Mörsdorf, M.A., Baggesen N.S., Yoccoz, N.G., Michelsen A., Elberling B., Ambus P.L., Cooper, E.J. 2019.

Deepened winter snow significantly influences the availability and forms of nitrogen taken up by plants in High Arctic tundra. *Soil Biology and Biochemistry* **135**:222-234

https://doi.org/10.1016/j.soilbio.2019.05.009

Mörsdorf, M.A., Baggesen N.S., Yoccoz, N.G., Michelsen A., Elberling B., Ambus P.L., Cooper, E.J. 2019.

Corrigendum to Mörsdorf et al. (2019) "Deepened winter snow significantly influences the availability and forms of nitrogen taken up by plants in High Arctic tundra" [Soil Biology & Biochemistry 135 222–234]

https://doi.org/10.1016/j.soilbio.2019.107654

- 1 Deepened winter snow significantly influences the availability and forms of nitrogen
- 2 taken up by plants in High Arctic tundra.
- 3 Martin A. Mörsdorf<sup>a</sup> (martinmoersdorf@gmx.de), Nanna S. Baggesen<sup>a,b</sup>
- 4 (nanna.baggesen@bio.ku.dk), Nigel G. Yoccoza (nigel.yoccoz@uit.no), Anders Michelsenb,c
- 5 (andersm@bio.ku.dk), Bo Elberling<sup>b</sup> (be@ign.ku.dk), Per Lennart Ambus<sup>b</sup> (peam@ign.ku.dk),
- 6 and Elisabeth J. Cooper<sup>a</sup> (elisabeth.cooper@uit.no)

7

- 8 aDepartment of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics,
- 9 UiT The Arctic University of Norway, Framstredet 39, 9037 Tromsø, Norway.
- <sup>b</sup>Center for Permafrost, Department of Geosciences and Natural Resource Management,
- 11 University of Copenhagen, 1350 Copenhagen K, Denmark.
- <sup>o</sup>Department of Biology, University of Copenhagen, 2100 Copenhagen Ø, Denmark.

13

- 14 Corresponding author: Martin A. Mörsdorf; UiT The Arctic University of Norway, Faculty of
- 15 Biosciences, Fisheries and Economics, Department of Arctic and Marine Biology;
- 16 Framstredet 39; 9037 Tromsø Norway; e-mail: martinmoersdorf@gmx.de
- 17 **Declarations of interest:** none.
- 18 **Keywords:** nutrients; Open Top Chamber (OTC); snow fences; soil and plant pools;
- 19 Svalbard; tundra

20

21

22

### **Abstract**

24

25

26

27

28

29

30

31

32

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47

Climate change may alter nutrient cycling in Arctic soils and plants. Deeper snow during winter, as well as summer warming, could increase soil temperatures and thereby the availability of otherwise limiting nutrients such as nitrogen (N). We used fences to manipulate snow depths in Svalbard for 9 consecutive years, resulting in three snow regimes: 1) Ambient with a maximum snow depth of 35 cm, 2) Medium with a maximum of 100 cm and 3) Deep with a maximum of 150 cm. We increased temperatures during one growing season using Open Top Chambers (OTCs), and sampled soil and vascular plant leaves throughout summer 2015. Labile soil N, especially inorganic N, during the growing season was significantly greater in *Deep* than *Ambient* suggesting N supply in excess of plant and microbial demand. However, we found no effect of *Medium* snow depth or short-term summer temperature increase on soil N, presumably due to minor impacts on soil temperature and moisture. The temporal patterns of labile soil N were similar in all snow regimes with high concentrations of organic N immediately after snowmelt, thereafter dropping towards peak growing season. Concentrations of all N forms increased at the end of summer. Vascular plants had high N at the start of growing season, decreasing as summer progressed, and leaf N concentrations were highest in Deep, corresponding to the higher soil N availability. Short-term summer warming was associated with lower leaf N concentrations, presumably due to growth dilution. Deeper snow enhanced labile soil organic and inorganic N pools and plant N uptake. Leaf <sup>15</sup>N natural abundance levels (δ<sup>15</sup>N) in *Deep* indicated a higher degree of utilization of inorganic than organic N, which was especially pronounced in mycorrhizal plants.

48

#### 1. Introduction

50

51 Major changes in precipitation and temperature patterns are occurring worldwide, but effects 52 are especially strong at high latitudes (ACIA, 2005; Barber et al., 2008; Shindell et al., 1999). 53 Warmer temperatures lead to increased precipitation during the winter, and may potentially change the functioning of Arctic terrestrial ecosystems (Bokhorst et al., 2016; Cooper, 2014; 54 Saha et al., 2006; Wrona et al., 2016). Greater snowfall can lead to deeper snow during 55 winter (Callaghan et al., 2011; Saha et al., 2006), increasing the insulating capacity of the 56 57 snow pack and resulting in enhanced soil respiration and nutrient mineralization rates (Blok et al., 2016; Grogan and Jonasson, 2006; Morgner et al., 2010; Nobrega and Grogan, 2007; 58 Schimel et al., 2004; Sturm et al., 2005). Furthermore, nutrient mineralization will be 59 increased by rising temperatures during the growing season (Epstein et al., 2000; 60 Nadelhoffer et al., 1991). Increased soil nitrogen (N) availability may be particularly 61 important, since this could stimulate plant growth, enhancing carbon sink potential (Epstein 62 et al., 2000; McGuire et al., 1992; Shaver and Chapin, 1980; Vitousek and Howarth, 1991). 63 However, it is still unclear how terrestrial N cycles in the Arctic will change in response to a 64 65 changing climate. In the Arctic, a large proportion of the annually produced labile soil N arises from de-66 polymerization and mineralization under the winter snow pack, and is determined by sub-67 nivean temperatures (Brooks et al., 2011; Giblin et al., 1991; Hobbie and Chapin, 1996; 68 69 Mikan et al., 2002; Schimel et al., 2004). During the melting phase this soil N is mobilized; possibly explained by the rapid change in environmental conditions causing osmotic stress 70 and breaking microbial cell walls, so that organic and inorganic N get into the soil solution 71 72 (Lipson et al., 1999; Schimel et al., 2007). However, the labile N release happens in pulses 73 during the melting phase and concentrations in soil solution might be amplified in enhanced 74 snow depths (Buckeridge and Grogan, 2010). Pulses of N may coincide with times of low 75 root- and microbial activity and large amounts of N may be lost as leachate (Brooks and Williams, 1999; Hobbie and Chapin, 1996). Anaerobic conditions during the thaw period also 76

promote processes such as denitrification, which increases N loss as gasses (Grogan et al., 2004; Mørkved et al., 2006; Sharma et al., 2006). In the High Arctic several years of artificially enhanced snow depths increased labile soil N (especially inorganic soil N) well into peak growing season (Semenchuk et al., 2015), showing that not all labile soil N from winter and melt-out phase is lost during thaw. There have been, to date very few studies on these processes ongoing in the High Arctic and the study by Semenchuk et al. (2015) is, to the best of our knowledge, the only one from the High Arctic, where enhanced snow depths are shown to increase labile soil N pools during the growing season. Besides the effects of enhanced snow depths on labile N during growing season, the N pool may be further modified by warmer summer temperatures. Labile soil organic and inorganic N pools are increased by warmer soil temperatures, due to higher microbial turnover and increased mineralization rates (Nadelhoffer et al., 1991; Rustad et al., 2001; Weedon et al., 2012). It is, however, still unclear whether snow related effects on N availability interact with warmer summer temperatures. Furthermore, the temporal patterns of different labile N forms (organic vs. inorganic N) throughout growing season may be changed under a warmer climate. During the melting period, there is usually a major peak of dissolved organic nitrogen (DON) and ammonium (NH<sub>4</sub><sup>+</sup>) (Edwards et al., 2006; Grogan et al., 2004; Grogan and Jonasson, 2003; Lipson et al., 1999). The period immediately following melting is characterized by N uptake by both microbes and plants, rendering labile soil N to be low or non-existent (Giblin et al., 1991; Schimel et al., 2004; Weintraub and Schimel, 2005). However, predicted climatic change may significantly alter those patterns. If labile soil N becomes more abundant in the High Arctic due to enhanced snow depths and warmer summers, N mineralization could occur during the peak growing season increasing the concentrations of inorganic soil N. This scenario is plausible under enhanced snow depths in the High Arctic (Semenchuk et al., 2015). The abundance of such inorganic soil N at specific times during growing season may be crucial for the structuring of plant communities in the Arctic, since tundra plant species

77

78

79

80

81

82

83

84

85

86

87

88

89

90

91

92

93

94

95

96

97

98

99

100

101

102

utilize different forms of N at various times throughout growing season, which may be a 104 requirement for their co-existence (McKane et al., 2002). 105 106 Besides potential N losses before summer, plants with overwintering roots are able to take 107 up some N during the melting phase or just a few weeks later, early in the growing season (Bilbrough et al., 2000; Chapin et al., 1980; Grogan et al., 2004; Grogan and Jonasson, 108 109 2003; Kreyling et al., 2007). In the High Arctic, enhanced winter snow depths and summer temperatures may thereby also lead to increased N uptake by plants, as indicated by higher 110 111 N concentrations of plant tissue during peak and late growing season (Blok et al., 2015; Semenchuk et al., 2015). However, even if the timing of available soil N coincides with 112 potential uptake via plant roots, immobilization by microbes can impose strong competition 113 for N at any time between the thaw period and the fall season (Andresen et al., 2008; 114 Jonasson et al., 1999; Lipson et al., 1999; Lipson and Monson, 1998; Schimel et al., 2004). 115 Plant acquisition of different forms of N relates to the incorporation of <sup>15</sup>N isotopes. The 116 natural concentration of <sup>15</sup>N in leaf tissue (δ<sup>15</sup>N) increases with higher N availability, and is 117 higher in plants that rely primarily on inorganic, rather than organic N (Craine et al., 2009; 118 Michelsen et al., 1998). N mineralization increases with enhanced microbial access to N-rich 119 organic material (Schimel and Bennett, 2004), and the released NH<sub>4</sub><sup>+</sup> is often enriched in <sup>15</sup>N 120 (Nadelhoffer et al., 1996; Yano et al., 2010). Plants from N poor ecosystems rely to a large 121 degree on organic N sources (Michelsen et al., 1998, 1996). Although a wide range of non-122 123 mycorrhizal and mycorrhizal plants are generally able to take up organic soil N (Näsholm et al., 2009), the latter plant group might be especially efficient in utilizing organic soil N in 124 tundra (Michelsen et al., 1996). This, in combination with discrimination of the heavier N 125 126 isotope at the fungi – plant interface (Hobbie and Hobbie, 2006) leads to δ<sup>15</sup>N levels that are often lower than those of non-mycorrhizal plants (Michelsen et al., 1998). Simulation of 127 enhanced snow depths increased tissue δ<sup>15</sup>N of mycorrhizal plants in the High Arctic, which 128 129 might be due to higher availability and uptake of inorganic N (Blok et al., 2015; Semenchuk et al., 2015). However, the N uptake capacity of tundra plants can be highly growth-form or 130

species-specific (Hansen et al., 2006; Welker et al., 2005), and root-type specific (mycorrhizal vs. non-mycorrhizal) differences in response to projected climate change scenarios are not clear. Furthermore, different sources of soil N (organic *versus* inorganic) might be partitioned between plant species in tundra at varies times throughout growing season (McKane et al., 2002).

The aim of this study was to trace the amounts of labile soil N during the complete course of the growing season (from green-up to senescence) and to test if organic and inorganic N uptake by five common High Arctic tundra plants is regulated by enhanced winter snow regimes and warmer summer temperatures. For the last 9 years we used a snow fence experiment on Svalbard to enhance snow depth during the wintertime. The fences enhanced snow depth to a maximum of 150 cm close to the leeward side of the fences (*Deep* regime), and to a maximum 100 cm snow depth further away (*Medium* regime). An *Ambient* regime of maximum 35 cm snow depth was defined near (but unaffected by) the fences. For one growing season (2015), we factorially crossed the three snow regimes with a passive warming treatment. As opposed to previous studies from our site (Semenchuk et al. 2015), we thereby investigate soil and plant N pools in response to two snow depths enhancements, summer warming and throughout the entire growing season. We also investigate N status of a larger amount of plant species to highlight the connection between soil and plant N pools.

We hypothesized that:

1) Due to higher soil microbial activity, plant available soil N during the growing season would be higher in plots of the long-term snow enhancement and in plots with short-term summer temperature enhancement. Snow enhancement may especially increase availability of inorganic N, as previously found at our site for the late growing season (Semenchuk et al., 2015). We considered potential interaction effects of both treatments; treatment interactions with the timing of sampling would also be expected, with enhanced snow depths and summer warming potentially promoting abundance of inorganic soil N during peak, or late, growing season.

2) Due to enhanced soil N availability, vascular plants would take up more N in enhanced snow depth regimes and at warmer summer temperatures. Thus, their leaf N concentrations would generally increase during growing season.

3) Because of  $^{15}N$  enriched soil N pools, the increased uptake of inorganic soil N (predicted due to enhanced snow depth and higher summer temperatures) will lead to higher leaf  $\delta^{15}N$  during the growing season.

Treatment effects on leaf N concentrations and  $\delta^{15}$ N levels may be species-specific and differently expressed in plants with different root types (such as mycorrhizal vs. non-mycorrhizal plants).

#### 2. Materials and Methods

2.1. Study Site and Experimental Setup

Our study was conducted in Adventdalen (78°10′N, 16°04′E) on Svalbard, High Arctic Norway. A local weather station at Svalbard airport, approximately 15 km away from our site, recorded mean annual precipitations of 228 mm (based on monthly data for the period 2009 to 2018). Mean annual temperatures for the same period were -2.5°C, whereas March was the coldest month (- 10.6°C) and July the warmest (7.4°C) (www.eklima.no). The experiment was set up in the flat bottom part of the glacially eroded U-shaped valley at an altitude between 25 and 100 m above sea level. Geological parental material consisted of basic calcareous sand, silt and shale stones, originating from Triassic, Jurassic and Cretaceous sedimentary bedrocks (Hjelle, 1993; Tolgensbakk et al., 2000). The soils typically had an organic layer on the surface, followed by an A-horizon that reached depths of maximum 10 cm before the B/C horizons commenced (Strebel et al., 2010). Along the soil profile, soil pH typically ranged between 5 and 6.5. The vegetation of the valley was classified as prostrate dwarf-shrub, herb tundra (CAVM Team, 2003), but a detailed classification by Elvebakk

(2005) described it as part of the middle Arctic tundra, with Cassiope tetragona heaths and Dryas octopetala -Tomentypnum nitens meadows being the dominant vegetation types. In autumn 2006, we established the experiment to address the effects of altered winter snow patterns on Arctic soils and vegetation (Cooper et al., 2011). Four experimental blocks were spread at least 500 m apart from each other, covering an area of approximately 2.5 x 1.5 km. Perpendicular to the main winter wind direction (south-east), three snow fences were erected within each block, each 1.5 m high and 6.2 m long. Snow accumulation was highest 3 to 12 meters behind the fence (henceforth termed "Deep"), affecting maximum snow depths (150 cm) and the onset of growing season (Table 1). The areas with medium snow depths (60 -100 cm, hereafter termed "Medium") were between 10 and 20 m behind the fence, while "Ambient" plots were placed in areas of natural snow conditions adjacent to each fence (Table 1). A data logger (Gemini Data Loggers TGP 4020, Tinytag, UK) with a soil temperature probe was installed at each fence within each snow regime, and measured soil temperature continuously since initiation of the experiment. The temperature probes were placed at approximately one cm below soil surface and placed in a representative part of the area of each snow regime. Soil winter temperatures were warmer within *Deep* than *Ambient* every year (Figure 1 in Semenchuk et al., 2013). At snowmelt 2015, we erected transparent polycarbonate open top chambers (OTCs, of 2m diameter) within each snow regime, to simulate increased summer temperatures (Marion et al., 1997). Each OTC was placed on a previously established vegetation plot. These plots were used in earlier studies on plant responses and were established in a stratified-random way, with plots being required to include Dryas octopetala L. as a focal species (Cooper et al., 2011). OTCs were placed in position when approximately 50% of the plot was snow free. Paired plots without OTCs in each snow regime were available for comparison. The first OTCs were set up in *Ambient* on 23 May, and the last were established in *Deep* on 17 June. All OTCs were removed on 11 September 2015. Simultaneously with the establishment of the OTCs we also installed temperature loggers within OTC plots at one cm depth and data

183

184

185

186

187

188

189

190

191

192

193

194

195

196

197

198

199

200

201

202

203

204

205

206

207

208

were recorded every 30 min. As opposed to the long-term snow enhancements in our site, OTC treatments were only applied during one growing season.

Twice a week, soil moisture within the uppermost five cm below surface of each plot was measured using a Theta Probe ML 2x (Delta-T Devices, Cambridge, UK). Moisture measurements in snow-free plots started on first of June (DOY 152), but complete measurements of moisture within each snow regime were possible from 12 June (DOY 163) onwards. The last moisture measurements were conducted on 8 September (DOY 251). We measured in four places around each plot and calculated an average value.

Since the start of the experiment, two of the fences were excluded due to breakages and soil subsidence, reducing the number of fences used from 12 to 10. Behind one of the fences, we did not establish plots within *Medium*, which all together reduced the number of experimental plots used for this study from the original 70 to 58 (Supplementary file 1, Table 1).

#### 2.2. Soil and Plant Samples

A representative area of 2 x 2 m was designated for sampling at all snow regimes and was paired with a smaller area within OTCs. We sampled soil and plant material within those defined areas through the snow-free period 2015. Soil was sampled once a week as soon as plots were 50 % snow free, and from 21 July (DOY 202) until 31 August (DOY 243) we sampled every second week. We took one soil sample per plot using a 3 cm diameter soil corer. Each sample was divided into two depth intervals (0-2 cm and 2-5 cm below surface), as we initially expected different N conditions between the uppermost two cm and the soil below (Semenchuk et al., 2015). The upper two cm of each sample represented a mixture of the organic layer and the A horizon, whereas the 2-5 cm depth interval of each sample was entirely within the soil's A horizon. All soil samples were transported to the lab on the same day, and stored in a fridge at 4 °C upon further processing in the lab (a maximum delay of one week). Chemical data from both depths were later averaged for each sample, since

snow enhancement and summer warming effects were the same in the uppermost soil and 236 the soil below (see 2.3. Statistical analyses). 237 238 The prostrate deciduous shrub Salix polaris Wahlenb.(nomenclature according to: 239 panarcticflora.org) was a common plant species in all our plots and we sampled leaf material 240 once a week, from 14 July 2015 (DOY 195) to 28 July 2015 (DOY 209), and thereafter, every 241 second week until 2 September (DOY 245). We collected two new leaves from three randomly chosen ramets per plot into paper bags. In addition, we collected leaf tissue of 242 243 other key plant species three times throughout the growing season (14 July – DOY 195; 6 August – DOY 218; 2 September – DOY 245). Those species included the herb Bistorta 244 vivipara (L.) Delarbre, the prostrate semi-evergreen shrub Dryas octopetala L. and the 245 246 graminoids Luzula confusa Lindeb. and Alopecurus borealis Trin. All plant samples were put 247 in paper bags and dried in a drying cabinet for 36 hours at 55° C (Semenchuk et al., 2015). 248 In the laboratory we suspended 3 g of fresh weight of each soil sample in 30 ml of distilled 249 water and shook for two hours at room temperature. We then transferred the extracts into 20 ml plastic vials using 0.45 µm syringe filters. Upon analyses, all extractions were stored at -250 251 18 °C in the freezer. We analyzed the extractions for concentrations of dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) concentrations, as well as for 252 concentrations of dissolved ammonium (NH<sub>4</sub> <sup>+</sup>) and nitrate (NO<sub>3</sub> <sup>-</sup>) using a flow injection 253 analyzer (Fiastar 5000, FOSS Analytical, Hilleroed, Denmark). We later calculated 254 255 concentrations as µg C or N per g dry weight of soil by using the dry weight to fresh weight 256 ratio of soil obtained from separate subsamples. 257 We manually ground all plant leaf samples of Salix polaris using a mortar. For samples of all other species, we used a grinding mill (Retsch Mixer Mill, Retsch GmbH, Haan, Germany) 258 until the material was a homogenous powder. After weighing approximately two mg of each 259 260 pulverized sample into tin capsules, we measured N concentrations as well as  $\delta^{15}$ N isotope signatures using IRMS (CE 1110 EA), which was coupled in continuous flow mode to a 261

Finnigan MAT Delta PLUS isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany).

On 12 July 2016 we randomly collected one ramet of each study species within each snow fence and snow regime therein. We cleaned roots of each plant sample in the lab, stained some of the roots with ink to investigate intraradical fungal structures, and screened all plants for mycorrhizal root associations under a stereo microscope. Additionally, a light microscope was adopted to study the fine roots, using 200 × magnification. This screening confirmed that all samples of *Salix polaris*, *Bistorta vivipara* and *Dryas octopetala* were associated with ectomycorrhizal fungal symbionts. The graminoids *Luzula confusa* and *Alopecurus borealis* had no mycorrhizal colonization.

# 2.3. Statistical Analyses

We first plotted daily averages of soil temperatures during winter 2014 - 2015, as well as soil temperatures and average soil moisture during summer 2015. Those figures were later used to discuss the results of our main analyses on soil and plant N pools.

Many of the soil samples in our study had nutrient concentrations which were too low to assure accurate quantification (Supplementary file 1, Table 2). Leaving out those values or replacing by zero leads to biased soil nutrient estimates towards higher (or, respectively lower) values (Helsel, 2006, 2005). We therefore randomly assigned values between zero and the respective quantification limits and used a Bayesian inference approach for analyzing such "left-censored" data (Kato et al., 2013). This approach did not increase the chance of Type I error when drawing conclusions from our study, since the proportions of left censored data were very similar in each treatment category (Supplementary file 1, Table 2).

To estimate the effects of experimental treatments and the time of the season, we fitted linear mixed effects models including the long-term alteration of snow regime (*Ambient*, *Medium*, *Deep*), the short-term alteration of summer temperature regime (no OTC, OTC) and

the sampling day (DOY as a categorical variable with 10 levels) and all of their two and three way interactions as fixed effects. In our data analyses, we defined the first day of sampling as the time when at least 85% of all plots in a respective snow regime were snow-free in order to have similar amounts of replicates for each treatment (i.e. to have a balanced dataset). The first analysed DOY therefore corresponded to 10 June (DOY 161) in the Ambient and Medium snow regime, and 17 June (DOY 168) in the Deep regime. For soil NH<sub>4</sub> <sup>+</sup> and NO<sub>3</sub> <sup>-</sup>, we were only able to use nine sampling dates, since there were almost no data above the limit of quantification on 21 July (DOY 202, Supplementary file 1, Table 2). We incorporated the experimental block as an additional fixed covariate and the snow fence as random intercepts to account for variation among fences. We defined a model set with a simpler model structure (removing interactions), and conducted model selection based on leave-one-out cross validation (loo function in loo library), using looic (Vehtari et al., 2016). Modelling for each soil variable was initially done separately for the two soil depth intervals (0-2 and 2-5 cm), but ranking the separate candidate models based on looic, rendered the same outcome for both depth intervals (Supplementary file 1, Tables 3 and 4). An additive model structure represented the most parsimonious model. In the final models, we therefore combined data of both soil depths and included the depth interval as an additional co-variate for the DOC and DON model, since this further improved looic (Supplementary file 1, Table 5). Since we wanted to investigate plant N patterns (leaf N concentrations and  $\delta^{15}$ N) with regard to patterns of soil N availability, we did not conduct a model averaging procedure for plant N data and kept the same additive model structure as we used for the soil data (Cox, 2007). All models were assessed in terms of homogeneous residual distribution (constant variance) and approximate normality (checking outliers in particular). For the soil chemistry data, we

288

289

290

291

292

293

294

295

296

297

298

299

300

301

302

303

304

305

306

307

308

309

310

311

312

313

314

and approximate normality (checking outliers in particular). For the soil chemistry data, we had to log transform all response variables to fulfill model assumptions. We extracted the effect sizes for each category of an altered snow regime, summer temperature regime and sampling day, including their 95 % credible intervals (CIs). For soil response variables, those

values were back-transformed to the measurement scale. Effect sizes thereby represent a proportional change within each experimental treatment compared to *Ambient* conditions, whereas effect sizes of plant chemistry models represent absolute changes. For soil chemistry data, effect sizes were termed to be statistically significant as long as their 95 % CIs did not overlap a value of one, which would imply no proportional change. For plant data, using absolute change, effect sizes not overlapping 0 at a 95% CI were considered statistically significant. All the analyses were done in R (version 3.3.0, R Core Team, 2016) and we used the STAN sampler to run MCMC chains in combination with rstanarm package for R (version 2.25.3, Stan Development Team, 2006). We used the non-informative default priors of the rstanarm package for all models. We ran four Markov chain Monte Carlo (MCMC) simulations for all models, using 2000 iterations with the first 1000 iterations to tune the samplers. We assessed the convergence of chains using Gelman and Rubin's convergence diagnostic (Gelman and Rubin, 1992), which showed that the chains converged well for all derived parameters in our study.

# 3. Results

3.1. Temperature and moisture conditions in snow and summer temperature regimes

During winter 2014 to 2015, soils were warmer within *Deep* than *Ambient* and *Medium* snow regimes, for approximately 175 days of the 227 days of sub-zero temperatures (i.e. 77% of the time) (Figure 1a). *Medium* soils were also warmer than in *Ambient*, but for a shorter duration. Also the minimum temperatures during winter were buffered in *Deep* (-10 °C) and *Medium* (-17.5 °C), and more stable than the highly fluctuating *Ambient* soil temperatures (min. -23.5 °C).

During summer 2015, daily average temperatures in July and August were slightly higher in OTC compared to non-OTC plots (Figure 1b). Plots with OTCs had generally lower soil

moisture and fewer temporal fluctuations than those without (Figure 1c).

(Approximate placement of Figure 1) 341 342 3.2. Soil chemistry and nitrogen availability 343 344 Our model selection revealed an additive parameter combination of long-term snow regime 345 treatments, short-term summer warming and the sampling day as the most parsimonious model for all soil chemistry variables (Supplementary file 1, Table 5). Interactions between 346 those parameters were therefore negligible and not reported here. 347 The geometric mean (median) of soil DOC was 190.0 µg g<sup>-1</sup> dry soil (with 75 and 435 being 348 349 the lower and upper limit of the 95 % CI; further noted as 95 % CI) in Ambient, and 350 concentrations did not significantly differ between snow regimes or summer temperature regimes (Table 2, Fig. 2a). During three sampling days in the middle of growing season 351 352 (DOY 175, 181, 202) DOC concentrations were significantly lower than at growing season 353 onset (Fig. 2a). 354 DON concentrations were 12.8 µg g<sup>-1</sup> dry soil (95 % CI 8.9 – 18.8) in *Ambient* and increased by 22 % in Deep (Table 2, Fig. 2b). The passive warming treatment (OTCs) had no effect on 355 356 DON concentrations, but for 6 out of 10 sampling days, soil DON concentrations were 357 significantly lower than at onset of growing season. 358 Soil NH<sub>4</sub> + concentrations were 2.1  $\mu$ g g<sup>-1</sup> dry soil (95 % CI 0.8 – 4.7) in *Ambient* and 359 increased by 82% in Deep (Table 2, Fig. 2c), but OTC treatment had no effect. On two 360 sampling days (DOY 175, 195), NH<sub>4</sub> \*concentrations were significantly lower than at onset of growing season. However, on the last sampling day, NH<sub>4</sub> + concentrations were 92 % higher 361 than at onset of growing season. 362  $NO_3$  concentrations were low; only 0.10  $\mu$ g g<sup>-1</sup> dry soil (95 % CI 0.03 – 0.37) in *Ambient*, but 363

were 360 % (i.e. 3.6 times) higher in *Deep* (Table 2, Fig. 2d), but OTC had no significant

effect. NO<sub>3</sub> - concentrations increased significantly from start towards the end of growing 365 season. 366 367 (Approximate placement of Figure 2) 368 369 3.3. Leaf N concentrations Leaf N concentrations of all tundra plants in this study were higher in *Deep* than in *Ambient* 370 371 (Table 3, Fig. 3), and for Salix polaris (Fig. 3a) and Alopecurus borealis (Fig. 3d) were also 372 higher in *Medium* than *Ambient* (Table 3). 373 Enhanced summer temperatures lowered leaf N concentrations in all plant species, and were 374 significant for Bistorta vivipara (Fig. 3b), Alopecurus borealis (Fig. 3d) and Luzula confusa (Table 3, Fig. 3e). 375 376 Temporal patterns of leaf N concentrations were similar for all plant species. Concentrations dropped significantly from the start towards the end of growing season (Table 3, Fig. 3.). 377 (Approximate placement of Figure 3) 378 379 3.4. Leaf δ<sup>15</sup>N 380 381 Leaf δ<sup>15</sup>N of the ectomycorrhizal plants Salix polaris, Bistorta vivipara and Dryas octopetala were significantly higher in *Deep* compared to *Ambient* (Table 4, Figs. 4a to c). The  $\delta^{15}$ N of 382 383 Alopecurus borealis leaves was lower in Deep than Ambient (Fig. 4d), but did not significantly change in Luzula confusa (Fig. 4e). 384 385 Enhanced summer temperatures had no effect on leaf  $\delta^{15}N$  in most species, with the exception of *Luzula confusa*, for which OTCs significantly increased leaf δ<sup>15</sup>N (Table 4, Fig. 386 4e). 387

There was no temporal effect in leaf  $\delta^{15}N$  throughout the growing season for most species with the exception of *Salix polaris* for which leaf  $\delta^{15}N$  increased significantly from the third towards the last sampling day.

4.1. Patterns of labile soil N within different snow and summer temperature regimes

(Approximate placement of Figure 4)

392

393

394

395

396

397

398

399

400

401

402

403

404

405

406

407

408

409

410

411

412

413

388

389

390

391

#### 4. Discussion

As we hypothesized (Hypothesis 1), the snow regime exerts significant effects on concentrations of labile soil N (organic and inorganic N) during the growing season, but there is no significant effect of short-term summer warming, or interactions between treatments (snow enhancement and OTC), on any of the soil chemical variables. Our data imply that a significant portion of surplus N from the winter period is in the soil solution in the *Deep* snow regime even after the period of snowmelt. For the peak growing season, these patterns were previously found at the present study site (Semenchuk et al., 2015) showing that the labile N produced via winter processes exceeds the summer demands of both microbes and plants in our tundra ecosystem. Our results are thereby opposed to previous findings from the Low Arctic by Buckeridge and Grogan (2010), who show that flushes of N during the melt-out phase contain more N in enhanced snow regimes, but that concentrations of labile soil N are similar to ambient regimes after the late thaw spring transition. Large amounts of labile N from below the snowpack at their site are presumably exported by drainage water out of the system or released as gasses (N<sub>2</sub>O, N<sub>2</sub>) due to de-nitrification (Buckeridge et al., 2010a; Grogan et al., 2004). At our High Arctic site, none of these processes seem to cause losses that offset the effects of increased labile organic and inorganic N in Deep after the melt-out phase. To some extent, the contrasting study outcomes may therefore relate to intrinsic site differences in environmental conditions, such as soil water contents and drainage. However, loss of labile soil N can also be due to

the uptake by microbes and plants during snow melt (Bilbrough et al., 2000; Schimel et al., 2004), although Arctic plants may take up very little N during that phase (Bilbrough et al., 2000). In different systems, the plant community appears to strongly influence soil N abundance during the growing season. In the Low Arctic, higher sink strength of plants within productive sites were shown to have stronger ability to exploit additional inorganic soil N compared to plants within unproductive sites (Vankoughnett and Grogan, 2014). In our High Arctic site, low temperatures exert strong limitation on productivity of many species during the growing season (Rumpf et al., 2014), which may partly explain why labile soil N is apparent throughout the entire study period, especially in enhanced snow regimes. Vegetation type related differences can also occur within study sites, as shown by (Vankoughnett and Grogan, 2014) for the Low Arctic. Previous findings from our site show that snow enhancement increases labile soil N more strongly in mesic meadow than in dry heath sites Semenchuk et al. (2015). However, those differences may relate to better soil drainage in heath, since the biomass of plants with high sink strength, such as graminoids, is higher in meadows than in heaths at our site (Mörsdorf et al., in prep.). We also relate the effects of enhanced snow regimes to the extent to which snow depths were experimentally increased. Buckeridge and Grogan (2010) enhanced snow to max 1.1m, which buffered minimum winter temperatures from -18 °C to -12 °C and extended the snow covered period for 1-2 weeks. Those changes correspond to our alterations in Medium regime, where, like them, we did not find any significant treatment effect. However, the absolute minimum temperatures during winter were considerably colder at our High Arctic site, and our lack of response in Medium may be due to the lower insulation capacity of the Medium snow pack and corresponding colder soil compared to Deep (Fig. 1a). Laboratory incubations of soils from the study area show that microbial respiration rates decline exponentially with decreasing temperature, though a substantial activity is measurable well below zero °C (Elberling, 2007). The variation of microbial activity with temperatures below zero °C is still unresolved. Some studies suggest an exponential decline in microbial activity

414

415

416

417

418

419

420

421

422

423

424

425

426

427

428

429

430

431

432

433

434

435

436

437

438

439

with decreasing temperature due to a reduction of liquid water films and pore space (Mikan et al., 2002; Tilston et al., 2010; Tucker, 2014), while another (Elberling and Brandt, 2003) suggests that a temperature sensitivity (reported as a Q10 value) above zero is appropriate at least down to -9 °C for some Arctic soils systems. However, generalizations of in vitro relationships between microbial activity and temperature cannot be transferred directly to field conditions. Controlled conditions during lab incubations show that the variation in relationships between microbial activity and temperature is strongly dependent on methodological approaches (e.g. length of incubation, range of the assessed temperature, water content and trapped CO<sub>2</sub> during incubation), the apparent microbial community and the quality of organic matter (Colman and Schimel, 2013; Elberling and Brandt, 2003; Hamdi et al., 2013). In contrast to our Hypothesis 1, we do not find effects of short-term summer warming on labile soil N during the growing season. Previous findings from laboratory- and in situ incubations of tundra soil show that litter mass loss, microbial activity and N mineralization rates increase under warmer summer temperatures (Blok et al., 2016; Nadelhoffer et al., 1991; Rustad et al., 2001). These studies did not directly investigate soil N pools in the field as we did, but microbial activities and N mineralization will ultimately affect labile soil N pools. However, significant increases of those processes presumably required stronger enhancements of summer temperatures than the ones we achieved in our experiment. In a meta-analysis, Rustad et al. (2001) found 46% increase of net N mineralization, which was induced by an average temperature increase of 2.4 °C across a range of sites. Temperature increases of comparable magnitude, caused by OTCs in our site were only found during particularly warm phases between July and August, potentially leading to minor overall effects of OTCs on soil N throughout the growing season (Fig. 1b). Additionally, litter mass loss and N mineralization are sensitive to soil moisture contents (Blok et al., 2016; Rustad et al., 2001). Blok et al. (2016) show reduced rates of litter mass loss and N mineralization at the soil surface, where experimentally increased soil temperatures (average of 0.6 °C) cause

441

442

443

444

445

446

447

448

449

450

451

452

453

454

455

456

457

458

459

460

461

462

463

464

465

466

drought at the soil surface and a reduction of microbial activity. OTC plots had consistently lower soil moisture than the non-OTC plots at our site too (Fig. 1c); although the induced changes in soil moisture may not have been sufficient to cause a significant difference in the amount of labile soil N. Comparing the effects of snow regime versus summer temperature treatments in our study, we have to consider potential long-term legacies of an altered snow regime and the temporal mismatch of the short-term summer warming. The 9 years of snow manipulation at our site led to significant changes of plant community composition, with a lower proportion of evergreen shrubs (Cassiope tertragona and Dryas octopetala) and a higher proportion of forbs in Deep (Cooper et al. 2018, in review). Several studies show that in situ decomposition rates and/or N mineralization rates depend on the quality of litter material (Buckeridge et al., 2010b; Cornelissen et al., 2007; McLaren et al., 2017). Higher abundance of woody plants within the community may cause increased input of recalcitrant litter material, which can reduce decomposition rates and thus contribute to lower N availability in the long-term (Cornelissen et al., 2007). A reduced input of recalcitrant litter, due to reduced shrub abundance, may thus contribute to greater amounts of soil N in Deep compared to Ambient at our site. We cannot assume major changes in plant community composition in the short time period of summer warming application at our site (one growing season). However, experimental (Elmendorf et al., 2012) and observational evidence (Myers-Smith et al., 2015) in the tundra suggest increased shrub expansion towards summer warming in future. As such, community composition changes resulting from summer warming may profoundly change litter quality and soil N availability in the long-term as well (Myers-Smith et al., 2011). In terms of soil N availability at our site, we still need to study whether those long-term effects are relevant, and potentially interacting, with the effects of enhanced snow regimes. Our hypothesis on treatment interactions with the temporal patterns of labile N pools (H1) has to be rejected as well. The temporal patterns of labile soil N abundance during growing season can be generalized for all treatments at our site. DON concentrations are initially high

468

469

470

471

472

473

474

475

476

477

478

479

480

481

482

483

484

485

486

487

488

489

490

491

492

493

and drop within the first three weeks of sampling; a similar pattern to that found for labile NH<sub>4</sub><sup>+</sup> - N. We assume that the first sampling dates are still characterized by N, potentially stemming from lysed microbial cells and NH<sub>4</sub>+, which are generated under the snow pack (Grogan and Jonasson, 2003; Lipson et al., 1999). The drop of dissolved organic carbon (DOC), and especially that of labile soil N, in the following period might be explained by a phase of microbial growth, plant uptake, and possibly denitrification (Edwards et al., 2006; Grogan et al., 2004; Grogan and Jonasson, 2003). The peak growing season is thereby characterized by relatively stable and low soil N concentrations, until there is an emerging tendency of increasing N concentrations from 4 August (DOY 216) until the last sampling day (31 August, DOY 243), corresponding with the period of leaf senescence. Bardgett et al. (2007) quantified soil and plant N pools in the surroundings of our site and showed that soil DON is tightly coupled to microbial N pools. Microbes became progressively more supplied with DON towards the end of growing season. Since DON availability to microbes is an important determinant of mineralization in N-limited systems (Bardgett et al., 2002; Schimel and Bennett, 2004) this may explain the increase of inorganic soil N pools towards the end of growing season we found.

511

512

513

514

515

516

517

518

519

520

495

496

497

498

499

500

501

502

503

504

505

506

507

508

509

510

#### 4.2. Leaf N concentrations of common vascular plants

Our data support Hypothesis 2 on increased leaf N concentrations in response to long-term snow enhancement, but not in response to short-term summer warming.

Higher leaf N concentrations have previously been found in snow manipulation experiments, and been attributed to higher N availability due to increased mineralization rates during winter (Semenchuk et al., 2015; Walsh et al., 1997; Welker et al., 2005). Welker et al. (2005) also mention the shortened growing season in enhanced snow regimes, and associated lack of leaf growth and N dilution, as a potential reason for increased leaf N. However, with regard to the higher amounts of labile soil N in *Deep* during the growing season, we assume that the

increased leaf N concentrations relate to a higher availability and uptake of N. Although there is no significant labile soil N response to Medium, there is a consistent and sometimes significant increase of leaf N concentrations. The data therefore indicate that N availability may be increased in *Medium* as well, but not to the same extent as in *Deep*. The direction of response towards snow regimes is the same for all plant species in our study, although N uptake of tundra plants can generally be growth form- (Hansen et al., 2006; Larsen et al., 2012) or species-specific (Aerts et al., 2009; Welker et al., 2005) due to a variety of root types. Leaf N concentrations however, have to be interpreted with caution. Species adapted to N poor environments, such as our site, often show higher leaf N concentrations in response to increased N availability, since conservatism in growth responses has advantages in N poor environments (Chapin, 1980). In our sampling year, 2015, we lack information on growth responses, but previous findings from our site show species-specific leaf growth responses to *Deep* for some of the studied plants (Rumpf et al., 2014; Semenchuk et al., 2015). Rumpf et al. (2014) found that leaves of Salix polaris are smaller in Deep, whereas other species such as Bistorta vivipara and Dryas octopetala respond with increased plant size. Semenchuk et al. (2015) revealed that leaf size of Salix polaris is not affected in *Deep*, but leaves of *Bistorta vivipara* and *Luzula confusa* are significantly larger in Deep than Ambient. The higher N concentrations of Salix polaris leaves in Deep we found here might therefore be confounded by reduced plant growth, but leaf isotopes patterns indicate increased uptake of inorganic N (see discussion below). Opposite effects are found in response to short-term summer warming at our site. Here, leaf N concentrations are consistently lower in OTCs for all vascular plants. These results are contrary to the findings of Welker et al. (2005), who report higher leaf N concentrations for all plants in response to summer warming. They interpreted their results to be due to higher mineralization rates in warmer summer regimes, which may be related to the longer application (6 years) of warming in their study. However, increased leaf N in response to warming may actually be transient, due to responses in growth traits (Hudson et al., 2011).

521

522

523

524

525

526

527

528

529

530

531

532

533

534

535

536

537

538

539

540

541

542

543

544

545

546

Increased leaf sizes thereby cause dilution effects and render leaf N concentrations to stay the same or to be even decreased, despite higher N supply (Chapin, 1980). The decreases in leaf N concentrations in this study are only significant for Bistorta vivipara and graminoid leaves. Tolvanen and Henry (2001) show opposite leaf N responses of dwarf shrubs, forbs and graminoids to warming. Dwarf shrubs responded with decreased leaf N, whereas the latter two growth forms maintained their leaf N status. They interpret the N uptake and growth response of forbs and graminoids to be more efficient than for dwarf shrubs. In our site, differences in growth rates, as outlined earlier, may cause the observed differences in leaf N response between growth forms, since dwarf shrubs have slower growth rates and a smaller demand for nutrients (Chapin, 1980). Our findings of altered leaf N chemistry in response to both climate change scenarios imply consequences for the ecosystem. As discussed in Welker et al. (2005), climate related increases in leaf N concentrations will accelerate the turnover rates of plant material by invertebrates, microbes and fungi (Enriquez et al., 1993) and improve forage quality for other herbivores. Those mechanisms may cause positive feedback effects and further speed up the N cycle within tundra. We also found decreasing leaf N concentrations for all vascular plants from start to the end of the growing season, especially declining rapidly during leaf senescence. N is usually

transported from leaves to other plant parts during late growing season (Bret-Harte et al.,
2002). Also, N may be re-allocated to roots, since below ground growth of tundra plants lags
behind leaf growth when lower soil layers are still frozen right after melt out (Chapin et al.,
1980), and roots continue to grow even after the leaves have senesced (D'Imperio et al.,
2018)

571

572

548

549

550

551

552

553

554

555

556

557

558

559

560

561

562

563

564

565

# 4.3. Leaf $\delta^{15}N$ of common vascular plants

Our data support Hypothesis 3; leaf  $\delta^{15}N$  is higher in *Deep*, but responses were species-573 specific. The short-term summer temperature increase has no significant effects on leaf δ<sup>15</sup>N 574 575 except for Luzula confusa. Levels of leaf  $\delta^{15}N$  indicate the plants' N source. On a worldwide scale foliar  $\delta^{15}N$  increases 576 with higher N availability, due to higher uptake of inorganic N (Craine et al., 2009). 577 Fractionation processes during microbial N mineralization lead to <sup>15</sup>N enrichment of inorganic 578 N (Michelsen et al., 1996; Nadelhoffer et al., 1996). Also in Arctic soils, hydrolysable NH<sub>4</sub> + 579 was found to be more enriched in <sup>15</sup>N than amino acids (Yano et al., 2010). The significantly 580 increased leaf δ<sup>15</sup>N of mycorrhizal plants in enhanced snow regimes of our study may 581 therefore indicate a higher proportion of inorganic N (in particular NH<sub>4</sub> +) than organic N 582 uptake as compared to Ambient regimes. In N poor environments where organic N is the 583 584 main N form available, mycorrhizal plants may be especially efficient in obtaining organic N, rendering low tissue δ<sup>15</sup>N levels (Michelsen et al., 1996; Nadelhoffer et al., 1996). In 585 586 combination with our soil N availability data, the leaf isotopes indicate that mycorrhizal plants 587 take up a higher proportion of inorganic N in Deep than in Ambient. The same direction of 588 response was previously shown for Salix polaris and Cassiope tetragona at our site (Blok et al., 2015; Semenchuk et al., 2015). However, our data shows that the N uptake response 589 seems to be species-specific. Levels of leaf  $\delta^{15}N$  for the graminoid *Alopecurus borealis* are 590 even lower in *Deep*. In relation to the significant increases of NO<sub>3</sub> - N in *Deep*, this species 591 592 may use a larger proportion of this N form. Nitrification is associated with a depletion of <sup>15</sup>N in NO<sub>3</sub> in comparison to that in NH<sub>4</sub> (Nadelhoffer et al., 1996) as long as denitrification rates 593 594 are not too high (Shearer et al., 1974). Luzula confusa did not show statistically significant responses in leaf  $\delta^{15}$ N towards enhanced snow, but the direction of response showed the 595 same patterns as in mycorrhizal plants. Since non-mycorrhizal plants are also able to obtain 596 597 organic N (Näsholm et al., 2009), we assume that this species exhibits a similar shift from 598 utilizing higher proportions of inorganic N to organic N in *Deep* than in *Ambient* regimes. Levels of δ<sup>15</sup>N were generally lower in mycorrhizal than non-mycorrhizal plants, which might 599

be due to discrimination against the heavier <sup>15</sup>N isotope at the fungi – plant interface (Hobbie and Hobbie, 2006). Our study does not reveal any effect of short-term summer warming on leaf  $\delta^{15}N$  for most species, which presumably relates to the lack of significant treatment effects on labile soil N. However, Luzula confusa has significantly higher leaf δ<sup>15</sup>N in OTCs, but underlying mechanisms for this pattern can only be speculated, since summer warming did not cause an increase of inorganic soil N at our site. As outlined above, this species has lower leaf N concentrations in OTCs, potentially indicating growth dilution. Higher sink strength in warmed plots may thereby increase the uptake of inorganic N across snow regimes, causing a parallel increase of leaf  $\delta^{15}N$  levels. Levels of leaf  $\delta^{15}N$  are relatively stable for all plants throughout the growing season, except for Salix polaris. Apart from Salix polaris, the data indicates that other species utilize largely the same N pools throughout the investigated timespan. Salix polaris leaves have higher δ<sup>15</sup>N as the growing season progressed. With its overwintering roots and a highly effective uptake capacity, including ectomycorrhizal fungi, this species may be very efficient in utilizing the organic N sources at snowmelt, potentially stemming from lysed microbial cells. Transportation of such N, likely <sup>15</sup>N depleted, from roots to other plant parts such as the leaves, may render the low δ<sup>15</sup>N levels during early sampling campaigns here. Late season N uptake may be characterized by a higher proportion of inorganic N uptake, which is then abundant at our site. Overall, the <sup>15</sup>N natural abundance data connect well to our findings on concentration characteristics of labile soil N at the tundra site and suggest that plants rely to a stronger degree on inorganic N sources in *Deep* compared to *Ambient*.

623

624

600

601

602

603

604

605

606

607

608

609

610

611

612

613

614

615

616

617

618

619

620

621

622

#### 4.4. Conclusions

For the High Arctic, our study provides further evidence for that the amount of labile soil N during growing season is significantly enhanced in *Deep* than *Ambient* snow regimes. In the deepest snow regime, the amount of labile N may exceed the uptake by microbes and plants throughout the growing season. Additional short-term summer warming during one growing season, with or without the combination of increased snow, does not have any significant short-term effects on the soil N pools at our site.

The data also indicate a strong link between soil and plant N pools. Significant amounts of labile N in *Deep* may be acquired by a range of common vascular plants. Higher leaf N concentrations could thereby have implications for the ecosystem, e.g. by changing the quality of herbivore forage and also affecting N cycling. The  $\delta^{15}$ N levels of leaf tissue provide insight into the acquired N forms and, in combination with soil N patterns, indicate that the proportion of inorganic to organic N uptake is generally greater in *Deep* than *Ambient*. This shift in utilized N pools with enhanced snow may be species-specific, but is especially obvious in plants with ectomycorrhizal symbionts, since those are efficient in exploiting the major N pools available in our system.

### **Acknowledgments**

This work was supported by the Norwegian Research Council [grant number 230970]; the FRAM Centre Terrestrial Flagship [SnoEcoFen project]; the Norwegian Centre for International Cooperation in Education (SIU) High North Program [grant number HNP2013/10092]; and the Danish National Research Foundation [grant number DNRF100]. We thank Saskia Bergmann and Yuko Kusama for assistance in the field, and the University Centre in Svalbard (UNIS) for logistical support. We are also grateful to Frans-Jan Parmentier, Philipp Semenchuk and Mikel Moriana Armendariz for their valuable feedback on the manuscript.

### References

- ACIA, 2005. Arctic climate impact assessment, Cambridge Univ. Press, U.K.
- Aerts, R., Callaghan, T. V., Dorrepaal, E., Van Logtestijn, R.S.P., Cornelissen, J.H.C., 2009.
- Seasonal climate manipulations result in species-specific changes in leaf nutrient levels
- and isotopic composition in a sub-arctic bog. Functional Ecology 23, 680–688.
- Andresen, L.C., Jonasson, S., Ström, L., Michelsen, A., 2008. Uptake of pulse injected
- nitrogen by soil microbes and mycorrhizal and non-mycorrhizal plants in a species-
- diverse subarctic heath ecosystem. Plant and Soil 313, 283–295.
- Barber, D.G., Lukovich, J. V, Keogak, J., Baryluk, S., Fortier, L., Henry, G.H.R., 2008. The
- changing climate of the Arctic. Arctic 61, 7–26.
- Bardgett, R.D., van der Wal, R., Jónsdóttir, I.S., Quirk, H., Dutton, S., 2007. Temporal
- variability in plant and soil nitrogen pools in a high-Arctic ecosystem. Soil Biology and
- 663 Biochemistry 39, 2129–2137.
- Bardgett, R. D., Streeter, T. C., Cole, L., Hartley, I. R., 2002. Linkages between soil biota,
- nitrogen availability, and plant nitrogen uptake in a mountain ecosystem in the Scottish
- Highlands. Applied Soil Ecology 19, 121–134.
- 667 Bilbrough, C.J., Welker, J.M., Bowman, W.D., 2000. Early spring nitrogen uptake by snow-
- covered plants: a comparison of Arctic and Alpine plant function under the snowpack.
- Arctic, Antarctic and Alpine Research 32, 404–411.
- Blok, D., Elberling, B., Michelsen, A., 2016. Initial stages of tundra shrub litter decomposition
- may be accelerated by deeper winter snow but slowed down by spring warming.
- 672 Ecosystems 19, 155–169.
- Blok, D., Weijers, S., Welker, J.M., Cooper, E.J., Michelsen, A., Löffler, J., Elberling, B.,
- 2015. Deepened winter snow increases stem growth and alters stem  $\delta^{13}$ C and  $\delta^{15}$ N in

evergreen dwarf shrub Cassiope tetragona in high-arctic Svalbard tundra. 675 Environmental Research Letters 10. doi:10.1088/1748-9326/10/4/044008 676 677 Bokhorst, S., Pedersen, S.H., Brucker, L., Anisimov, O., Bjerke, J.W., Brown, R.D., Ehrich, D., Essery, R.L.H., Heilig, A., Ingvander, S., Johansson, C., Johansson, M., Jónsdóttir, 678 I.S., Inga, N., Luojus, K., Macelloni, G., Mariash, H., McLennan, D., Rosqvist, G.N., 679 Sato, A., Savela, H., Schneebeli, M., Sokolov, A., Sokratov, S.A., Terzago, S., 680 Vikhamar-Schuler, D., Williamson, S., Qiu, Y., Callaghan, T. V, 2016. Changing Arctic 681 682 snow cover: a review of recent developments and assessment of future needs for observations, modelling, and impacts. Ambio 45, 516-537. 683 684 Bret-Harte, M.S., Shaver, G.R., Chapin, F.S.I., 2002. Primary and secondary stem growth in Arctic shrubs: implications for community response to environmental change. Journal of 685 686 Ecology 90, 251-267. 687 Brooks, P.D., Grogan, P., Templer, P.H., Groffman, P., Öquist, M.G., Schimel, J., 2011. Carbon and nitrogen cycling in snow-covered environments. Geography Compass 5, 688 682-699. 689 690 Brooks, P.D., Williams, M.W., 1999. Snowpack controls on nitrogen cycling and export in 691 seasonally snow-covered catchments. Hydrological Processes 13, 2177–2190. 692 Buckeridge, K.M., Cen, Y.P., Layzell, D.B., Grogan, P., 2010a. Soil biogeochemistry during the early spring in low arctic mesic tundra and the impacts of deepened snow and 693 enhanced nitrogen availability. Biogeochemistry 99, 127-141. 694

arctic shrub tundra are enhanced by litter feedbacks. Plant and Soil 330, 407–421.

Buckeridge, K.M., Grogan, P., 2010. Deepened snow increases late thaw biogeochemical

Buckeridge, K.M., Zufelt, E., Chu, H., Grogan, P., 2010b. Soil nitrogen cycling rates in low

pulses in mesic low arctic tundra. Biogeochemistry 101, 105–121.

695

696

697

- 699 Callaghan, T. V, Johansson, M., Brown, R.D., Groisman, P.Y., Labba, N., Radionov, V.,
- Bradley, R.S., Blangy, S., Bulygina, O.N., Chistensen, T.R., Colman, J.E., Essery,
- R.L.H., Forbes, B.C., Forchhammer, M.C., Golubev, V.N., Honrath, R.E., Juday, G.P.,
- Meshcherskaya, A. V, Phoenix, G.K., Pomeroy, J., Rautio, A., Robinson, D.A., Schmidt,
- N.M., Serreze, M.C., Shevchenko, V.P., Shiklomanov, A.I., Shmakin, A.B., Sköld, P.,
- Sturm, M., Woo, M., Wood, E.F., 2011. Multiple effects of changes in Arctic snow
- 705 cover. AMBIO 40, 32-45.
- 706 CAVM Team. 2003. Circumpolar Arctic Vegetation Map. (1:7,500,000 scale), Conservation of
- Arctic flora and fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, Anchorage,
- 708 Alaska. http://www.arcticatlas.org/maps/themes/cp/
- 709 Chapin, F.S.I., 1980. The mineral nutrition of wild plants. Annual Review of Ecology and
- 710 Systematics 11, 233–260.
- 711 Chapin, F.S.I., Johnson, D.A., McKendrick, J.D., 1980. Seasonal movement of nutrients in
- 712 plants of differing growth form in an Alaskan tundra ecosystem: implications for
- 713 herbivory. Journal of Ecology 68, 189–209.
- Colman, B.P., Schimel, J.P., 2013. Drivers of microbial respiration and net N mineralization
- at the continental scale. Soil Biology and Biochemistry 60, 65–76.
- Cooper, E.J., 2014. Warmer shorter winters disrupt Arctic terrestrial ecosystems. Annual
- 717 Review of Ecology, Evolution, and Systematics 45, 271–295.
- Cooper, E.J., Dullinger, S., Semenchuk, P., 2011. Late snowmelt delays plant development
- 719 and results in lower reproductive success in the High Arctic. Plant Science 180, 157–
- 720 167.
- 721 Cornelissen, J.H.C., van Bodegom, P.M., Aerts, R., Callaghan, T. V, van Logtestijn, R.S.P.,
- Alatalo, J., Chapin, F.S., Gerdol, R., Gudmundsson, J., Gwynn-Jones, D., Hartley, A.E.,
- Hik, D.S., Hofgaard, A., Jónsdóttir, I.S., Karlsson, S., Klein, J.A., Laundre, J.,

- Magnusson, B., Michelsen, A., Molau, U., Onipchenko, V.G., Quested, H.M., Sandvik,
- S.M., Schmidt, I.K., Shaver, G.R., Solheim, B., Soudzilovskaia, N.A., Stenström, A.,
- Tolvanen, A., Totland, Ø., Wada, N., Welker, J.M., Zhao, X., Team, M., 2007. Global
- negative vegetation feedback to climate warming responses of leaf litter decomposition
- rates in cold biomes. Ecology Letters 10, 619–627.
- Cox, D.R., 2007. Applied statistics: a review. The Annals of Applied Statistics 1, 1–16.
- 730 Craine, J.M., Elmore, A.J., Aidar, M.P.M., Bustamante, M., Dawson, T.E., Hobbie, E.A.,
- Kahmen, A., Mack, M.C., Mclauchlan, K.K., Michelsen, A., Nardoto, G.B., Pardo, L.H.,
- Peñuelas, J., Reich, P.B., Schuur, E.A., Stock, W.D., Templer, P.H., Virginia, R.A.,
- Welker, J.M., Wright, I.J., 2009. Global patterns of foliar nitrogen isotopes and their
- relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen
- availability. New Phytologist 183, 980–992.
- D'Imperio, L., Arndal, M. F., Nielsen, C. S., Elberling, B., Schmidt, I. K., 2018. Fast
- responses of root dynamics to increased snow deposition and summer air temperature
- in an Arctic wetland. Frontiers in Plant Science 9, doi: 10.3389/fpls.2018.01258.
- 739 Edwards, K.A., McCulloch, J., Kershaw, G.P., Jefferies, R.L., 2006. Soil microbial and
- nutrient dynamics in a wet Arctic sedge meadow in late winter and early spring. Soil
- Biology and Biochemistry 38, 2843–2851.
- 742 Elberling, B., 2007. Annual soil CO<sub>2</sub> effluxes in the High Arctic: the role of snow thickness
- and vegetation type. Soil Biology and Biochemistry 39, 646-654.
- 744 Elberling, B., Brandt, K.K., 2003. Uncoupling of microbial CO<sub>2</sub> production and release in
- frozen soil and its implications for field studies of arctic C cycling. Soil Biology and
- 746 Biochemistry 35, 263-272.

- 747 Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., 2012. Global assessment of
- experimental climate warming on tundra vegetation: heterogeneity over space and
- 749 time. Ecology Letters, 15, 164–175.
- 750 Elvebakk, A., 2005. A vegetation map of Svalbard on the scale 1:3.5 mill. Phytocoenologia
- 751 35, 951–967.
- For Enriquez, S., Duarte, C., Sand-Jensen, K., 1993. Patterns in decomposition rates among
- photosynthetic organisms: the importance of detritus C: N: P content. Oecologia 94,
- 754 457–471.
- 755 Epstein, H.E., Walker, M.D., Chapin, F.S., Starfield, A.M., 2000. A transient, nutrient-based
- model of arctic plant community response to climatic warming. Ecological Applications
- 757 10, 824–841.
- 758 Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences.
- 759 Statistical Science 7, 457–472.
- Giblin, A.E., Nadelhoffer, K.J., Shaver, G.R., Laundre, J.A., McKerrow, A.J., 1991.
- 761 Biogeochemical diversity along a riverside toposequence in Arctic Alaska. Ecological
- 762 Monographs 61, 415–435.
- Grogan, P., Jonasson, S., 2006. Ecosystem CO2 production during winter in a Swedish
- subartic region: the relative importance of climate and vegetation type. Global Change
- 765 Biology 12, 1479–1495.
- Grogan, P., Jonasson, S., 2003. Controls on annual nitrogen cycling in the understory of a
- subarctic birch forest. Ecology 84, 202–218.
- Grogan, P., Michelsen, A., Ambus, P., Jonasson, S., 2004. Freeze-thaw regime effects on
- 769 carbon and nitrogen dynamics in sub-arctic heath tundra mesocosms. Soil Biology and
- 770 Biochemistry 36, 641–654.

- Hamdi, S., Moyano, F., Sall, S., Bernoux, M., Chevallier, T., 2013. Synthesis analysis of the
- temperature sensitivity of soil respiration from laboratory studies in relation to
- incubation methods and soil conditions. Soil Biology and Biochemistry 58, 115–126.
- Hansen, A.H., Jonasson, S., Michelsen, A., Julkunen-Tiitto, R., 2006. Long-term
- experimental warming, shading and nutrient addition affect the concentration of
- phenolic compounds in arctic-alpine deciduous and evergreen dwarf shrubs. Oecologia
- 777 147, 1–11.
- Helsel, D.R., 2006. Fabricating data: how substituting values for nondetects can ruin results,
- and what can be done about it. Chemosphere 65, 2434–2439.
- Helsel, D.R., 2005. Insider censoring: distortion of data with nondetects. Human and
- 781 Ecological Risk Assessment: An International Journal 11, 1127–1137.
- Hjelle, A., 1993. Geology of Svalbard, Norsk Polar Institutt, Oslo.
- Hobbie, J.E., Hobbie, E.A., 2006. <sup>15</sup>N in symbiotic fungi and plants estimates nitrogen and
- carbon flux rates in arctic tundra. Ecology 87, 816–822.
- Hobbie, S.E., Chapin III, F.S., 1996. Winter regulation of tundra litter carbon and nitrogen
- dynamics. Biogeochemistry 35, 327–338.
- Hudson, J.M.G., Henry, G.H.R., Cornwell, W.K., 2011. Taller and larger: shifts in Arctic
- tundra leaf traits after 16 years of experimental warming. Global Change Biology 17,
- 789 1013–1021.
- Jonasson, S., Michelsen, A., Schmidt, I.K., 1999. Coupling of nutrient cycling and carbon
- 791 dynamics in the Arctic, integration of soil microbial and plant processes. Applied Soil
- 792 Ecology 11, 135–146.
- Kato, T., Miura, T., Okabe, S., Sano, D., 2013. Bayesian modeling of enteric virus density in
- wastewater using left-censored data. Food and Environmental Virology 5, 185–193.

- Kreyling, J., Beierkuhnlein, C., Pritsch, K., Schloter, M., Jentsch, A., 2007. Recurrent soil freeze-thaw cycles enhance grassland productivity. New Phytologist 177, 938–945.
- Larsen, K.S., Michelsen, A., Jonasson, S., Beier, C., Grogan, P., 2012. Nitrogen uptake
  during fall, winter and spring differs among plant functional groups in a subarctic heath
  ecosystem. Ecosystems 15, 927–939.
- Lipson, D.A., Monson, R.K., 1998. Plant-microbe competition for soil amino acids in the alpine tundra: effects of freeze-thaw and dry-rewet events. Oecologia 113, 406–414.
- Lipson, D.A., Schmidt, S.K., Monson, R.K., 1999. Links between microbial population
  dynamics and nitrogen availability in an alpine ecosystem. Ecology 80, 1623–1631.
- Marion, G.M., Henry, G.H.R., Freckman, D.W., Johnstone, J., Jones, G., Jones, M.H.,
   Lévesque, E., Molau, U., Mølgaard, P., Parsons, A.N., Svoboda, J., Virginia, R.A.,
   1997. Open-top designs for manipulating field temperature in high-latitude ecosystems.
- 807 Global Change Biology 3, 20–32.
- McGuire, A., Melillo, J., Joyce, L., Kicklighter, D., Grace, A., Moore III, B., Vorosmarty, C.,

  1992. Interactions between carbon and nitrogen dynamics in estimating net primary

  productivity for potential vegetation in North America. Global Biogeochemical Cycles 6,

  101–124.
- McKane, R.B., Johnson, L.C., Shaver, G.R., Nadelhoffer, K.J., Rastetter, E.B., Fry, B., Giblin,
  A.E., Kielland, K., Kwiatkowski, B.L., Laundre, J.A., Murray, G., 2002. Resource-based
  niches provide a basis for plant species diversity and dominance in arctic tundra.

  Nature 415, 68–71.
- McLaren, J.R., Buckeridge, K.M., van de Weg, M.J., Shaver, G.R., Schimel, J.P., Gough, L.,
  2017. Shrub encroachment in Arctic tundra: *Betula nana* effects on above- and
  belowground litter decomposition. Ecology 98, 1361–1376.

- Michelsen, A., Quarmby, C., Sleep, D., Jonasson, S., 1998. Vascular plant <sup>15</sup>N natural
- abundance in heath and forest tundra ecosystems is closely correlated with presence
- and type of mycorrhizal fungi in roots. Oecologia 115, 406–418.
- Michelsen, A., Schmidt, I.K., Jonasson, S., Quarmby, C., Sleep, D., 1996. Leaf <sup>15</sup>N
- abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and
- non-and arbuscular mycorrhizal species access different sources of soil nitrogen.
- 825 Oecologia 105, 53–63.
- Mikan, C.J., Schimel, J.P., Doyle, A.P., 2002. Temperature controls of microbial respiration in
- arctic tundra soils above and below freezing. Soil Biology and Biochemistry 34, 1785-
- 828 1795.
- Morgner, E., Elberling, B., Strebel, D., Cooper, E.J., 2010. The importance of winter in
- annual ecosystem respiration in the High Arctic: effects of snow depth in two vegetation
- 831 types. Polar Research 29, 58–74.
- 832 Mørkved, P.T., Dörsch, P., Henriksen, T.M., Bakken, L.R., 2006. N₂O emissions and product
- ratios of nitrification and denitrification as affected by freezing and thawing. Soil Biology
- and Biochemistry 38, 3411–3420.
- Myers-Smith, I.H., Elmendorf, S.C., Beck, P.S.A., Wilmking, M., Hallinger, M., Blok, D., Tape,
- K.D., Rayback, S.A., Macias-Fauria, M., Forbes, B.C., Speed, J.D.M., Boulanger-
- Lapointe, N., Rixen, C., Levesque, E., Schmidt, N.M., Baittinger, C., Trant, A.J.,
- Hermanutz, L., Collier, L.S., Dawes, M.A., Lantz, T.C., Weijers, S., Jørgensen, R.H.,
- Buchwal, A., Buras, A., Naito, A.T., Ravolainen, V., Schaepman-Strub, G., Wheeler,
- J.A., Wipf, S., Guay, K.C., Hik, D.S., Vellend, M., 2015. Climate sensitivity of shrub
- growth across the tundra biome. Nature Climate Change 5, 887-891.
- Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D.,
- Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P.,
- Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.A., Schmidt,

845 N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Ménard, C.B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E., 846 847 Hik, D.S., 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters 6, doi:10.1088/1748-848 849 9326/6/4/045509. 850 Nadelhoffer, K., Shaver, G., Fry, B., Giblin, A., Johnson, L., McKane, R., 1996. <sup>15</sup>N natural abundances and N use by tundra plants. Oecologia 107, 386-394. 851 852 Nadelhoffer, K.J., Giblin, A., Shaver, G.R., Laundre, J.A., 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. Ecology 72, 242-253. 853 854 Näsholm, T., Kielland, K., Ganeteg, U., 2009. Uptake of organic nitrogen by plants. New 855 Phytologist 182, 31–48. 856 Nobrega, S., Grogan, P., 2007. Deeper snow enhances winter respiration from both plantassociated and bulk soil carbon pools in birch hummock tundra. Ecosystems 10, 419-857 858 431. R Core Team, 2016. R: A language and environment for statistical computing. R Foundation 859 860 for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/. 861 Rumpf, S.B., Semenchuk, P.R., Dullinger, S., Cooper, E.J., 2014. Idiosyncratic responses of High Arctic plants to changing snow regimes. PloS One 9, e86281. 862 863 doi:10.1371/journal.pone.0086281 Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., 864 Cornelissen, J.H.C., Gurevitch, J., 2001. A meta-analysis of the response of soil 865 respiration, net nitrogen mineralization, and aboveground plant growth to experimental 866 ecosystem warming. Oecologia 126, 543-562. 867 868 Saha, S.K., Rinke, A., Dethloff, K., 2006. Future winter extreme temperature and

precipitation events in the Arctic. Geophysical Research Letters 33, 1-4.

- Schimel, J., Balser, T.C., Wallenstein, M., 2007. Microbial stress-response physiology and its
- implications for ecosystem function. Ecology 88, 1386–1394.
- 872 Schimel, J.P., Bennett, J., 2004. Nitrogen mineralization: challenges of a changing paradigm.
- 873 Ecology 85, 591–602.
- 874 Schimel, J.P., Bilbrough, C., Welker, J.M., 2004. Increased snow depth affects microbial
- activity and nitrogen mineralization in two Arctic tundra communities. Soil Biology and
- 876 Biochemistry 36, 217–227.
- Semenchuk, P.R., Elberling, B., Amtorp, C., Winkler, J., Rumpf, S., Michelsen, A., Cooper,
- 878 E.J., 2015. Deeper snow alters soil nutrient availability and leaf nutrient status in high
- Arctic tundra. Biogeochemistry 124, 81–94.
- 880 Semenchuk, P.R., Elberling, B., Cooper, E.J., 2013. Snow cover and extreme winter
- warming events control flower abundance of some, but not all species in high arctic
- 882 Svalbard. Ecology and Evolution 3, 2586–2599.
- Sharma, S., Szele, Z., Schilling, R., Munch, J.C., Schloter, M., 2006. Influence of freeze-thaw
- stress on the structure and function of microbial communities and denitrifying
- populations in soil. Applied and Environmental Microbiology 72, 2148–2154.
- Shaver, G.R., Chapin, F., 1980. Response to fertilization by various plant growth forms in an
- 887 Alaskan tundra: nutrient accumulation and growth. Ecology 61, 662–675.
- Shearer, G., Duffy, J., Kohl, D.H., Commoner, B., 1974. A steady-state model of isotopic
- fractionation accompanying nitrogen transformations in soil. Soil Science Society of
- 890 America Journal 38, 315-322.
- 891 Shindell, D.T., Miller, R.L., Schmidt, G.A., Pandolfo, L., 1999. Simulation of recent northern
- winter climate trends by greenhouse-gas forcing. Nature 399, 452–455.
- 893 Stan Development Team, 2016. Stan modeling language users guide and reference manual,
- http://mc-stan.org/documentation/.

895 Strebel, D., Elberling, B., Morgner, E., Knicker, H.E., Cooper, E.J., 2010. Cold-season soil respiration in response to grazing and warming in High-Arctic Svalbard. Polar Research 896 897 29, 46-57. 898 Sturm, M., Schimel, J., Michaelson, G., Welker, J.M., Oberbauer, S.F., Liston, G.E., Fahnenstock, J., Romanovsky, V.E., 2005. Winter biological processes could help 899 convert arctic tundra to shrubland. BioScience 55, 17-27. 900 901 Tilston, E.L., Sparrman, T., Öquist, M.G., 2010. Unfrozen water content moderates 902 temperature dependence of sub-zero microbial respiration. Soil Biology and Biochemistry 42, 1396-1407. 903 904 Tolgensbakk, J., Soerbel, L., Hoegvard, K., 2000. Adventdalen, geomorphological and 905 quaternary geological map, Svalbard 1:100000. Spitsbergen sheet C9Q, Norsk Polarinstitutt Temakart nr. 32. Norsk Polarinstitutt, Tromsø. 906 907 Tolvanen, A., Henry, G.H.R., 2001. Responses of carbon and nitrogen concentrations in high 908 Arctic plants to experimental warming. Canadian Journal of Botany 79, 711–718. Tucker, C., 2014. Reduction of air- and liquid water-filled soil pore space with freezing 909 910 explains high temperature sensitivity of soil respiration below 0 °C. Soil Biology and 911 Biochemistry 78, 90–96. 912 Vankoughnett, M.R., Grogan, P., 2014. Nitrogen isotope tracer acquisition in low and tall 913 birch tundra plant communities: a 2 year test of the snow-shrub hypothesis. 914 Biogeochemistry 118, 291–306. 915 Vehtari, A., Gelman, A., Gabry, J., 2016. Practical bayesian model evaluation using leave-916 one-out cross-validation and WAIC. Statistics and Computing 1–20, doi:10.1007/s11222-016-9696-4. 917 Vitousek, P.M., Howarth, R.W., 1991. Nitrogen limitation on land and in the sea: how can it 918

occur? Biogeochemistry 13, 87-115.

| 920 | Walsh, N.E., McCabe, T.R., Welker, J.M., Parsons, A.N., 1997. Experimental manipulations                   |
|-----|--|
| 921 | of snow-depth: effects on nutrient content of caribou forage. Global Change Biology 3,                     |
| 922 | 158–164.   |
| 923 | Weedon, J.T., Kowalchuk, G.A., Aerts, R., Van Hal, J., Van Logtestijn, R., Taş, N., Röling,                |
| 924 | W.F.M., Van Bodegom, P.M., 2012. Summer warming accelerates sub-arctic peatland                            |
| 925 | nitrogen cycling without changing enzyme pools or microbial community structure.                           |
| 926 | Global Change Biology 18, 138–150.   |
| 927 | Weintraub, M.N., Schimel, J.P., 2005. Seasonal protein dynamics in Alaskan arctic tundra                   |
| 928 | soils. Soil Biology and Biochemistry 37, 1469–1475.  |
| 929 | Welker, J.M., Fahnestock, J.T., Sullivan, P.F., Chimner, R.A., 2005. Leaf mineral nutrition of             |
| 930 | Arctic plants in response to warming and deeper snow in northern Alaska. Oikos 109,                        |
| 931 | 167–177.   |
| 932 | Wrona, F.J., Johansson, M., Culp, J.M., Jenkins, A., Mård, J., Myers-Smith, I.H., Prowse,                  |
| 933 | T.D., Vincent, W.F., Wookey, P.A., 2016. Transitions in Arctic ecosystems: ecological                      |
| 934 | implications of a changing hydrological regime. Journal of Geophysical Research:                           |
| 935 | Biogeosciences 121, 650–674.   |
| 936 | Yano, Y., Shaver, G.R., Giblin, A.E., Rastetter, E.B., 2010. Depleted <sup>15</sup> N in hydrolysable-N of |
| 937 | arctic soils and its implication for mycorrhizal fungi — plant interaction. Biogeochemistry                |
| 938 | 97, 183–194.   |
| 939 |  |
| 940 |  |
| 941 |  |
| 942 |  |
| 943 |  |

## **Tables**

Table 1. Effects of snow fence treatments and properties of the corresponding snow regimes. Presented are treatment specific maximum snow depths during winter (measured in 2015), melt out dates during year 2015 (observations when first plots within the respective snow regime were 50% snow free) and plot locations.

| max. snow  | first plots melt out | approx. plot locations     |  |  |  |  |
|------------|----------------------|----------------------------|--|--|--|--|
| depth (cm) |                      |                            |  |  |  |  |
| 35         | 23 May (Day 143)     | adjacent to snowfence      |  |  |  |  |
| 100        | 1 June (Day 152)     | 10 - 20 m behind snowfence |  |  |  |  |
| 150        | 17 June (Day 168)    | 3 - 12 m behind snowfence  |  |  |  |  |
|            | depth (cm) 35 100    | depth (cm)  35             |  |  |  |  |

Table 2. Soil chemistry variables and effect strengths of snow regime, summer warming (by open top chambers, OTC) and sampling day (day of the year, DOY). We present the medians of each effect (in bold), including their 95% credible intervals (lower and upper value to the left and the right). Effects strengths are thereby back-transformed from log scale and represent relative changes compared to *Ambient*, no OTC, DOY 161. Effect strengths with credible intervals not overlapping one were termed to be statistically significant and are marked with "\*".

|              |        | DOC conc.                | DON conc.                | NH4 <sup>+</sup> conc.   | NO <sub>3</sub> conc.      |
|--------------|--------|--------------------------|--------------------------|--------------------------|----------------------------|
| Parameter    |        | effect strength          | effect strength          | effect strength          | effect strength            |
| snow regime  | Medium | (0.75 <b>1.03</b> 1.44)  | (0.77 <b>0.89</b> 1.04)  | (0.83 <b>1.09</b> 1.42)  | (0.87 <b>1.20</b> 1.62)    |
|              | Deep   | (0.89 <b>1.23</b> 1.72)  | (1.04 <b>1.22</b> 1.42)* | (1.39 <b>1.82</b> 2.37)* | (2.62 <b>3.60</b> 4.94)*   |
| summer       | ОТС    | (0.75 <b>0.98</b> 1.28)  | (0.94 <b>1.06</b> 1.20)  | (0.78 <b>0.96</b> 1.19)  | (0.77 <b>0.98</b> 1.25)    |
| warming      |        |                          |                          |                          |                            |
| sampling day | 168    | (0.29 <b>0.59</b> 1.17)  | (0.63 <b>0.87</b> 1.20)  | (0.62 <b>1.07</b> 1.83)  | (0.77 <b>1.38</b> 2.57)    |
|              | 175    | (0.19 <b>0.36</b> 0.72)* | (0.45 <b>0.62</b> 0.85)* | (0.13 <b>0.22</b> 0.38)* | (0.55 <b>1.00</b> 1.83)    |
|              | 181    | (0.09 <b>0.17</b> 0.34)* | (0.15 <b>0.20</b> 0.28)* | (0.48 <b>0.78</b> 1.34)  | (0.64 <b>1.17</b> 2.13)    |
|              | 188    | (0.54 <b>1.02</b> 2.02)  | (0.44 <b>0.61</b> 0.83)* | (0.75 <b>1.27</b> 2.11)  | (1.62 <b>2.93</b> 5.45)*   |
|              | 195    | (0.36 <b>0.69</b> 1.37)  | (0.41 <b>0.57</b> 0.79)* | (0.33 <b>0.55</b> 0.94)* | (0.98 <b>1.77</b> 3.26)    |
|              | 202    | (0.08 <b>0.15</b> 0.30)* | (0.33 <b>0.45</b> 0.62)* |                          |                            |
|              | 216    | (0.64 <b>1.24</b> 2.44)  | (0.37 <b>0.51</b> 0.71)* | (0.57 <b>0.97</b> 1.61)  | (3.07 <b>5.65</b> 10.61)*  |
|              | 230    | (0.73 <b>1.43</b> 2.81)  | (0.59 <b>0.82</b> 1.13)  | (0.86 <b>1.45</b> 2.45)  | (3.39 <b>6.12</b> 11.34)*  |
|              | 243    | (0.58 <b>1.12</b> 2.17)  | (0.64 <b>0.87</b> 1.20)  | (1.14 <b>1.92</b> 3.22)* | (9.94 <b>17.93</b> 32.66)* |

Table 3. Plant leaf N concentrations (% dry weight) and the effect strengths of snow regime, summer warming (by open top chambers, OTC) and sampling day (day of the year, DOY). Presented are means of each effect strength (in bold), including their 95% credible intervals (lower and upper value to the left and the right). Effects strengths are thereby on measurement scale and represent absolute changes (in terms of % dry weight) compared to *Ambient* (and no OTC, DOY 195). Effect strengths with credible intervals not overlapping zero are termed to be statistically significant and labelled with "\*".

|                   |        | Salix polaris effect strength |       |                 | Bistorta vivipara |       |                 | Dryas octopetala effect strength |       |         | Alope           | curus bo | orealis         | Luzula confusa |       |                 |  |
|-------------------|--------|-------------------------------|-------|-----------------|-------------------|-------|-----------------|----------------------------------|-------|---------|-----------------|----------|-----------------|----------------|-------|-----------------|--|
| Parameter         |        |                               |       |                 | effect strength   |       | effect strength |                                  |       |         | effect strength |          |                 |                |       |                 |  |
| snow regime       | Medium | (0.14                         | 0.24  | 0.34)*          | (-0.01            | 0.13  | 0.27)           | (-0.11                           | 0.05  | 0.21)   | (0.21           | 0.51     | 0.82) *         | (-0.01         | 0.21  | 0.42)           |  |
|                   | Deep   | (0.62                         | 0.72  | 0.82) *         | (0.55             | 0.68  | 0.82) *         | (0.31                            | 0.49  | 0.65) * | (0.76           | 1.07     | 1.38) *         | (0.50          | 0.70  | 0.91) *         |  |
| summer<br>warming | отс    | (-0.17                        | -0.09 | -0.01)          | (-0.27            | -0.16 | -0.05) *        | (-0.26                           | -0.13 | 0.01)   | (-0.67          | -0.43    | -0.19) <b>*</b> | (-0.34         | -0.17 | -0.01) *        |  |
| sampling day      | 202    | (-0.50                        | -0.36 | -0.22) <b>*</b> |                   |       |                 |                                  |       |         |                 |          |                 |                |       |                 |  |
|                   | 209    | (-0.52                        | -0.38 | -0.23) <b>*</b> |                   |       |                 |                                  |       |         |                 |          |                 |                |       |                 |  |
|                   | 218    |                               |       |                 | (-0.41            | -0.27 | -0.14) <b>*</b> | (-0.20                           | -0.04 | 0.13)   | (-0.33          | -0.03    | 0.27)           | (-0.57         | -0.36 | -0.17) <b>*</b> |  |
|                   | 224    | (-0.71                        | -0.57 | -0.42) <b>*</b> |                   |       |                 |                                  |       |         |                 |          |                 |                |       |                 |  |
|                   | 238    | (-1.32                        | -1.18 | -1.04) <b>*</b> |                   |       |                 |                                  |       |         |                 |          |                 |                |       |                 |  |

Table 4. Plant leaf  $\delta^{15}N$  (‰) and the effect strengths of snow regime, summer warming (by open top chambers, OTC) and sampling day (day of the year, DOY). Presented are means of each effect strength (in bold), including their 95% credible intervals (lower and upper value). Effects strengths are thereby on measurement scale and represent absolute changes (in terms of ‰) compared to *Ambient* (and no OTC, DOY 195). Effect strengths with credible intervals not overlapping zero are termed to be statistically significant and labelled with "\*".

|              |        | Salix p         | olaris |                | Bistor          | ta vivipa | ra              | Dryas  | octopet | ala             | Alopec | urus bo | realis          | Luzula | confus | а      |
|--------------|--------|-----------------|--------|----------------|-----------------|-----------|-----------------|--------|---------|-----------------|--------|---------|-----------------|--------|--------|--------|
| Parameter    |        | effect strength |        | effect s       | effect strength |           | effect strength |        |         | effect strength |        |         | effect strength |        |        |        |
| snow regime  | Medium | (-0.10          | 0.29   | 0.67)          | (-0.07          | 0.66      | 1.38)           | (0.16  | 0.78    | 1.40)*          | (-1.78 | -0.58   | 0.59)           | (-0.45 | 0.06   | 0.58)  |
|              | Deep   | (1.24           | 1.63   | 2.04)*         | (2.09           | 2.77      | 3.43) <b>*</b>  | (0.85  | 1.50    | 2.17)*          | (-2.57 | -1.38   | -0.13) <b>*</b> | (-0.12 | 0.37   | 0.88)  |
| summer       | отс    | (-0.05          | 0.27   | 0.59)          | (-0.27          | 0.31      | 0.88)           | (-0.38 | 0.13    | 0.67)           | (-1.30 | -0.33   | 0.60)           | (0.07  | 0.48   | 0.88)* |
| warriing     |        |                 |        |                |                 |           |                 |        |         |                 |        |         |                 |        |        |        |
| sampling day | 202    | (-0.44          | 0.12   | 0.67)          |                 |           |                 |        |         |                 |        |         |                 |        |        |        |
|              | 209    | (0.05           | 0.63   | 1.18) <b>*</b> |                 |           |                 |        |         |                 |        |         |                 |        |        |        |
|              | 218    |                 |        |                | (-0.77          | -0.08     | 0.60)           | (-0.48 | 0.20    | 0.87)           | (-0.88 | 0.27    | 1.39)           | (-0.23 | 0.26   | 0.73)  |
|              | 224    | (0.38           | 0.94   | 1.51) <b>*</b> |                 |           |                 |        |         |                 |        |         |                 |        |        |        |
|              | 238    | (0.91           | 1.45   | 2.00)*         |                 |           |                 |        |         |                 |        |         |                 |        |        |        |
|              | 245    | (0.53           | 1.08   | 1.63) <b>*</b> | (-1.26          | -0.57     | 0.09)           | (-0.94 | -0.26   | 0.41)           | (-0.98 | 0.24    | 1.47)           | (-0.45 | 0.06   | 0.60)  |

## **Figure Captions**

Figure 1. Daily averages of soil temperatures across all plots within respective treatments, in a depth of approx. one cm below soil surface. Temperatures are shown for (a) winter season 2014/2015 and (b) summer season 2015. In the figure legend, "A" represents *Ambient*, "M" the *Medium* and "D" the *Deep* snow regime. "T" represents plots within snow regimes that were temperature enhanced during summer, using OTCs. (C) Shows average volumetric soil moisture content across all plots for each treatment combination.

Figure 2. Soil chemistry and N pools for each category of snow regime, summer temperature regime and sampling day. Categories of experimental treatments and sampling day are presented separately, since interactions between them were not significant. Symbols represent the medians for each treatment category and error bars represent 95 % credible intervals. "A" represents *Ambient*, "M" *Medium* and "D" *Deep* snow regimes. "OTC" and "no OTC" represent whether an OTC was present or not. The numbers on x-axes represent the sampling day as Julian days. Statistically significant effect strengths of each treatment category compared to *Ambient*, no OTC, DOY 161, are marked with "\*".

Figure 3. Leaf N concentrations of common tundra plants for each category of snow regime, summer temperature regime and sampling day. In connection to patterns of soil N pools, categories of experimental treatments and sampling day are presented separately and no interactions are included. Symbols represent means (equal to the median for this data) as % dry weight for each treatment category and error bars represent 95 % credible intervals. All other labels are according to Figure 2. Note that different species cover different ranges on the y-axis.

Figure 4. Leaf  $\delta^{15}N$  of common tundra plants, presented for each category of snow regime, summer temperature regime and sampling day. In connection to patterns of soil N pools, categories of experimental treatments and sampling day are presented separately and no interactions are included. Symbols represent means (equal to the median for this data) for each treatment category and error bars represent 95 % credible intervals. All other labels are according to Figure 2 and 3. Note that different species cover different ranges on the y-axis.







