



Grazing intensity in subarctic tundra affects the temperature adaptation of soil microbial communities



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ABSTRACT

Grazing by large ungulates, such as reindeer (*Rangifer tarandus* L.), in subarctic tundra exerts a considerable effect on the soil microclimate. Because of higher insulation by the aboveground vegetation in light versus heavily grazed areas, soil temperatures during the growing season are considerably higher under heavy grazing. Here, we hypothesized that these grazer-induced changes in soil microclimate affect the temperature sensitivity of soil microbial activity. To test this hypothesis, we conducted soil incubations at different temperatures (4 °C, 9 °C and 14 °C) for six weeks using soils from sites with contrasting long-term grazing intensities. Microbial respiration at low temperature (4 °C) was significantly higher in soils under light grazing than in soils under heavy grazing; however, grazing intensity did not affect respiration rates at 9 °C and 14 °C. In soils under light grazing, post-incubation β-glucosidase (BG) activity at 4 °C was higher in soils that had been incubated at 4 °C than in soils incubated at 14 °C, suggesting functional adaptation of the soil microbial community to low temperature. Similar adaptation was not detected in soils under heavy grazing. Ion Torrent sequencing of bacterial 16S rRNA genes showed major differences in the bacterial community composition in soils incubated at different temperatures. Overall, our results indicate that tundra soil microorganisms may be more cold-adapted under low than high grazing intensity. Due to this difference in temperature adaptation, the consequences of climate warming on soil microbial processes may be dependent on the grazing intensity.

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1. Introduction

Grazing by large mammals, such as reindeer (*Rangifer tarandus* L.), exerts important effects on vegetation across the circumpolar Arctic (Grellmann, 2002; Olofsson et al., 2004; van der Wal and Brooker, 2004; Gornall et al., 2009; Zamin and Grogan, 2013). The compositional changes of the dominant vegetation induced by grazing affect the quantity and quality of plant litter input to soil (Olofsson and Oksanen, 2002; Olofsson et al., 2004; Stark et al., 2007), which has important consequences for soil microbial processes because of changes in substrate availability for soil microorganisms (Stark et al., 2002, 2012; Olofsson et al., 2004; Stark and Väisänen, 2014). The fertilisation effect of urine and faeces by

grazing mammals frequently increases soil nutrient availability (van der Wal et al., 2004; Stark and Väisänen, 2014; Barthelemy et al., 2015). However, another major mechanism by which large grazers may alter soil microbial activities is the decreased insulatory effect of vegetation on soil, which increases soil temperatures during the growing season (van der Wal et al., 2001; Olofsson et al., 2004; Macías Fauria et al., 2008; Gornall et al., 2009). Recently, soil microbial communities have been acknowledged as possessing a strong capacity to acclimate their functions to temperature (Allison et al., 2011; Wallenstein et al., 2011; Wallenstein and Hall, 2012; Bradford, 2013). Whether this acclimation is by physiological adaptation or shifts in microbial community structure is still not well understood. To date, it has not been investigated if the temperature sensitivity of soil microbial activity differs at the different levels of grazing intensity. Identifying such an interaction would be important, especially in northern ecosystems that experience substantial changes in climate and where limited organic matter decomposition caused by low temperatures has resulted in

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considerable stocks of accumulated soil carbon (C) (Davidson and Janssens, 2006; Karhu et al., 2014).

Soil microbial communities generally adapt to changing temperatures by a number of mechanisms that operate over a range of timescales. For example, temperatures alter the production rate and structure of extracellular enzymes that catalyse organic matter degradation (Wallenstein et al., 2011; Wallenstein and Hall, 2012; Steinweg et al., 2013). Extracellular enzymes synthesized by soil microorganisms show remarkable plasticity and can function at different temperatures because of modifications to the structural characteristics of the enzymes (Lützow and Kögel-Knabner, 2009; Wallenstein et al., 2011; German et al., 2012). The adaptation of enzymes to cold conditions may constitute a trade-off between the capacity to increase process rates along with temperature and capacity to maintain structural stability at high temperatures (Conant et al., 2011; Wallenstein et al., 2011; Wallenstein and Hall, 2012). Temperatures also influence the soil microbial community composition and relative activity of different taxa (Yergeau et al., 2012; Xiong et al., 2014). Therefore, the adaptation of soil microbial functions to temperature may be mediated by a combination of enzymatic adaptations within soil microbial communities and shifts in the relative activity and abundance of microbial taxa adapted to different temperature regimes (Wallenstein and Hall, 2012).

Here, we hypothesized that soil microbial communities could show specific temperature adaptations depending on the level of long-term grazing intensity. We predicted that adaptation to low soil temperatures could constitute a more important functional trait (*sensu* Wallenstein and Hall, 2012) in soils under light grazing where soil temperatures during the growing season are lower. In contrast, the capacity to increase reaction rates with temperature could constitute a more important functional trait in soils under heavy grazing where soil temperatures are higher. We tested these predictions with laboratory incubations at different temperatures using soils collected from tundra sites that experience contrasting long-term grazing intensities. Previous studies of the sites have demonstrated that the mean soil temperatures during the growing season can be 2.5 °C higher in heavily grazed areas relative to lightly grazed areas (Olofsson et al., 2004). First, we predicted that soil microbial respiration and extracellular enzyme activities

(EEAs), such as BG activity, at low temperature would be higher in soils under light grazing. Second, we predicted that soil microbial respiration and EEAs would show a stronger increase with increased soil temperatures under heavy grazing. Soil incubation at different temperatures would also provide novel insights into the responses of soil microbial abundance and community composition to temperature. Because of lower soil temperatures during the growing season under light grazing, we thirdly predicted that the bacterial community composition would be more sensitive to increased temperatures in these soils than in heavily grazed soils.

2. Materials and methods

2.1. Study site, sampling and laboratory incubation

We used a mesic tundra heath (Raisduoddar, Norway [69°39'N, 27°30'E]) in the suboceanic section of northernmost Fennoscandia (Oksanen and Virtanen, 1995) for this study. Because of a pasture rotation fence built in the 1960s, one sub-section in Raisduoddar is only briefly used by the reindeer for passage (hereafter referred to as light grazing). Another sub-section has been subjected to intensive grazing for the past 50 years during the annual reindeer migration period that occurs in the first half of August (hereafter referred to as heavy grazing). Vegetation under light grazing is dominated by evergreen and deciduous dwarf shrubs, and the soil is N poor, whereas vegetation under heavy grazing is dominated by graminoids (*Carex* sp.) and has high plant productivity, and the soil is N rich (Table 1; Stark et al., 2002; Olofsson et al., 2004). The soil temperature was monitored (at approximately 3 cm depth) using temperature data loggers ($N = 3$, EasyLog EL-USB-1, Lascar Electronics) set to record the temperature every hour. The minimum and maximum soil temperatures were lower in the lightly grazed area than in the heavily grazed area during the summer months (mean + S.E. for June through August (2010–2012) of 7.5 ± 0.3 °C and 9.0 ± 0.3 °C in the lightly and heavily grazed areas, respectively). The soil temperatures in the lightly grazed area increased slowly after snow-melt, which resulted in a soil environment with temperatures below 9 °C for most of the growing season (Fig. 1).

Table 1
A. Soil properties and dominant plant species and their abundances in lightly and heavily grazed subarctic tundra heath in Raisduoddar. Vegetation abundance data have been previously published in Väisänen et al. (2013) and Väisänen et al. (2014). B. The concentrations of NH₄-N and NO₃-N before and after soil incubations at different temperatures (4 °C, 9 °C, and 14 °C) in soils collected from lightly and heavily grazed tundra. Values are the mean and S.E. in parentheses, $N = 5$ (soil properties) or $N = 8$ (plant abundances).

	Lightly grazed	Heavily grazed
A.		
OM%	75.6 (2.3)	68.4 (8.0)
pH	5.1 (0.1)	5.2 (0.1)
OM stock (kg m ⁻²)	3.6 (0.3)	4.1 (0.3)
<i>Humus layer depth (cm)</i>		
Dominant plant species (abundances described as hits/100 pins; mean + S.E.)	<i>Empetrum hermaphroditum</i> (75.0 ± 12.0), <i>Vaccinium vitis-idaea</i> (40.0 ± 8.0), <i>V. uliginosum</i> (19.7 ± 5.9), <i>Betula nana</i> (19.1 ± 5.7), graminoids (18.1 ± 5.8), <i>V. myrtillus</i> (3.8 ± 2.7), bryophytes (66.6 ± 6.9)	Graminoids (208.1 ± 44.8), <i>Empetrum hermaphroditum</i> (32.2 ± 25.2), <i>V. vitis-idaea</i> (15.6 ± 4.6), <i>Betula nana</i> (2.5 ± 2.2), bryophytes (36.9 ± 10.4)
B.		
NH ₄ -N initial (mg kg ⁻¹ OM)	15.0 (5.6)	61.7 (29.1)
NO ₃ -N initial	3.1 (0.2)	9.8 (6.3)
NH ₄ -N		
Post-incubation 4 °C	14.1 (4.3)	95.9 (54.4)
Post-incubation 9 °C	17.1 (2.7)	73.3 (31.7)
Post-incubation 14 °C	11.9 (5.1)	55.9 (25.5)
NO ₃ -N		
Post-incubation 4 °C	2.9 (0.2)	8.9 (5.5)
Post-incubation 9 °C	3.2 (0.3)	10.1 (6.2)
Post-incubation 14 °C	2.9 (0.3)	9.3 (5.4)

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