs.).

Data analysis

The results were tested in two different ways, first after calculating values per g soil OM, and second, after an automated analyzer (EA 1110, CHNS-O, CE Instruments).

Mineralization of N and C

For assessing the effect of reindeer grazing on the organic matter (OM) quality at the contrasting study sites, laboratory measurements for potential gross and net N mineralization and soil respiration rates were conducted. Gross N mineralization was determined using the isotope dilution method (Hart et al. 1994). After 2-day preincubation, 10 ml of dilute (0.04 g ammonium sulphate ²⁵N-atom% 97.5 in 1 dm³ distilled water) (²⁵NH₄)₂SO₄ solution was added to 200 cm³ of soil, and a subsample was immediately extracted with 0.5M K₂SO₄ for the recovery of ²⁵NH₄⁺ and the initial ²⁵NH₄⁺/²⁴NH₄ isotope ratio. The rest of the soil was incubated at +20°C for three days, and after the incubation a subsample was extracted with 0.5M K₂SO₄. The NH₄⁺ contents of the extracts were analysed as described earlier. The samples for ¹⁵N isotope ratio analysis were prepared by vaporizing NH₄Cl from the extracts and diffusing into 0.01M H₂SO₄ which was then dried at +45°C. Diffusion and drying were repeated until a sufficient amount of NH₄⁺ for the ¹⁵N analysis was obtained. The ¹⁵N/¹⁴N ratio was analysed by mass spectrometry (Europa Scientific ANCA system) and the rates of gross N mineralization and immobilization were calculated by the equation of Kirkham and Bartholomew (1954). Potential net N mineralization was measured by incubating a subsample in field moisture for 12 weeks at +20°C, and the initial and final NH₄⁺-N contents were determined as above.

Soil respiration (carbon mineralization) was analysed using a respirometer (Nordgren 1988, Nordgren et al. 1988). Soil moisture was adjusted to 250% of the weight of OM (Nordgren 1988). Basal respiration was analysed as the rate of CO₂-C efflux for 40 h of incubation at +20°C. Substrate-induced respiration (SIR), an index of microbial biomass C, was analysed by adding 313.8 mg of substrate (200 mg of glucose, 103.7 mg of (NH₄)₂SO₄ and 10.1 mg of KH₂PO₄) to fresh weight equivalent to 1 g OM (Anderson and Domsch 1978, Ohtonen 1994). The metabolic quotient of the soil microflora (q.CO₂) was calculated as a ratio of basal respiration to SIR. The lag time between the addition of substrate and the start of the exponential increase in the respiration rate was also measured as an indicator of microbial activity (Nordgren 1988, Ohtonen 1994).
calculating values per dm$^3$, because these two ways of presenting the results give different information in some cases. Measurements expressed per soil OM reflect the quality of the substrate for the soil organisms, and represent the reindeer-mediated chemical changes in soil quality, but values per soil volume also include the integrated effects of grazer-mediated changes in OM content and bulk density, and are often more appropriate to use when comparing different ecosystems (Cheng et al. 1998).

The assumption of homogeneity of variances was tested by Levene’s test, and in the case of unequal variances, logarithmic and reciprocal square root transformations were used. The data were analysed statistically by split-plot ANOVA with grazing, vegetation type and site as the main factors. Study site, a random factor, was nested with the vegetation type. The error d.f. for evaluating the main effect of grazing and the interaction between grazing and vegetation type was calculated as MS [grazing × site (vegetation type)]. The error d.f. for evaluating the main effect of forest type was calculated as MS [site (vegetation type)]. The error d.f. for evaluating the main effect of study site was calculated as MS [grazing × site (vegetation type)], and error d.f. for calculating the interaction between grazing and study site was calculated as MS (error). In parameters where ANOVA showed a significant interaction between grazing and site (vegetation type), $t$-test for each site individually was conducted. A non-parametric test (Mann-Whitney U-test) for each site individually was also used for net N mineralization that contained both positive and negative values and equal variances could not be obtained with any transformation. Data analysis was performed using the SPSS for Windows 8.0.

**Fig. 1.** Soil NH$_4^+$, extractable organic N, extractable microbial N and total N contents per soil volume (means ± S.E., n = 8, except in Raisduoddar, where n = 6). J = Jesnalvaara, N = Nuortitunturi (subcontinental study sites) and L = Lagisduoddar and R = Raisduoddar (suboceanic study sites).
Results

N mineralization and immobilization

Grazing increased gross N mineralization and immobilization rates on both OM and volume basis irrespective of vegetation type (Fig. 2, Tables 1 and 2). Due to the small soil NH$_4^+$-N content, we were unable to obtain reliable measures on every replicate in Jesnalvaara.

The microbial N uptake relative to supply was high in all laboratory incubations, resulting in negative net microbial N mineralization on a volume basis (net immobilization) in soils from all study sites except Jesnalvaara, being 9.4 ± 1.3, and 3.5 ± 1.5 µg dm$^{-3}$ d$^{-1}$ in grazed and ungrazed areas, respectively. In Jesnalvaara, grazing increased potential net N mineralization on a volume basis (Mann-Whitney test, $P = 0.023$). Otherwise, due to a very large variation among replicates, there were no significant differences in net N mineralization in relation to grazing. Net N mineralization was $-18.9 ± 13.5$ and $-12.9 ± 18.0$ µg dm$^{-3}$ d$^{-1}$ in grazed and ungrazed areas in Nuortitunturi, $-46.9 ± 40.1$ and $-75.2 ± 16.6$ µg dm$^{-3}$ d$^{-1}$ in grazed and ungrazed areas in Lagisduoddar, and $-1.75 ± 0.57$ and $-1.16 ± 0.39$ mg dm$^{-3}$ d$^{-1}$ in grazed and ungrazed areas in Raisduoddar, respectively.

Soil respiration, SIR and $q$CO$_2$

On the volume basis, grazing significantly enhanced soil respiration in the suboceanic tundra heaths but not in the subcontinental tundra heaths (grazing × vegetation type interaction; Tables 1 and 3). There were no effects on soil respiration on the OM basis, or on SIR, but basal respiration to SIR values ($q$CO$_2$) were significantly increased by grazing in the suboceanic tundra heaths but not in the subcontinental tundra heaths (grazing × vegetation type interaction; Tables 1 and 3). The effect on time lag before exponential growth of respiration after substrate addition was limited to only some of the study sites (grazing × site (vegetation type) interaction), and was significantly shorter on the grazed than the ungrazed plots in Raisduoddar ($P = 0.019$; t-test).

Soil and microbial N and P contents

Soil NH$_4^+$-N concentrations were affected by grazing in only some of the sites (grazing × site (vegetation type) interaction; Fig. 1, Tables 1 and 3), and was significantly increased by grazing in Raisduoddar ($P = 0.004$; t-test). Similar trend was found in extractable organic N concentrations ($N_{org}$; grazing × site (vegetation type) interaction, $P < 0.10$), which was significantly higher on the grazed than on the ungrazed plots in Raisduoddar ($P = 0.049$, t-test). The NO$_3^-$ -N and total dissolved P concentrations were negligible or below the detection limit (values not shown).

The effect of grazing on microbial N was limited to only some of the study sites with no consistent impact within the vegetation type (grazing × site (vegetation type) interaction; Tables 1 and 3). Grazing significantly increased microbial N in Jesnalvaara ($P = 0.034$, t-test) and in Lagisduoddar ($P < 0.001$, t-test). Extractable microbial P was 27.0 ± 15.9 mg dm$^{-3}$ in grazed and 8.9 ± 2.4 in ungrazed plots in Jesnalvaara, 2.7 ± 0.6 in grazed and 8.6 ± 5.4 in ungrazed plots in Nuortitunturi, and 27.9 ± 4.7 in grazed and 10.9 ± 1.7 in ungrazed side in Lagisduoddar. Grazing significantly increased microbial P in Lagisduoddar ($P = 0.024$, t-test).

Total N concentrations on the volume basis were higher on the grazed than on the ungrazed plots in the suboceanic but not in the subcontinental tundra heaths (Fig. 1, grazing × vegetation type interaction in Table 1). However, there was no significant influence on total N when the values were calculated per OM (Tables 1 and 2).

Soil properties

Soil OM and moisture contents were significantly higher in the suboceanic than in the subcontinental tundra heaths, and there were no effects in relation to reindeer grazing (Tables 1 and 4). Bulk density on a dry weight basis, however, was significantly increased by grazing irrespective of the vegetation type.

Discussion

Grazing significantly increased organic matter decomposition rates in the suboceanic but not in the subcontinental tundra heaths. Grazing also increased soil respiration to SIR ratio, a carbon availability index (CAI) (Cheng et al. 1998) or microbial metabolic activity ($q$CO$_2$) (Nordgren 1988, Ohtonen 1994), in the suboceanic tundra heaths. The results indicate that reindeer-mediated changes in soil C quality differ between the suboceanic and the subcontinental tundra heaths, and thus conform to our study hypothesis. The shorter lag upon grazing in Raisduoddar indicates especially improved availability of labile C for soil microbes, because they respond quickly to added glucose if they are adjusted to using it (Nordgren 1988). However, grazing enhanced the rate of gross N mineralization in both nutrient-poor and nutrient-rich tundra heaths. Thus, the direction of the impact on soil nutrient availability was the same in both vegetation types, which was not predicted by the hypothesis.
Table 1. ANOVA table for reindeer effects on microbial and soil properties tested on soil OM and volume basis. The transformations to meet the assumptions of ANOVA are indicated by numbers: 1) logarithm 2) reciprocal square root. *F* and *P* values obtained by nested ANOVA (grazing hypothesis df = 1, error df = 2; vegetation type hypothesis df = 1, error df = 2; site (vegetation type) df = 2, error df = 2; grazing × vegetation type hypothesis df = 1, error df = 2; grazing × site (vegetation type) hypothesis df = 2, error df = 51).

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(continued...)
Reindeer grazing often increases the proportion of graminoids in the tundra heaths (Oksanen and Virtanen 1995, Kumpula et al. 1996, Manseau et al. 1996, Post and Klein 1996, Olofsson et al. 2001). Graminoids – although a food resource preferred by reindeer – gain from grazing because of their capability of fast regrowth and large investment of biomass in the root system, which makes them less sensitive to the loss of biomass than dwarf shrubs (Chapin 1980, Chapin et al. 1986). Thus, changes in vegetation promoted by grazing are results of both food selection by herbivores and differences in grazing tolerance among plant species and growth forms (Bryant et al. 1983, Chapin et al. 1986, Augustine and McNaughton 1998). In suboceanic tundra heaths, soil C transformations were higher in the grazed relative to ungrazed areas, presumably because graminoid litter decomposes faster than litter of dwarf shrubs (Hobbie 1996), and because graminoids have more fine roots that probably exudate more low molecular weight organic substances, which is easily available substrate for soil microbes (Ruess and Seagle 1994, Bardgett et al. 1998).

The urine and faeces produced by mammalian herbivores also affect the soil microbial processes, because slowly decomposable plant material is transformed into labile and N-rich organic substances (Mckendrick et al. 1980, Ruess and McNaughton 1987, Frank and Groffman 1998). Interestingly, graminoids gain from increased nutrient availability more than dwarf shrubs (Mckendrick et al. 1980, Jonasson 1992, Chapin and Shaver 1996, Grellmann 2001), and the increase in graminoids by grazing may be a result of both a better tolerance for biomass removal and efficient absorption of increased amount of nutrients (Olofsson et al. 2001). This view is supported by the result of Grellmann (2001), who found that in the absence of mammalian waste products as an underlying mechanism, herbivores decreased the abundance of graminoids in the arctic plant community and had a decelerating effect on soil nutrient cycling.
There was some site-specific variation in the strength of the reindeer effects on various microbial processes, which can be related to spatial variation in grazing intensity and timing, as these factors in turn affect the nutrient sink strength of the vegetation. Microbial biomass N and P were strongly increased by reindeer grazing in Lagisduoddar, indicating increased microbial nutrient immobilization. As a comparison, there was a non-significant elevation in microbial biomass due to grazing in Raisduoddar, but the soil NH$_4^+$-N and organic N contents were markedly increased. The contrast in the reindeer effects coincides with the differences in the impacts of reindeer grazing on vegetation, discussed by Olofsson et al. (2001). They suggested that, in Lagisduoddar, the dominance of graminoids is suppressed by the continuously high grazing pressure, while graminoids have established better in Raisduoddar due to the intensive but periodic grazing. As changes in plant communities are dependent on grazing pressure and temporal patterns, local variation in the changes in soil processes is also expected. In Lagisduoddar, plant production is limited by severe grazing and is probably indifferent to N availability. A decline in the sink strength of nutrients in plants may result in a considerable increase in the microbial biomass N and P (Jonasson et al. 1999b), which was the case in Lagisduoddar. By contrast, in Raisduoddar, plant productivity was significantly higher in the heavily grazed relative to ungrazed area (Olofsson et al. 2001), and soil nutrients were efficiently assimilated into plant rather than microbial biomass. Thus, soil nutrient availability was increased by grazing at both of the suboceanic study sites, but targeted to different components of biota.

**Subcontinental tundra heaths**

In nutrient-deficient lichen heaths, reindeer grazing changes the overall composition of material entering the decomposer foodweb by the decrease in the lichen biomass. In heavily grazed areas, lichens form very little necromass (Ahti 1977, Helle and Aspi 1982), and thus produce little dead organic matter for the soil decomposer community. As grazing did not change soil respiration in subcontinental tundra heaths, this suggests that, even though lichens produce litter that decomposes extremely slowly (Moore 1984), a reduction in the relative amount of lichen litter does not necessarily
improve litter or soil quality. Gross N mineralization rates were, yet, increased by reindeer grazing. Thus, in the subcontinental tundra heaths, increase in soil N contents due to the fertilization by urine and faeces probably enhance soil N mineralization rates, despite organic matter decomposition rates are not affected.

In arctic-alpine ecosystems, soil microbes contain a large proportion of the soil nutrient pool, particularly in nutrient-poor soils (Jonasson et al. 1999b). At the lichen-dominated sites, vegetation was dominated by slow-growing lichens that acquire their nutrients from atmospheric deposition, while, at the same time, large amounts of nutrients are stored in the microbial biomass. However, Jesnalvaara was the only area where measurable potential net mineralization took place during the laboratory incubation. This agrees with the field measurements of Giblin et al. (1991) and Cheng et al. (1998), who measured net N mineralization during the growing season in lichen heaths by contrast to net immobilization in some other vegetation types. Mineralization measurements by incubation and in the absence of living plant roots have proved to be problematic in the arctic, as the measurements often lead to net immobilization (Jonasson et al. 1999a). Assuming a likely control of microbial activity by easily available C, the low respiration rates in Jesnalvaara indicate that only a small proportion of total organic C was readily available to soil microbes (Nadelhofer et al. 1991), resulting in low microbial N uptake and mobilization rather than immobilization of the mineralized N.

There are some differences in the grazing effects on soil microbial processes between the lichen heaths and the lichen-dominated boreal forests, and these may provide insight into some of the underlying mechanisms. Reindeer grazing decreases soil respiration in the humus layer of lichen-dominated boreal forests (Väre et al. 1996, Stark et al. 2000), while net N mineralization is simultaneously enhanced (Stark et al. 2000). Thus, in lichen-dominated forests with a very thin humus layer, reindeer grazing causes a C limitation for the soil microbes, but does not seem to do so in arctic-alpine lichen heaths. In arctic-alpine ecosystems, considerable storage of organic matter takes place through accumulation, and, as C availability does not limit microbial growth, N is immobilized in microbial biomass to a much greater extent than in the boreal forest (Giblin et al. 1991, Jonasson et al. 1996, 1999a). Consequently, increased nutrient availability by reindeer grazing may lead to increased microbial N immobilization in arctic-alpine areas, but not in the boreal forests, where soil microbes face strong C limitation due to grazing. The view that microbes at high altitudes are not only C-limited but limited by both C and nutrients (Körner 1999) is well supported by the differences in the soil microbial responses to reindeer grazing between boreal and arctic-alpine ecosystems. Whether soil microbes are limited by C or nutrients may therefore be one of the key determinants in the effects of herbivory on soil microbial processes, especially on the balance between microbial nutrient mobilization and immobilization.

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