Variable responses of carbon and nitrogen contents in vegetation and soil to herbivory and warming in high-Arctic tundra

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Abstract. Chemical responses of tundra vegetation and tundra soil to environmental changes are likely to differ, with implications for ecosystem functioning, yet they are rarely compared. Here, we aimed at comparing sensitivity and magnitude of short-term carbon and nitrogen responses of three main tundra ecosystem compartments: vascular plants, mosses, and soil, to two environmental perturbations: herbivore disturbance and warming. In a full-factorial field experiment in the high-Arctic Svalbard, we simulated herbivore disturbance as spring grubbing activity by pink-footed geese (*Anser brachyrhynchus*) and passively increased summer temperatures using open-top chambers. Manipulations were set up within three habitats that differ in soil moisture and carried out for two consecutive growing seasons. Overall, we found small and few significant responses to herbivore disturbance and warming, suggesting that carbon and nitrogen contents of high-Arctic ecosystems are relatively resistant to these perturbations, at least in the short term. However, the three ecosystem compartments still differed in their sensitivity to perturbations (vascular plants > soil > mosses), and this was exacerbated by their differential sensitivity across habitats (mesic > moist > wet). Also, while vascular plants responded to herbivore disturbance in mesic and wet habitats and to warming in mesic and moist habitats, soil and mosses only responded to herbivore disturbance in mesic and wet habitats, respectively. Responses to treatments were generally consistent across the two growing seasons, despite great differences in temperature conditions and large between-year variations in the chemical composition of the three ecosystem compartments. These findings highlight the potential for environmental perturbations to have small, yet differential short-term impacts on the carbon and nitrogen contents of vascular plants, mosses, and soil, both within and between tundra habitats. Our results imply that assessments of a single ecosystem compartment in a given context cannot be extrapolated to the whole ecosystem, thus stressing the importance of considering both vegetation and soil carbon and nitrogen responses, and how they display across habitats, in order to better understand how environmental changes might affect biogeochemical processes in the tundra. Longer-term studies should dig deeper into the relative role of (simulated) global change drivers vs. natural inter-annual climatic fluctuations for tundra ecosystem carbon and nitrogen dynamics.

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Introduction

The biogeochemistry of tundra ecosystems is largely controlled by the slow turnover rates of carbon (C) and nutrients between soil and vegetation (Hobbie et al. 2002). The low soil temperatures cause slow organic matter decomposition (Cornelissen et al. 2007), which in turn limits nutrient mineralization rates (Nadelhoffer et al. 1991). The slow nutrient cycling rates (particularly of nitrogen [N]) constrain plant growth and thus ecosystem C gain through primary productivity (Shaver et al. 1992). Under such conditions, any factors that modify C and N contents of soil and vegetation can have large effects on the functioning of the ecosystem.

Studying the extent to which C and N contents of soil and vegetation respond to perturbations may help us understand the capacity of tundra ecosystems to resist disturbance and maintain their functioning. For instance, alterations in the C content of soil and vegetation may reflect changes in C exchange rates and C budget of ecosystems, while modifications in their N content may alter ecosystem N cycling (Jonasson et al. 1999, Hobbie et al. 2002). Yet, C and N contents and their ratio (C:N) in soil and vegetation (vascular plants and mosses) differ widely (Shaver et al. 1992). In addition, these ecosystem compartments might differ in their capacity to immediately respond, that is, in their short-term responsiveness, to perturbations. As soil and vegetation jointly regulate whole-ecosystem processes (Bardgett et al. 2013), differential sensitivity and magnitude of soil and vegetation C and N responses may have important implications for C and N dynamics in tundra ecosystems. Most studies have quantified chemical responses of a single ecosystem compartment, and it is unclear whether they can be translated to other compartments of the ecosystem. Here, we aimed at comparing the extent to which three main ecosystem compartments (vascular plants, mosses, and soil) differ in their short-term responsiveness, that is, in sensitivity and magnitude of their C and N contents and C:N ratio responses, to two environmental perturbations (warming and herbivory) in the Arctic tundra.

With an increase in average annual temperature by 0.75°C over the past decade, Arctic regions are warming faster than any other areas on Earth (Post et al. 2019). Several experimental studies have investigated the effects of warming on C and N contents of either tundra vegetation or tundra soil, yet a direct comparison of their responses is lacking. While over long time scales (i.e., 10–20 yr), vascular plants (Hudson et al. 2011), mosses (Sorensen et al. 2012), and soil (Sistla et al. 2013) appear to at least partially restore their chemical composition that could have initially changed in response to elevated temperatures, shorter-term chemical responses may still differ between these ecosystem compartments. Two to six years of experimentally imposed higher summer temperatures caused detectable changes in C and N contents of vascular plants in a range of low-Arctic (Welker et al. 2005, Aerts et al. 2009) and high-Arctic (Tolvanen and Henry 2001, Doiron et al. 2014) ecosystems. Mosses and soil are generally less responsive than vascular plants, though changes in their C and N contents following short-term (2- to 4-yr) experimental warming have been observed (Biasi et al. 2008, Deane-Coe et al. 2015). It is thus likely that, in general, responsiveness to elevated temperatures increases in the order: vascular plant > moss ≥ soil compartment.

Herbivores are a key component of Arctic ecosystems (Barrio et al. 2016) and strongly influence their functioning (Mulder 1999). The dramatic increase of migratory goose populations in the Arctic (Fox and Madsen 2017) suggests that the impacts of geese on C and N contents of tundra ecosystems may be considerable. During the pre-breeding period in spring, migratory geese of the genera *Anser* and *Chen* forage on belowground plant parts, that is, roots and rhizomes, through grubbing (Fox et al. 2006). Grubbing is a disturbance that occurs at the landscape scale (Fig. 1a), although each affected tundra patch can be small in extent (Fig. 1b) (Ravolainen et al. 2020). By disrupting the moss mat structure and by provoking rapid vegetation loss, which may even lead to soil erosion, goose grubbing can cause severe disturbance to tundra ecosystems (Jefferies and Rockwell 2002). Hence, grubbing by geese might be expected to elicit more similar C and N responses across ecosystem compartments (vascular plants ≈ mosses ≈ soil) compared with those caused by warming. The archipelago of Svalbard, in the European high-Arctic, has
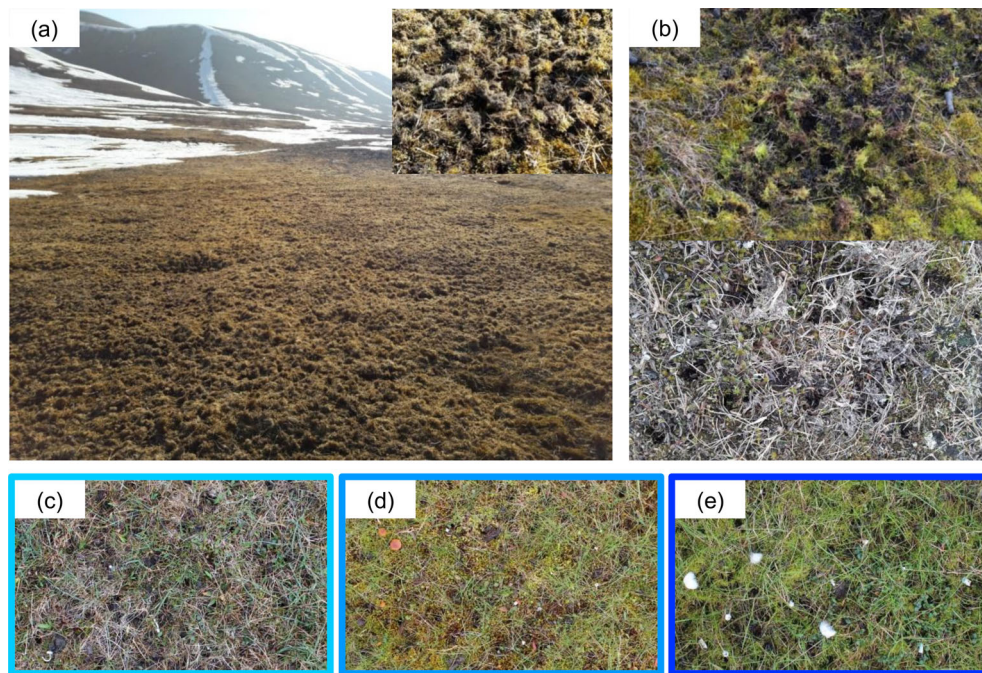
Fig. 1. Natural and simulated spring grubbing by pink-footed geese. (a) Extensive natural grubbing as found in many pre-breeding sites in Svalbard. In the upper-right corner, a closer visualization of a heavily grubbed tundra patch is shown. (b) Natural beak-sized bites in a relatively moist [top] and dry [bottom] tundra patch. Examples of the goose disturbance simulation in (c) mesic [ME], (d) moist [MO], and (e) wet [WE] habitats. Pictures were taken (a, b) in the study area in spring 2017 and (c–e) in experimental plots during fieldwork in July 2017.

experienced a noticeable rise in both the number of pink-footed geese (*Anser brachyrhynchus*—from 15,000 individuals in 1965 up to 90,000 individuals in 2017; Madsen et al. 2017) and average summer temperatures (0.7°C/decade for the period 1991–2018; Nordli et al. 2020). It therefore represents a relevant system where to study whether these three main ecosystem compartments differ in their responsiveness to goose disturbance, and further explore whether interactive effects with warmer summers are at stake.

Arctic ecosystems contain a mosaic of different habitats due to fine-scale heterogeneities in topography and hydrological conditions (Walker 2000), where the vegetation is characterized by plants that differ in their C and N contents (Welker et al. 2005). Tundra vegetation is usually dominated by mosses. Generally, mosses have lower N content than vascular plants (Aerts et al. 2009, Turetsky et al. 2012), but are effective in competing for available nutrients deposited from, for example, animal excreta (Sjögersten et

al. 2010, Barthelemy et al. 2017). Moreover, the moss layer can insulate the soil and thus play an important role in mediating processes and dynamics of soil and vascular plant compartments (van der Wal and Brooker 2004, Gornall et al. 2007). Yet, moss abundance varies widely between habitats, suggesting that these mediating effects may be stronger in wetter habitats, where the moss mat is thicker compared with drier habitats (Speed et al. 2010). Further, Arctic habitats are featured by diverse soil types, which also differ in their C and N contents (Bardgett et al. 2007). Evidence suggests that tundra ecosystem responses to drivers of environmental changes are contingent upon the characteristics of a system (Shaver et al. 2000). Therefore, although no studies have, to our knowledge, compared C and N responses of vascular plant, moss, and soil compartments across the heterogeneous Arctic landscape, one might expect their responsiveness to environmental perturbations to differ between habitats.

The overall objective of this study was to determine whether and to what extent vascular plants, mosses, and soil differ in the sensitivity and magnitude of their short-term C, N, and C:N ratio responses to goose disturbance and warming. To achieve this, we simulated pink-footed goose grubbing activity in spring and passively increased summer temperatures in a two-year full-factorial field experiment in a high-Arctic ecosystem in Svalbard. In order to understand whether chemical responses of the three ecosystem compartments vary across the tundra landscape, perturbations were imposed in three habitats that differ in soil moisture, from relatively dry, through moist, to wet. We measured C and N contents of vascular plants, mosses, and soil within the experiment at the peak of the growing season in both years. In addition to the expectations given above, we predicted stronger responses after two years of experimental manipulations.

MATERIAL AND METHODS

Study area

The study was carried out in Adventdalen, which is a wide valley in Svalbard, Norway (78°10′ N, 16°05′ E) (Fig. 2a), during the summers of 2016 and 2017. The average annual temperature for the period 1988–2017 was −4.2°C, with a mean of −0.1°C in 2016 and −2.2°C in 2017. The two experimental seasons largely differed in spring and summer temperatures. Spring 2016 was unusually warm (May mean temperature: 1.4°C; average for the period 1988–2017: −2.4°C), whereas spring 2017 was unusually cold (May mean temperature: −3.9°C). Also, mean summer (June to August) temperature was 6.6°C in 2016 and 5.9 in 2017 (average for the period 1988–2017: 5.4°C) (Nordli et al. 2020; data from Svalbard airport, approximately 10 km from the study area).

Adventdalen becomes snow-free relatively early and is thus heavily utilized by pink-footed geese as feeding ground during the pre-breeding period in spring (Fox et al. 2006). Snowmelt generally begins in mid-May, but the date at which the tundra becomes snow-free differs from year to year and depends on climatic conditions (Pelt et al. 2016). The onset of the growing season was particularly early in 2016 and delayed in 2017,

reflecting spring temperature differences between the two years. The start of the growing season also varies at the landscape scale due to different snow accumulation patterns in winter, yet aboveground plant biomass generally reaches an average peak in late July/early August in most habitats (van der Wal and Stien 2014). Additional details on environmental characteristics of the study area and its trophic system are given in Appendix S1: Table S1 and Appendix S2.

Study design and experimental treatments

In order to capture habitats that differ in hydrology within the experimental units of this study, we selected seven sites within a 5-km^2 area on the southern side of Adventdalen (Fig. 2b), each hosting mesic (ME), moist (MO), and wet (WE) habitats (Fig. 2c). Distance between sites (300–1500 m) was greater than the distance between habitats within sites (30–100 m). ME habitats mainly develop on flat terrains that dry out as the summer progresses and have relatively thin snow cover in winter. MO habitats are found on gently sloping grounds and are characterized by considerable seepage of water in the soil above the permafrost throughout the season and by having a moderate snow cover in winter. WE habitats are generally confined in depressions, which feature the presence of standing water in spring, close to water-saturated soil in summer, and an appreciable snow cover in winter.

Habitats were chosen based on the descriptions of Rønning (1996) and are important pink-footed goose habitats in Svalbard (Fox et al. 2006). ME habitats are characterized by the rush *Luzula wahlenbergii*, which co-occurs with dwarf shrubs, grasses, and forbs (common species are *Dryas octopetala*, *Salix polaris*, *Alopecurus ovatus*, *Poa arctica*, and *Bistorta vivipara*). The moss compartment is dominated by *Sanionia uncinata*, *Tomentypnum nitens*, *Polytrichastrum alpinum*, *Hylocomium splendes*, and *Dicranium* spp. MO and WE habitats lack both rushes and evergreen dwarf shrubs. MO habitats are ruled by grasses such as *A. ovatus* and *Calamagrostis neglecta*, the deciduous dwarf shrub *S. polaris*, the vascular cryptogam *Equisetum arvense*, and forbs such as *B. vivipara*. Other graminoids found in WE habitats, such as *Dupontia fisheri* and *Eriophorum scheuchzeri*, occur in MO habitats only in small quantities. The moss compartment is mainly
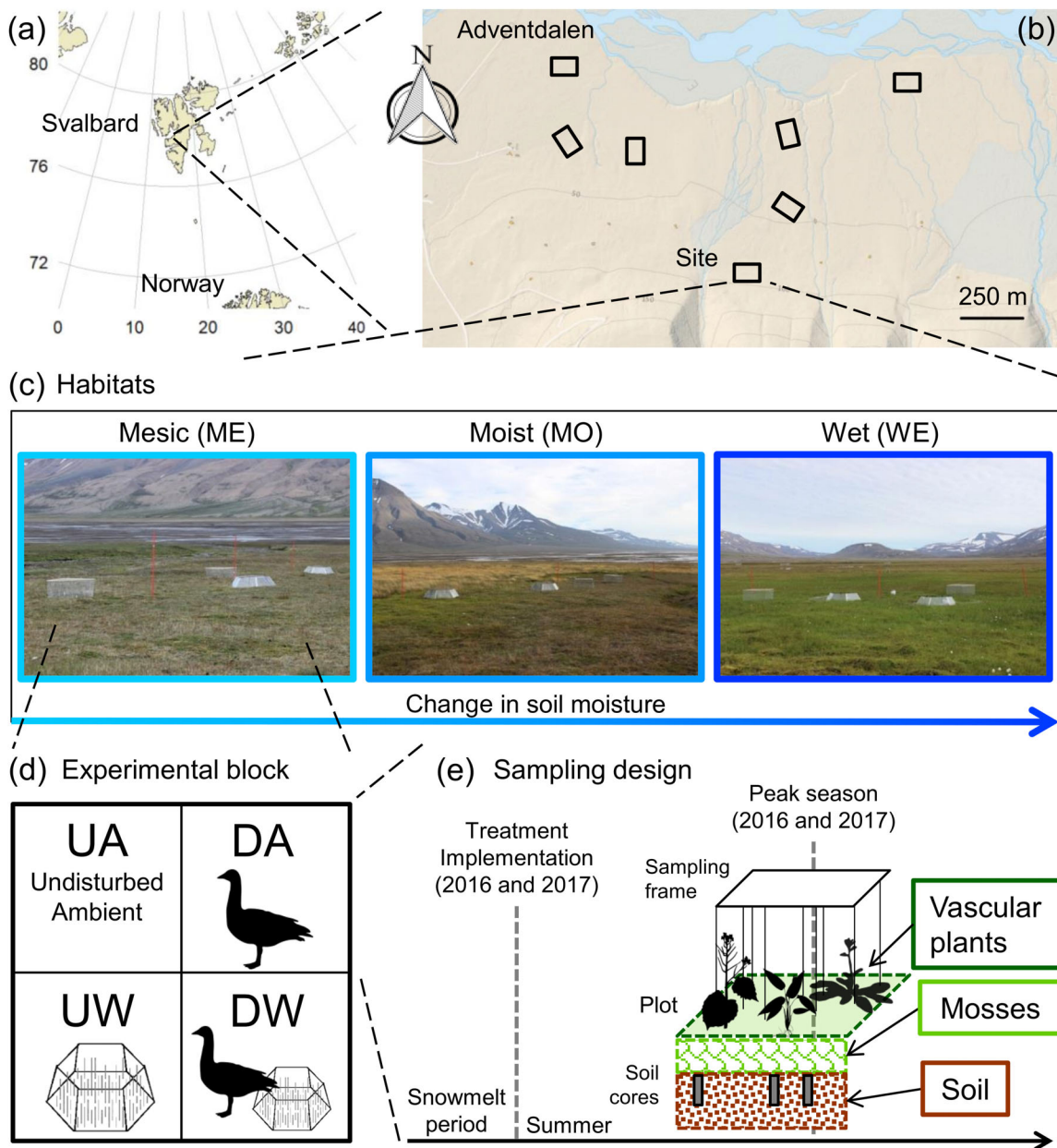
Fig. 2. Study and sampling design. (a) Study location, (b-d) hierarchical spatial structure of the study design, and (e) sampling design adopted for vascular plant, moss, and soil sample collection in summer 2016 and 2017. Color coding for (c) habitats (mesic [ME], moist [MO], and wet [WE]) and (e) ecosystem compartments (vascular plants, mosses, and soil) and *silhouettes* and acronyms for (d) treatment combinations (UA = undisturbed/ambient, DA = disturbed/ambient, UW = undisturbed/warming, and DW = disturbed/warming) presented in this figure will be consistent throughout the manuscript. Pictures in (c) were taken during fieldwork in July 2016.

characterized by species from the genus *Aulacomnium*, *Dicranium*, and *T. nitens*. In WE habitats, the vegetation is largely dominated by grasses (predominantly *D. fisheri* and *C. neglecta*) and the

sedge *E. scheuchzeri*. Other species, such as *S. polaris* and *B. vivipara*, occur only occasionally. *Calliergon* and *Scorpidium* are the dominant genera of the moss compartment. Vascular plant names

follow the Pan-Arctic Flora (http://nhm2.uio.no/paf), whereas moss names follow Frisvoll and Elvebakk (1996).

To investigate C and N contents and C:N ratio responses of tundra ecosystem compartments (i.e., vascular plants, mosses, and soil) to herbivory and warming, we used a full-factorial randomized block design with simulated spring goose disturbance (two levels: disturbed [D] and undisturbed [U]) and summer warming (two levels: warming [W] and ambient [A]), leading to a total of four treatment combinations in all three habitats (Fig. 2d). Within each habitat, an experimental block was established in a patch with homogenous vegetation that was large enough to include all plots. Four plots (80 × 80 cm) were laid out at least 2 m apart in each block (minimum 80% of the plot had to be vegetated), for a total of 84 plots. Treatment combinations were randomly assigned to plots. Due to a flooding in early summer 2016, one of the selected blocks in WE habitats had to be excluded (WE habitats, n = 6).

Spring goose disturbance simulation.—The treatment was applied in the period 5–12 June in 2016 and 15–22 June in 2017, at the peak of the grubbing season. Temporal differences in treatment application reflected different snowmelt patterns in the two years (see Material and Methods: Study area). To simulate natural pink-footed goose beak-sized bites, which are typically found to a depth of 2–8 cm from the moss surface in different habitats (Fox et al. 2006), we used a sharpened steel tube (20 mm Ø) that was inserted to a depth of approximately 5 cm and twisted to remove material from the plot, following Speed et al. (2010). Grubbing was implemented in a regular fashion to approximately 33% of the plot surface (Fig. 1c–e) (cf. low-intensity grubbing treatment in Speed et al. 2010). We then added 120 g of fresh goose feces (approximately 45 g dry weight, hereafter termed %dw) uniformly spread out as single droppings. Feces were collected each spring within the experimental area. Feces addition was based upon observations of the feces distribution patterns within naturally grubbed areas found in Adventdalen. To quantify how much N was added in "disturbed" plots, 20 fresh goose droppings were randomly selected each spring and analyzed for C and N contents (means %dw ±

SD in 2016: C = 37.8 ± 6.7, N = 1.71 ± 0.62; in 2017: C = 36.8 ± 3.0, N = 1.73 ± 0.30) using a CN analyzer (Vario EL Cube, Elementar Analysesysteme GmbH, Hanau, Germany). Thus, approximately 1.2 g/m^2 of N was added to "disturbed" plots through goose droppings in both spring 2016 and 2017.

The intensity of our spring goose disturbance treatment was comparable to what we observed in naturally grubbed areas typically found in MO habitats. We observed somewhat lower intensity of goose disturbance in ME habitats and somewhat higher intensity in WE habitats, as reported in previous studies (e.g., Speed et al. 2009). However, by keeping a consistent goose disturbance intensity, we could compare sensitivity and magnitude of ecosystem compartment responses across habitats (cf. Speed et al. 2010). Moreover, following their population increase, pink-footed geese have started exploiting less suitable, drier habitats (Pedersen et al. 2013). Hence, the intensity of our simulation may be a likely scenario for ME habitats in the coming years if the pink-footed goose population will continue to rise (Jensen et al. 2008).

Summer warming simulation.—The treatment was implemented by hexagonal open-top chambers (OTCs, made of LEXAN polycarbonate—1.4 m diameter), following specs in the International Tundra Experiment (ITEX) protocol (Henry and Molau 1997). We used larger OTCs than the plot size to minimize edge effects. OTCs are passive warming devices that have been successfully used in numerous ecological studies to increase plot-level temperatures (see, e.g., the review by Elmendorf et al. 2012). Throughout the summer, OTCs generally increase average air temperature by 1.5–1.9°C and maximum air temperature by ~3.5°C (Marion et al. 1997, Hollister and Webber 2000). However, OTCs may also alter other microclimatic variables, such as soil moisture and air humidity (see Marion et al. 1997, Hollister and Webber 2000 for further details concerning OTC performances). In 2016, OTCs were set up during the implementation of the goose disturbance treatment, when all plots had already been snow-free for 7–10 d. In 2017, OTCs were set up as soon as snow conditions allowed (i.e., period 2-8 June). To prevent potential confounding effects of uneven snow accumulation (Bokhorst et al. 2011), OTCs were removed

before the first snowfall in autumn and throughout the winter period.

To avoid natural herbivory as a possible confounding factor, cages were set up on all plots at the same time as setting up the OTCs. We used cages made of metal net (90 × 90 cm area × 50 cm height; mesh size 1.9 × 1.9 cm) to exclude herbivore activities from "ambient" plots. In "warmed" plots, a metal net was used to close the open-top part of each OTC, which then acted as an herbivore exclosure throughout the summer. As for OTCs, cages were removed during winter.

Micro-environment monitoring

We measured soil moisture at the peak of the growing season in 2016 and 2017 within each plot using a soil moisture probe attached to a moisture logger (ML3 Theta Probe and HH2 Moisture Meter Logger, Delta-T Devices Ltd., Cambridge, UK). Air temperature at 5 cm above the moss surface was registered in three "ambient" and three "warmed" plots per habitat every 30 min throughout the two growing seasons using temperature loggers (U23-003/UA-001 HOBO, Onset Computer, Bourne, Massachusetts, USA; accuracy: ±0.2°C) equipped with solar radiation shields. Temperature loggers (DS1921G-F5 Thermochron iButtons, Homechip, Ltd, Milton Keynes, UK; accuracy: ±0.5°C) were also used to register surface moss mat (−2 cm from the moss surface) temperature in three-to-four plots of each treatment per habitat every 2 h throughout the two growing seasons. We obtained July average and maximum temperatures by extracting mean and maximum daily temperatures from each temperature logger and by averaging these values for the period 1–31 July.

Sample collection and processing

To quantify chemical responses of tundra ecosystem compartments to spring goose disturbance and summer warming, we collected vascular plant, moss, and soil samples from each plot in both 2016 and 2017 and determined their C and N contents (%dw), and C:N ratio. All samples were collected at the peak of the growing season (2016: 19–29 July; 2017: 20–28 July), as defined by Macias-Fauria et al. (2017).

Vascular plant C and N contents.—Vascular plant sampling was designed to minimize disturbance and was performed randomly within each plot by placing a metal frame (50 × 50 cm) with 25 evenly distributed points in the center of each plot. Nine woody sticks (numbered from 1 to 9) were lowered down vertically to the tundra from 9 randomly selected points within the frame (Fig. 2e). From stick 1 to 9, the species for which the uppermost leaf had touched the stick was registered. The same species was not registered twice. Hence, the second closest species to a stick was registered when the stick would have provided a species already encountered. Three to five fresh leaves of each registered species were collected in each plot at different sticks, starting from the first stick at which the species was registered and continuing with the subsequent sticks. The sampling led to a total of 9–27 leaves depending on the number of dominant species found in that plot, which ranged between a minimum of three (2.5% of the plots, all in WE habitats) and a maximum of nine (5% of the plots, all in ME habitats) (on average 5.4 ± 1.3 species). We did not aim at sampling all the species within a plot, but rather at sampling the species that built up most of the biomass in that plot. Across habitats, we collected leaves from 14 species belonging to seven broadly classified plant functional types (PFTs), namely forbs, grasses, rushes, sedges, deciduous and evergreen dwarf shrubs, and horsetails (Appendix S1: Table S2). Their combined biomass encompassed in average over 99% (range: 89–100%) of the aboveground vascular plant biomass within plots (own data; see Vascular plant C and N contents and Appendix S1: Fig. S1). In this study, we used the collected leaves to calculate C and N community-weighted contents (%dw) of the vascular plant compartment as a whole, that are the average C and N contents in the vascular plant community weighted by the species' relative abundances (see Vascular plant C and N contents for the procedure adopted).

During fieldwork, the 3-5 leaves from each species and plot were stored together in a separate tea filter bag and pressed in a plant press within max 10 h after collection. After 72 h, leaf samples were oven-dried at 60°C for 48 h. All leaves were analyzed for C and N contents (% dw) with near-infrared reflectance spectroscopy (NIRS) using a FieldSpec 3 (ASD, Boulder, Colorado, USA) in 350 − 2500 nm range and equipped with a 4-mm light adapter for full-leaf analysis

(Petit Bon et al. 2020*a*). For each leaf, between 3 and 10 measurements were taken (on average 3.7 ± 1.2), depending on the size of the leaf. Each measurement was converted to C and N contents using prediction models based on milled and tableted plant samples (Murguzur et al. 2019) and correction factors for full leaves (Petit Bon et al. 2020*a*). We first calculated the median of the replicate measurements of each leaf and then averaged the medians of the 3–5 leaves to obtain mean C and N contents for each species within a plot. Additional details on sample collection and chemical analyses with NIRS are provided in Appendix S3 (for a similar approach, see Petit Bon et al. 2020*b*).

To derive vascular plant C and N community-weighted contents, we assessed aboveground vascular plant biomass by using point intercept frequency method (PIM—Bråthen and Hagberg 2004). Two subplots (25 × 25 cm) were randomly selected within each plot after snowmelt in 2016 and PIM was performed within these at peak season in both 2016 and 2017 by using a sampling frame with 25 evenly distributed intercepts. Due to time constraints, 12 intercepts were randomly selected and used in 2016, whereas all 25 intercepts were used in 2017. Such difference is assumed to be irrelevant since a pin density of 12 pins per ˜0.06 m^{-2} area (the area of our subplots) is already largely above the threshold after which an increase in number of pins has a negligible effect on the accuracy of biomass estimates (Bråthen and Hagberg 2004). Within each subplot, we vertically lowered a pin (3 mm diameter) through the selected intercepts and counted the number of contacts between the pin and each live vascular plant species. Number of contacts for each species was first averaged between the two subplots within plot and then converted into biomass values (g/m^2) (see Vascular plant C and N contents).

A total of 17 25 × 25 cm plots were selected for destructive harvesting within the study area at the peak of the growing season in 2016. Plots were selected to encompass the three habitats and a high degree of variation in both aboveground vascular plant biomass and species (and PFT) composition. At each plot, we performed PIM as described above using a frame (25 × 25 cm) with 50 evenly distributed intercepts. Live aboveground vascular plant biomass from each plot was then harvested and sorted in PFTs, oven-dried at 60°C for 48 h, and weighted with an accuracy of ±0.001 g. By fitting weighted linear regression models (Bråthen and Hagberg 2004), we calculated the relationships between PIM data and grams of biomass (g/m^2) for each PFT (Appendix S1: Table S3). These PFT-specific relationships were used to calculate plant species biomass (g/m^2) in our experimental plots.

Finally, vascular plant C and N community-weighted contents were obtained following Garnier et al. (2004): vascular plant C or N content (%dw) = $\sum_{i=1}^{n} = p_i \times$ (C or N content)$_i$, where *n* is the number of species in a plot, p_i is the relative contribution of species *i* to the overall plot biomass, and (C or N content)$_i$ are C and N contents (%dw) of species *i*, respectively.

Moss C and N contents.—We randomly collected moss shoots within each plot using the same metal frame as for vascular plant sampling (see Material and Methods: Sample collection and processing: Vascular plant C and N contents; Fig. 2e). Moss shoots were collected at each of the nine sticks used to sample vascular plant leaves. We sampled about the same amount of moss material at each stick (i.e., 7–10 moss shoots, for a total of 63–90 shoots per plot). Moss shoots were oven-dried at 60°C for 48 h, and shoots of the same plot were pooled prior to analyses. For each moss sample, we separated the green, photosynthetically active part of the shoots from the brown, nearly decomposed part and only the former was used in the analyses. Samples were milled using a ball mill (Retsch Mixer Mill MM 400, Haan, Germany) (milling time: 40 min; milling intensity: 15 Hz). After milling, a 4–6 mg subsample was analyzed for its C and N contents (%dw) using the CN analyzer. Since we collected any moss species that was randomly hit by the sticks and about the same number of shoots from each stick, estimates of C and N contents are considered approximate community-weighted C and N contents of the moss compartment as a whole.

Soil C and N contents.—The organic soil layer in Svalbard is thin and often forms a continuum with the lower part of the moss mat, which can be found at different stages of decomposition. Hence, the distinction between soil and moss compartments can be challenging due to heterogeneous profiles, which also vary between

habitats. Here, the moss–soil interface was defined as the point where the moss tissue was no longer distinguishable by eye from the organic soil. Three samples of organic soil were collected from each plot using a soil sample cylinder (20 mm diameter and 30–40 mm deep) (Fig. 2e). Spots for soil sample collection within each plot were randomly selected, and the moss layer was removed before inserting the soil corer into the ground. Soil samples were stored in a refrigerator at 3–4°C after collection. Within one week, the three samples of organic soil belonging to a plot were pooled together and oven-dried at 60°C for 48 h. Samples were first mixed and homogenized and subsequently sieved with a 2-mm mesh size soil sieve. A 5–9 mg subsample was analyzed for its C and N contents (%dw) using the CN analyzer.

Statistical analyses

We analyzed the data using linear mixed-effects models (LMM) fitted with the lme function from the nlme package (Pinheiro et al. 2015) in the R environment version 3.6.1 (https://www.r-project.org). We used "spring goose disturbance" (two-level factor: undisturbed [U] and disturbed [D]), "summer warming" (two-level factor: ambient [A] and warming [W]), "year" (two-level factor: 2016 and 2017) and their interactions as predictors in full models with C and N contents (%dw) and C:N ratio as response variables, separately for each ecosystem compartment (vascular plants, mosses, and soil) and habitat (ME, MO, and WE), for a total of 27 models. In all models, we specified "site" as random term to account for the hierarchical spatial structure of the study design. Moreover, "plot" was nested within "site" to account for the repeated sampling in 2016 and 2017. Response variables in each model were $\log_e(y)$-transformed prior to analyses in order to achieve homogeneity in the residual variance.

By using likelihood ratio test on full LMMs (fitted using maximum likelihood—ML), we simplified the fixed-effects structure of each model. First, we attempted to select the better, but common, fixed-effects structure for all the analyses in order to obtain estimates for the same model parameters in all 27 models. The common model structure included "spring goose disturbance," "summer warming," and "year" as additive fixed terms and "spring goose disturbance × year" and

"summer warming × year" as interaction fixed terms. However, these interactions were found to be important as deemed by the statistical significance of the interaction term in only 4 out of the 27 models. Such across-year statistical consistency in C, N, and C:N ratio responses of ecosystem compartments to experimental treatments was considered of interest in light of our expectation of stronger chemical responses following two years of manipulations. Thus, we show results from models with the better, most parsimonious fixed-effects structure. Model estimates for these models are provided in Appendix S1: Tables S4–S6. To enable comparisons between the different sets of models, we provide model estimates for the models with common fixed-effects structure in Appendix S1: Tables S7–S9.

We present C, N, and C:N ratio responses of vascular plants, mosses, and soil to spring goose disturbance and summer warming, separately for the three habitats. We display the main effects of the experimental treatments since their interaction was not found to be statistically significant in any of the models (see this section). We also report natural variation in ecosystem compartment C and N contents and C:N ratio between 2016 and 2017 to allow comparisons with treatment effects.

In order to facilitate the comparison of effect sizes regardless of positive or negative responses, we present each response in terms of absolute values of standardized estimates. The direction of each response is also provided. Standardized estimates have the standard deviation (SD) as their unit and thus indicate how many additional SDs the response variable changes in response to treatments for every change of 1 SD of the response variable in un-manipulated control plots. Standardized estimates were obtained by extracting standardized coefficients from model outputs (fitted by restricted ML) following Gelman (2008).

Statistically significant effects were defined as having their 95% confidence interval (CI) not crossing zero. In addition, we also evaluated and defined effects where the 90% CI did not cross zero. We considered both these responses as biologically meaningful in the *Results* because the effect sizes were very similar. We validated each model by assessing normality and homogeneity of variances in the residuals for the fixed-effects and checking for approximate linearity between observed and fitted values.

Results

Micro-environmental characteristics

Micro-environmental characteristics measured throughout the warmest month (July) varied between habitats and years and were modified to a different extent by experimental treatments (Fig. 3).

Soil moisture differed between habitats (ME: ˜43%, MO: ˜67%, WE: ˜95%; averages across years and treatments), whereas differences between years and treatments were comparatively small (Fig. 3a). Across years and habitats, average and maximum air temperatures in warmed plots were ˜0.7° and ˜3.7°C higher, respectively, compared with ambient plots (Fig. 3b). OTCs also increased moss mat temperatures (Fig. 3c): average and maximum moss mat temperatures in warmed plots were ˜0.8° and ˜1.4°C higher, respectively, than in ambient plots. Conversely, herbivore disturbance had more variable between-year and between-habitat effects on moss mat temperatures compared with warming, and no clear patterns were identified (Fig. 3c). OTCs had little effects on air relative humidity and soil pH (Appendix S1: Fig. S2).

Differences in ambient average temperatures between years were greater than within-year effects of experimental warming (Fig. 3b,c). Across habitats, air and moss mat temperatures were ˜1.6° and ˜1.2°C higher, respectively, in 2016 than 2017. Differences between the two years in ambient maximum temperatures were instead smaller than within-year effects of OTCs.

C and N contents and C:N ratio of ecosystem compartments in un-manipulated controls

Ecosystem compartments varied widely in their chemical composition (Fig. 4). C content was much lower in soil (average between the two years ±SD: 7.1 ± 3.8%) than in the two vegetation compartments (vascular plants: 43.7 ± 1.3%; mosses: 42.4 ± 2.3%) (Fig. 4a-c). N content was lowest in soil (0.44 ± 0.26%), intermediate in mosses (1.04 ± 0.25%), and highest in vascular plants (2.86 ± 0.40%) (Fig. 4d–f). C:N ratio was highest in mosses (43.4 ± 11.9) and comparable between soil (16.4 ± 2.1) and vascular plants (15.6 ± 2.4) (Fig. 4g–i). There was high variability in the chemical composition of each ecosystem compartment, as expressed by the large SDs.

Chemical composition of ecosystem compartments showed strong differences between the two years (Fig. 4). In all habitats, C and N contents of vascular plants were higher and C:N ratio was lower in 2017 than 2016 (Fig. 4a, d, g). Mosses had lower C content in 2017 than 2016 in all habitats, whereas N content was higher in 2017 compared with 2016 in WE habitats and C:N ratio was lower in 2017 than 2016 in MO and WE habitats (Fig. 4b, e, h). Soil had lower C content in 2017 than 2016 in MO and WE habitats, lower N content in 2017 compared with 2016 in WE habitats, and lower C:N ratio in 2017 than 2016 in all habitats (Fig. 4c, f, i).

C, N, and C:N ratio responses of ecosystem compartments to goose disturbance and warming

Out of a total of 58 treatment effects assessed across models, we found nine effects where the 95% confidence interval (CI) did not cross zero and three effects where the 90% CI did not cross zero, corresponding to 21% of the assessed parameters (Fig. 5). The three ecosystem compartments differed in their sensitivity to treatments. Out of these 12 responses, eight were detected in vascular plants, three in soil, and one in mosses. As a result, 40% of the assessed chemical parameters in vascular plants, 15% in soil, and 6% in mosses responded to the imposed manipulations. While vascular plants responded to both goose disturbance (three responses) and warming (five responses), mosses and soil only responded to goose disturbance.

When considering all 58 treatment effects, chemical responses of vascular plants were stronger (as expressed by standardized effect sizes) compared with those of mosses and soil. However, when only considering the 12 significant responses, their magnitude was similar across ecosystem compartments (Fig. 5). Differences in C and N contents and C:N ratio of ecosystem compartments between the two years were up to threefold larger than their chemical responses to either goose disturbance or summer warming (cf. effect sizes in Figs. 4, 5).

Ecosystem compartments differed between habitats in their chemical sensitivity to treatments (Fig. 5). Vascular plants responded to goose disturbance in ME and WE, but not MO habitats, and all responses were consistent across the two years. Vascular plant responses to
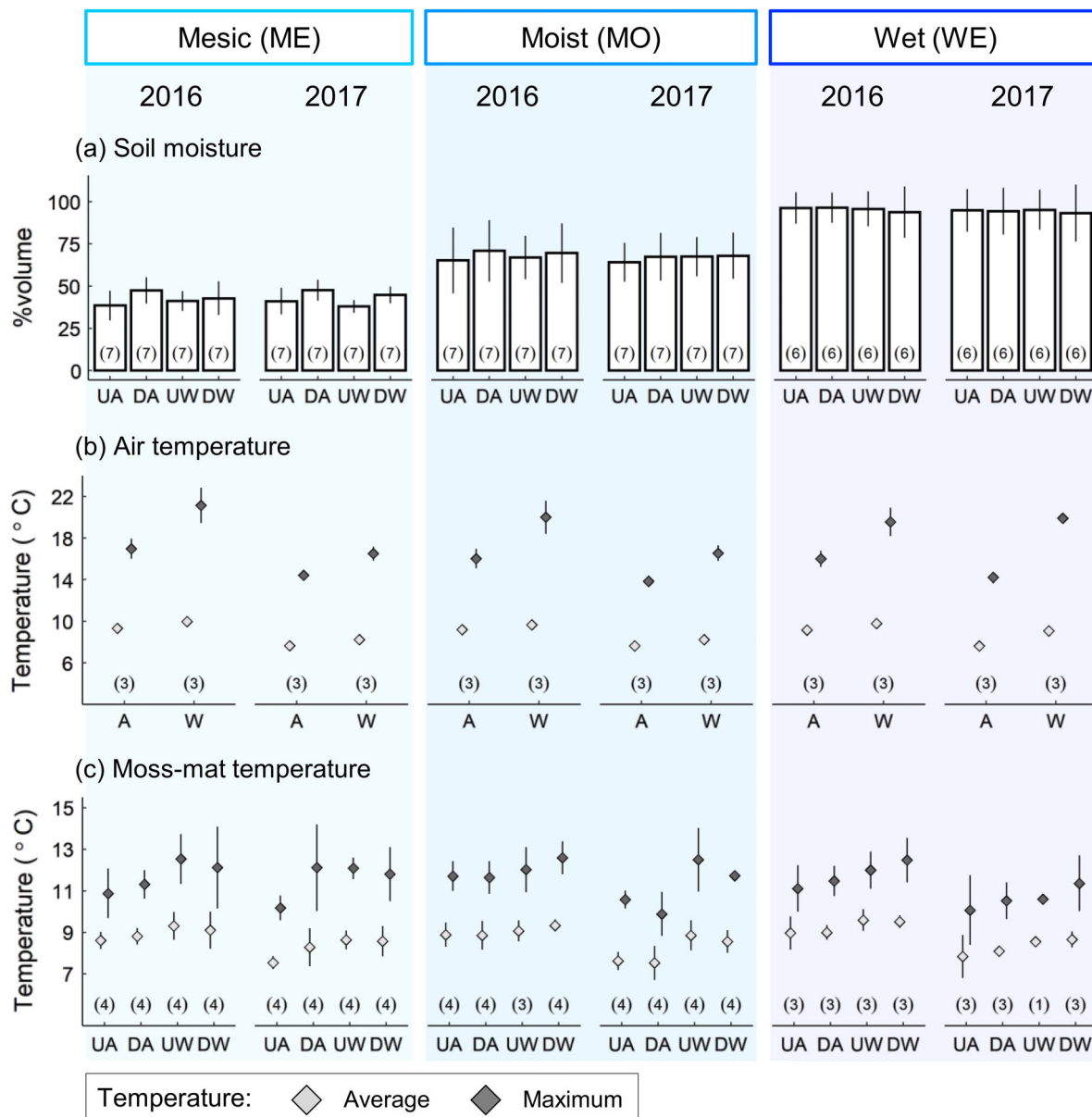
Fig. 3. Micro-environmental characteristics of habitats and treatments in summer 2016 and 2017. (a) Peak season soil moisture (as %volume) averaged from five readings at each plot and average and maximum (b) air temperatures and (c) moss mat temperatures throughout the warmest month (July) in 2016 and 2017. Bars represent the standard deviation of the mean. A few temperature loggers showed malfunctioning, and thus, data were excluded before calculating the summary statistics presented here (numbers in parentheses refer to the number of monitored plots). Acronyms used to identify treatment combinations (x-axis) are described in Fig. 2.

warming occurred in ME and MO, but not WE habitats; whereas they were consistent across the two years in MO habitats, they only became significant in ME habitats in 2017 (i.e., following two years of elevated temperatures). All responses of soil to goose disturbance occurred in ME habitats and while C and N contents only responded in the first year (i.e., 2016), C:N ratio was consistently affected across the two years. The only response of mosses was detected in WE
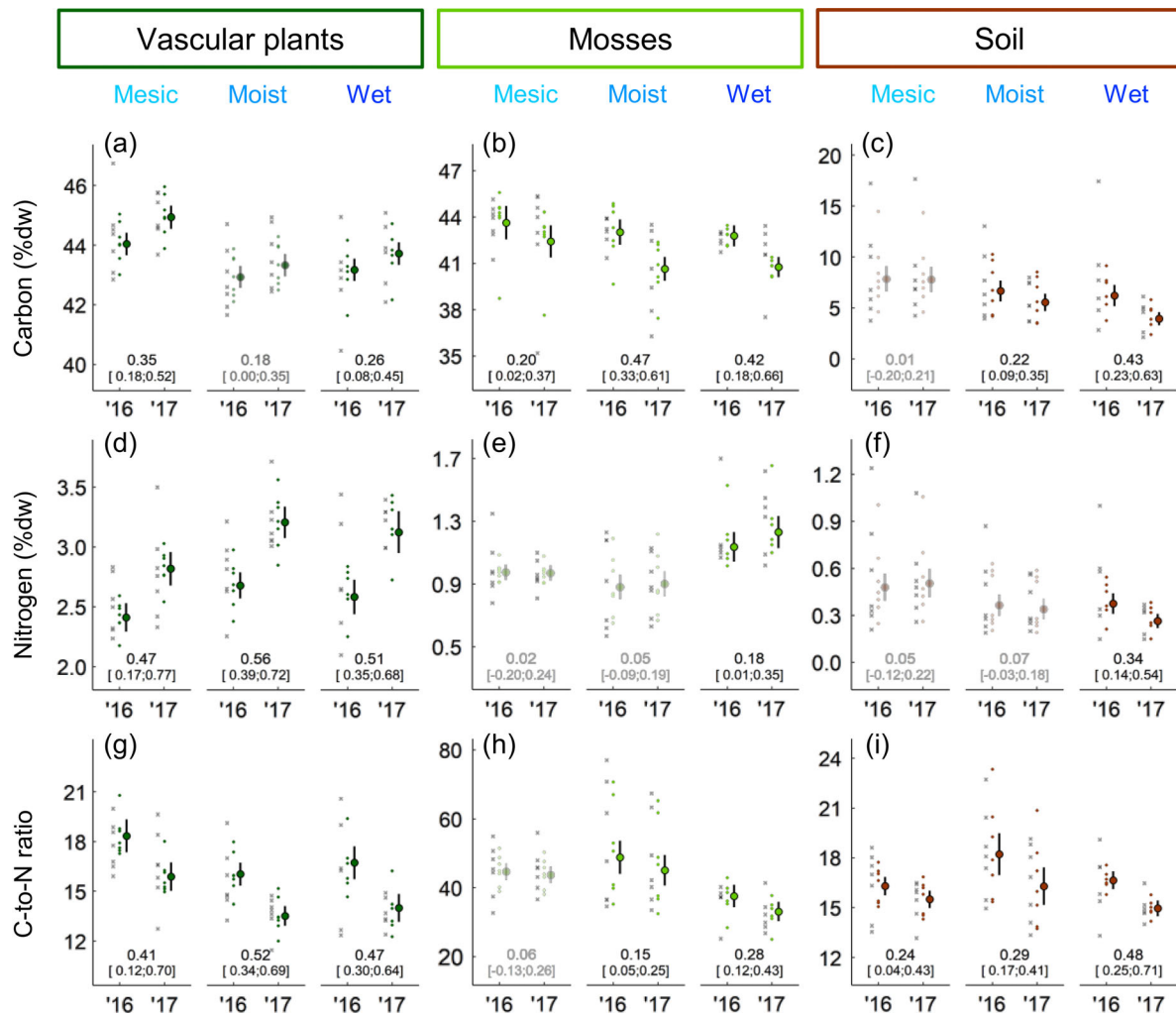
Fig. 4. Chemical composition of the three ecosystem compartments in the un-manipulated controls in summer 2016 and 2017. (a–c) Carbon [C] and (d–f) nitrogen [N] content (% of dry weight – %dw) and (g–i) C-to-N ratio [C:N] in vascular plants, mosses, and soil within the three habitats (mesic [ME], moist [MO], and wet [WE]) in 2016 and 2017. Main dots represent model predictions ± their standard error (SE), colored dots represent fitted values from the models, and gray dots represent raw values. Data were back-transformed from the $\log_e(y)$-scale prior to presentation; note the different scales of y-axis. Model predictions (and their SE) in bold colors highlight statistically significant differences (i.e., 95% confidence interval [CI] not overlapping zero) between the two years. Predictions (and their SE) in half-shaded colors highlight statistically close to significant differences (i.e., 90% CI not overlapping zero) between the two years. Predictions (and their SE) in fully shaded colors highlight non-statistically significant differences between the two years. At the base of each panel, absolute values of standardized effect sizes (and their 95% CI) for the difference between the two years are reported in order to allow comparisons with treatment effects (color shading reflects statistical differences as explained in this caption).

habitats, where goose disturbance affected their C content in both years.

C, N, and C:N ratio responses of ecosystem compartments to treatments had comparable standardized effect sizes in all three habitats (Fig. 5). In ME habitats, responses of ecosystem compartments to treatments were similar in magnitude to that of differences in chemical composition between the two years (cf. Figs. 4, 5 [ME panel]). Yet, between-year differences in chemical
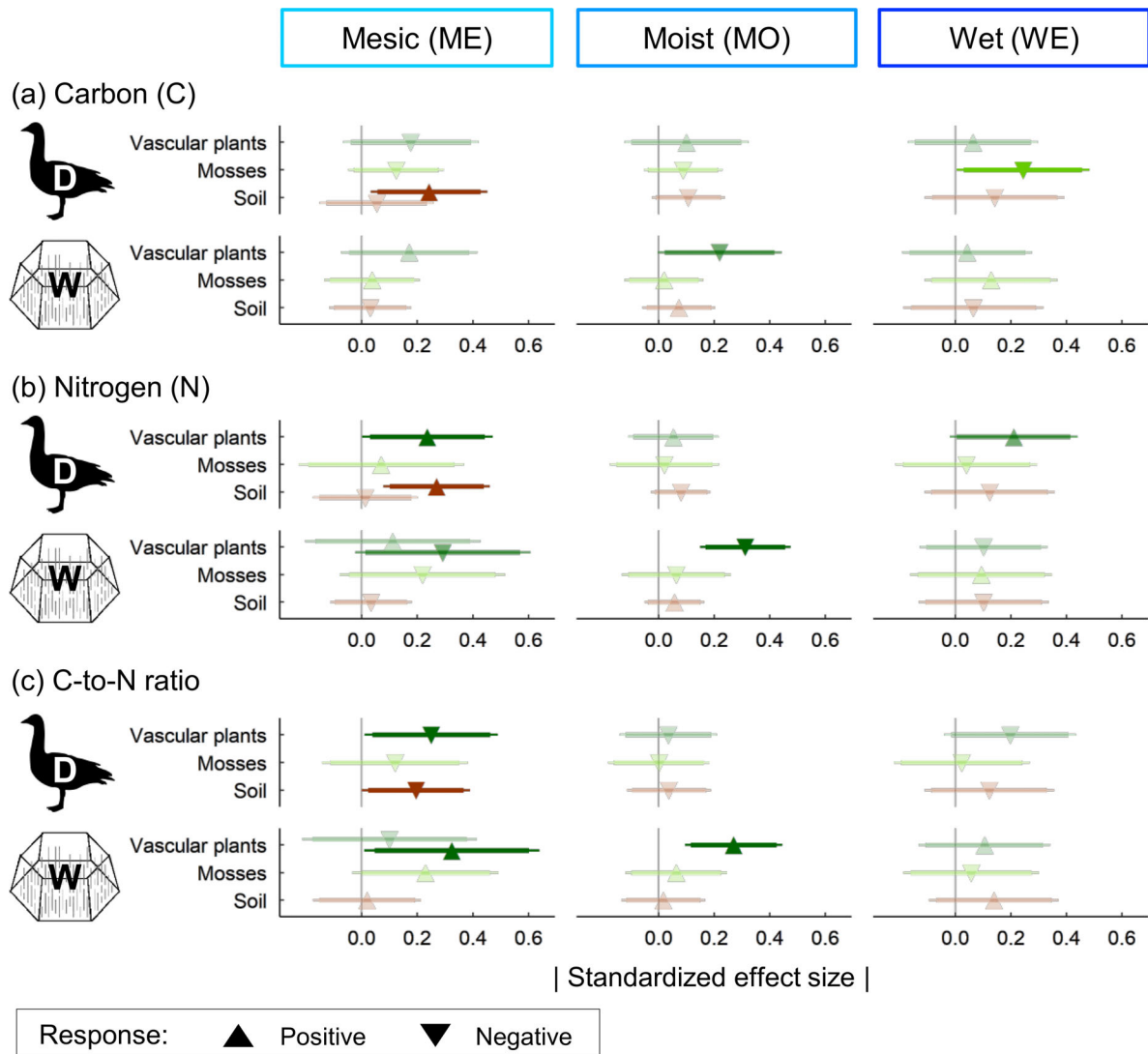
Fig. 5. Change in chemical composition of the three ecosystem compartments in response to simulated perturbations. Absolute values of standardized effect sizes for changes in (a) carbon [C], (b) nitrogen [N], and (c) C-to-N ratio [C:N] of vascular plants, mosses, and soil in response to spring goose disturbance (D vs. undisturbed plots [U—the reference level]) and summer warming (W vs. ambient plots [A— the reference level]) in the three habitats (mesic [ME], moist [MO], and wet [WE]). The reference level is denoted with the gray line at 0 effect size. Standardized effect sizes, their 90% confidence interval [CI] (thick line), and their 95% CI (thin line) are given for the main effects of treatments since their interaction was not found to be statistically significant in any of the models (see Statistical Analysis for details). (a–c [ME]) For the four models in which a statistically significant "treatment × year" interaction was found (see Statistical Analysis for details), standardized effect sizes are presented separately for year 2016 (top) and year 2017 (bottom). Effect sizes (and their CI) in bold colors highlight statistically significant effects (i.e., 95% CI not overlapping zero). Effect sizes (and their CI) in half-shaded colors highlight statistically close to significant effects (i.e., 90% CI not overlapping zero). Effect sizes (and their CI) in fully shaded colors highlight non-statistically significant effects. Upward-pointing triangles denote positive standardized effect sizes (i.e., positive responses), whereas downward-pointing triangles denote negative standardized effect sizes (i.e., negative responses).

composition of ecosystem compartments in MO and WE habitats were up to threefold larger than their responses to treatments (cf. effect sizes in Figs. 4, 5 [MO and WE panels]).

Discussion

The novelty of this study is that we compared the extent to which three main tundra ecosystem compartments, vascular plants, mosses, and soil, differ in their short-term responsiveness, that is, sensitivity and magnitude of their short-term carbon (C), nitrogen (N), and C:N ratio responses, to perturbations. We found that, although the high-Arctic ecosystem studied here showed relatively small and few significant responses to simulated spring goose disturbance and summer warming, ecosystem compartments still differed in their sensitivity to treatments, both within and across habitats. Overall, vascular plants showed higher sensitivity compared with soil and mosses and ecosystem compartments in drier habitats showed higher sensitivity compared with those in wetter habitats. We did not find any consistent responses of the three ecosystem compartments within the same treatment × habitat combination. This substantial variation in short-term C, N, and C:N ratio responses of vascular plants, mosses, and soil to herbivore disturbance and warming indicates that these responses are contingent on the environmental driver considered as well as abiotic and biotic habitat contexts. Through these variable effects, environmental perturbations, such as those imposed here, are likely to alter the immediate distribution of C and N across the tundra landscape.

The result that only 21% of the assessed parameters responded to treatments, indicating that the C and N contents of this ecosystem were relatively resistant to perturbations, supports the view that high sensitivity of high-Arctic ecosystems may only be observed after certain thresholds of disturbance are crossed (Hudson and Henry 2010, Lamb et al. 2011). A possible explanation for such resistance may be found in the fine-scale spatial distribution of C and N in this high-Arctic ecosystem. The between- and within-plot differences, that is the variation between and within tundra patches, in soil, moss, and vascular plant C and N contents, can be so pronounced that responses are unlikely to emerge as

a consistent pattern, at least in the short term. There are two indicators for this. First, there was a high variation in C and N contents and C:N ratio of soil, mosses, and vascular plants across un-manipulated control plots (Fig. 4). Second, we found large confidence intervals for the assessed responses (Fig. 5), which suggest that C and N contents of a given ecosystem compartment in a plot may partly dictate its responsiveness to perturbations. A considerable between-plot variability across short distances (i.e., a few meters) has also been shown to commonly characterize other attributes of tundra ecosystems, such as anti-herbivore defenses in plants (Soininen et al. 2013) and microbial diversity in soil (Lamb et al. 2011), while much less is known about within-plot variation. Our results might be indicative of a conspicuous small-scale spatial variability, both between and within tundra patches, in the C and N contents of ecosystem compartments, and call for a better understanding of how such variation contributes to tundra ecosystem resistance to perturbations.

We set out to investigate whether goose disturbance in spring might interact with higher summer temperatures in affecting C and N contents of this high-Arctic ecosystem. Indeed, the importance of considering herbivory to understand tundra ecosystem responses to warming (and vice versa) has been repeatedly emphasized. For instance, previous studies from the Arctic indicate that vertebrate herbivores can regulate the effects of elevated temperatures on plant community productivity (Post and Pedersen 2008), as well as modulate warming-induced changes in the C exchange rates of ecosystems (Cahoon et al. 2012). Yet, whether these two perturbations together can elicit multiplicative C and N responses in the main compartments of tundra ecosystems has not been explored. We did not find signs of significant interactive effects between herbivore disturbance and higher temperatures across any ecosystem compartment × habitat combinations, suggesting that each of these drivers did not modulate sensitivity and magnitude of vegetation and soil C and N responses to the other driver. Further, significant effects of either driver alone in the same ecosystem compartment × habitat combination were detected only sporadically (Fig. 5b, c—mesic habitats). Together, these results indicate that

spring goose disturbance and summer warming affect the immediate C and N contents of vascular plants, mosses, and soil of this high-Arctic ecosystem in an additive way and that in many cases, even if operating simultaneously, only one of these perturbations determines ecosystem compartment responses in a given context.

Congruent with our expectations, all ecosystem compartments responded to goose disturbance, although vascular plants and soil showed higher sensitivity compared with mosses, while responses to warming were restricted to the vascular plant compartment. Results from previous Arctic studies suggest that relatively fast chemical responses of single vascular plant species to either goose herbivory (e.g., Bazely and Jefferies 1985, Beard et al. 2019) or higher temperatures (e.g., Tolvanen and Henry 2001, Welker et al. 2005) should be expected. Species-level responsiveness, however, may not mirror community-level responsiveness (the focus of our study). Such contrast is particularly relevant in ecosystem-level research, where species-specific responses can fail to describe changes in ecosystem properties that depend on the abundance of each species in the community (Grime 1998). The community-weighted contents (Garnier et al. 2004) for C and N contents and C:N ratio we report here show that the chemistry of the whole vascular plant compartment of tundra ecosystems can also be relatively sensitive to spring goose disturbance and summer warming and that its sensitivity is higher compared with that of mosses and soil. To what extent such differential short-term sensitivity to environmental perturbations has implications for the relative role that these tundra ecosystem compartments have in whole-ecosystem C and N dynamics (Jonasson et al. 1999, Hobbie et al. 2002) is yet to be explored.

The almost total unresponsiveness of the moss compartment to the goose disturbance simulation was surprising, considering the ability of Arctic mosses to quickly sequester available nutrients (Sjögersten et al. 2010, Barthelemy et al. 2017) that we here deposited in the form of added feces. In experimentally disturbed plots, the photosynthetically active part of the moss layer seemed to dry out during the summer, even in wet habitats (M. Petit Bon, *personal observation*), likely as a consequence of the reduced water-holding capacity of the disturbed moss colonies (Elumeeva et al. 2011). As mosses are unable to stay physiologically active when dry (Turetsky et al. 2012), the simulated goose grubbing may have prevented any changes in their chemistry and allowed nutrients leaching from goose droppings to reach the rooting zone of vascular plants. These findings suggest that the capacity of mosses to constrain the fertilizing effects of animal excreta on forage species may be inhibited by some other herbivore-related activities, such as goose grubbing.

Differences between habitats in the sensitivity of vascular plant and soil C and N contents to the simulated perturbations may partly be attributed to different abiotic and biotic characteristics. The vascular plant compartment exhibited the highest sensitivity to warming in MO habitats, had intermediate sensitivity in ME habitats, and did not respond in WE habitats. Welker et al. (2005) also found C and N contents of vascular plants to be more affected by warming in moist than dry tundra habitats. Tolvanen and Henry (2001) did not observe any changes in the C and N contents of the sedge *Carex stans* growing in a close to water-saturated high-Arctic meadow exposed to warming, while plant species from relatively drier habitats responded to higher temperatures. These observations suggest that soil moisture could mediate C and N responses of vascular plants to warming, thus supporting the consideration that moisture availability is a key context variable that influences the ecological impacts of perturbations on tundra ecosystems (le Roux et al. 2013). All but one response of vascular plants and soil to goose disturbance were found in ME habitats. The higher resistance of wetter habitats may be because the soil, and thus the rooting zone of vascular plants, is protected from disturbance by a thick moss layer, which is shallower in drier habitats. Though we did not measure moss depth directly, it varied between ME, MO, and WE habitats (M. Petit Bon, *personal observation*), likely matching that of the *Dryas/Luzula* heath (~6 cm), moss tundra (~10 cm), and freshwater mire (~11 cm), respectively, studied by Speed et al. (2010) in the same high-Arctic valley. They found that the capacity of these and other high-Arctic plant communities to withstand goose grubbing was indeed positively related to soil moisture, hence moss cover (Speed

et al. 2010). Collectively, these results point toward a high degree of contextual sensitivity in C, N, and C:N ratio responses of ecosystem compartments to perturbations and indicate that spatially neighboring tundra habitats may have different resistance to environmental changes.

The large difference in C and N contents and C:N ratio of vascular plants, mosses, and soil that we found between the two summers shows that, in addition to the pronounced spatial variation in ecosystem compartment chemical composition, there is a strong temporal component. The large between-year variability in abiotic conditions that characterizes Arctic ecosystems (Pelt et al. 2016, Nordli et al. 2020) may thus be accompanied by substantial between-year differences in the chemistry of the main ecosystem compartments, as has been shown, for example, for primary productivity (Gauthier et al. 2011, van der Wal and Stien 2014). The two growing seasons encompassed by this study markedly differed in their climatic conditions; indeed, their temperature differences were greater than the effects of our experimental treatments on plot-level temperatures (Fig. 3). Accordingly, the between-summer variation in ecosystem compartment chemical composition was larger than the changes in chemistry induced by our manipulations (cf. Figs. 4, 5). This highlights the challenge to quantify the relative importance of simulated perturbations vs. natural variability in dictating changes in high-Arctic ecosystem C and N contents and possibly biogeochemical processes. We propose that longer-term experiments should more often focus on partitioning response variability due to treatment effects and response variability due to natural inter-annual climatic fluctuations, which would help us better interpret the ecological relevance of (simulated) environmental changes. Noteworthy, however, goose disturbance and warming still caused detectable changes in the C and N contents of this high-Arctic ecosystem. This suggests that the net effect of short-term perturbations might be that of exaggerating background variations in the chemical composition of vascular plants, mosses, and soil across contrasting years.

In summary, we have here examined whether and to what extent vascular plants, mosses, and soil in tundra ecosystems differ in their short-term C and N responses to environmental

perturbations. Though the system's total C and N contents were relatively resistant to both simulated spring herbivore disturbance and summer warming, the three ecosystem compartments still differed in their sensitivity to perturbations (vascular plants > soil > mosses), and this was exacerbated by their differential sensitivity across habitats (mesic > moist > wet). In order to unravel to what extent environmental changes may alter tundra ecosystem C and N dynamics, and eventually develop conceptual models focusing on the impact of perturbations across the heterogeneous Arctic landscape, future efforts could benefit from taking these variable responses into account. Our findings imply that assessments of a single ecosystem compartment are unlikely to reflect whole-system impacts of perturbations, suggesting that addressing vegetation and soil responses in diverse habitat contexts can advance our predictive capability of how the biogeochemistry of tundra ecosystems responds to environmental changes.

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Data Availability

Data are available from DataverseNO UiT Open Research Data Repository: https://doi.org/10.18710/RHERMM.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3746/full