This article has been published in the Journal of Ecology, please cite it as follows

Deschamps, L., Maire, V., Chen, L., Fortier, D., Gauthier, G., Morneault, A., Hardy-Lachance, E., Dalcher-Gosselin, I., Tanguay, F., Gignac, C., McKenzie, J. M., Rochefort, L., & Lévesque, E. (2022). Increased nutrient availability speeds up permafrost development, while goose grazing slows it down in a Canadian High Arctic wetland. *Journal of Ecology*, *00*, 1–15. https://doi.org/10.1111/1365-2745.14037

The present version is the accepted manuscript before final editing.

Research paper

Title: Increased nutrient availability speeds up permafrost development, while goose grazing slows it down in a Canadian High Arctic wetland

Authors: Lucas Deschamps[1,2,3]*, Vincent Maire[1,2,3], Lin Chen[4], Daniel Fortier[3,5], Gilles Gauthier[3,6], Amélie Morneault[1,2], Elisabeth Hardy-Lachance[3,5], Isabelle Dalcher-Gosselin[1,2], François Tanguay[1,2], Charles Gignac[3,7], Jeffrey M. McKenzie[8], Line Rochefort[3,7], Esther Lévesque[2,3]

Address:

1 Chaire en Écologie Fonctionnelle Arctique, Université du Québec à Trois-Rivières, Trois Rivières, QC, G9A 5H7, Canada;

2 Département des sciences de l'environnement, Université du Québec à Trois-Rivières, Trois Rivières, QC, G9A 5H7, Canada;

3 Centre d'études nordiques, Université Laval Québec, QC, G1V 0A6, Canada;

4 Department of Environmental Sciences, University of California, Riverside, CA 92521, USA;

5 Département de géographie, Université de Montréal, Montréal, QC, H3T 1J4, Canada.

6 Département de biologie, Université Laval, QC, G1V 0A6, Canada

7 Département de Phytologie, Université Laval, Quebec City, QC, G1V 0A6, Canada

8 Department of Earth and Planetary Sciences, McGill University, Montréal, QC H3A 0E8, Canada

*** Author for correspondence:**

Lucas Deschamps

Tel: +1 819 524-0245

Email: lucas.deschamps@uqtr.ca

Word count:

Total word count (excluding summary and legends): 8938

Summary: 332/350; Introduction: 1067; Materials and Methods: 1848; Results: 690; Discussion: 2282; Acknowledgements: 159; References: 2892; Figures: 5; Tables: 3; No of supporting Information files: 1

Summary

1) It is of prime importance to understand feedbacks due to the release of carbon (C) stored in permafrost soils (permafrost-climate feedback) and direct impacts of climatic variations on permafrost dynamics therefore received considerable attention. However, indirect effects of global change, such as the variation in soil nutrient availability and grazing pressure, can alter soil and surface properties of the Arctic tundra, with the potential to modify soil heat transfers toward the permafrost and impact resilience of Arctic ecosystems.

2) We determined the potential of nutrients availability and grazing to alter soil energy balance using a 16-year split-plot experiment crossing fertilization at different doses of nitrogen (N) and phosphorus (P) with protection from goose grazing. Moss biomass and some determinants of the surface energy budget (leaf area index (LAI), dead vascular plant biomass and albedo) were quantified and active layer thaw depth repeatedly measured during three growing seasons. We measured soil physical properties and thermal conductivity and used a physical model to link topsoil organic accumulation processes to heat transfer.

3) Fertilization increased LAI and albedo, whereas grazing decreased dead vascular plant biomass and albedo. Fertilization increased organic accumulation at the top of the soil leading to drier and more porous topsoil, whereas grazing increased water content of topsoil. As a result, topsoil thermal conductivity was higher in grazed plots than in ungrazed ones. Including these properties into a simulation model, we showed that, after 16 years, nutrient addition tended to shallow the active layer whereas grazing deepened mean July active layer by 3.3 cm relative

to ungrazed subplots. As a result of OM accumulation at the surface, fertilization increased permafrost vertical aggradation rate by almost an order of magnitude (up to 5 mm·year^{-1} instead of 0.7 mm·year^{-1}), whereas grazing slowed down permafrost aggradation by reducing surface uprising and deepening thaw depth.

4) *Synthesis:* We demonstrated that long-term grazing and N and P addition, through their impact on vegetation and soil properties have the potential to impact permafrost dynamics to the same extent as contemporary temperature increase in High Arctic polygonal wetlands.

KEYWORDS: Active layer; Albedo; Fertilization; Global change ecology; Greater snow goose; Organic matter; Polygons; Tundra

Résumé

1) Afin de comprendre les rétroactions causées par la respiration du carbone (C) stocké dans le pergélisol (rétroaction pergélisol-climat), les impacts directs du changement climatique sur la dynamique du pergélisol ont reçu une attention considérable. Toutefois, les effets indirects du changement climatique, telles que la disponibilité en nutriments du sol et la pression de broutement, peuvent altérer les propriétés du sol et de surface de la toundra Arctique, avec le potentiel de modifier les transferts de chaleur vers le pergélisol et d'impacter la résilience des écosystèmes Arctiques.

2) Nous avons déterminé l'effet potentiel d'une disponibilité accrue en nutriment et du broutement sur la balance énergétique du sol grâce à une expérimentation en tiroir croisant différents niveaux de fertilisation en azote (N) et phosphore (P) à une protection contre le broutement durant 16 ans. La biomasse des plantes vasculaires et des mousses, ainsi que plusieurs déterminants du budget radiatif de surface ont été quantifiés (indice de surface foliaire (LAI), biomasse de plantes vasculaires mortes et albédo). La profondeur de la couche active a été mesurée à répétition durant trois saisons de croissance. Les propriétés physiques du sol et sa conductivité thermique ont été mesurées, et nous avons utilisé un modèle physique de simulation pour lier l'accumulation de matière organique en surface aux transferts de chaleur dans le sol.

3) L'indice de surface foliaire et l'albédo ont augmenté dans les traitements de fertilisation, alors que le broutement a diminué la biomasse de plantes vasculaires mortes et l'albédo. La fertilisation a causé l'ajout de nouveaux horizons organiques peu décomposés sous la surface du sol, menant à des conditions plus sèches et à un sol plus poreux. À l'inverse, le broutement a augmenté la teneur en eau du sol. En conséquence, la conductivité thermique du sol était plus élevée dans les sous-parcelles broutées que dans celles non-broutées. En incluant ces propriétés dans un modèle de simulation, nous avons montré que l'addition de

nutriments a diminué la profondeur de la couche active, tandis que le broutement l'a approfondie de 3.3 cm en moyenne. En conséquence de la création de nouveaux horizons organiques en surface, la fertilisation a augmenté le taux d'aggradation vertical du pergélisol par un ordre de grandeur (jusqu'à 5.5 $mm \cdot an^{-1}$ au lieu de 0.7 $mm \cdot an^{-1}$), tandis que le broutement a ralenti l'aggradation du pergélisol en limitant l'élévation de la surface et en approfondissant la couche active.

4) ***Synthèse*** *:* Nous avons montré que l'effet à long-terme du broutement et de l'ajout de N et P influençait la dynamique du pergélisol dans la même mesure que les augmentations de températures contemporaines, et ce en impactant la végétation et les propriétés du sol dans les marais polygonaux du Haut-Arctique.

Introduction

Thawing of the active layer (AL), the near-surface part of permafrost seasonally warming above 0 °C, has important impacts on net carbon emission in the Arctic biome and may turn it from a carbon sink to a carbon source (Schuur *et al.*, 2009; Koven *et al.*, 2011; Miner et al., 2022). Much effort has been devoted to understanding the response of the AL to increased radiative forcing and air temperature, both with modelling (Schädel *et al.*, 2018) and empirical (Hollister *et al.*, 2006) approaches. Physical properties of the land surface influence transmission of radiation and energy partitioning among heat fluxes and may slow or accelerate AL thaw rate and increase depth depending upon topsoil characteristics and vegetation cover (Yi *et al.*, 2007). Surface properties are strongly influenced by vegetation, for example through its influence on snow accumulation (Myers-Smith *et al.*, 2011) or shading (Blok *et al.*, 2010). Because Arctic vegetation is driven by indirect influences of climate (for instance nutrient availability, Gough *et al.*, 2016; hydrology, Hodkinson *et al.*, 1999) and other unrelated forces (for instance grazing, Pouliot *et al.*, 2009), global change may alter local AL dynamic in unexpected ways.

Nutrient availability may alter AL thaw through its impact on tundra vegetation. Nutrient availability is expected to increase in terrestrial Arctic ecosystems following an increase of topsoil temperature (Hartley *et al.*, 1999, Koven *et al.*, 2015). Arctic vegetation growth has been demonstrated to be co-limited by N and P (Shaver & Chapin, 1995; Gough & Hobbie, 2003). Grasses (Liu *et al.*, 2020; Ylänne *et al.*, 2020) and deciduous shrubs (Shaver *et al.*, 2001; van Wijk *et al.*, 2004; Gu & Grogan, 2020) benefit generally the most from increased nutrient availability in topsoils, at the expense of mosses, which become submitted to severe light limitation (Grellman, 2002; Gough *et al.*, 2016). The net effect of such

vegetation change on active layer depth is however not evident. An increase in dead vascular plant and grass cover increases albedo (te Beest *et al.*, 2016), while an increase in shrub cover and height diminishes it (Juszak *et al.*, 2014), decreasing and increasing the quantity of energy available to warm the system, respectively. Higher vascular plant leaf area index (LAI) reduces radiative input at the soil surface by shading (Juszak *et al.*, 2016 and 2017), potentially reducing the available energy to thaw the active layer (Blok *et al.*, 2010). The reduction in moss cover potentially removes an insulative layer at the top of the soil column (Gornall *et al.*, 2009, Soudzilovskaia *et al.*, 2013) and can increase AL depth (Gornall *et al.*, 2007). Altogether, these changes all represent potential vegetation-mediated feedback between global warming and active layer depth, as nutrient availability is expected to increase along with Arctic temperatures.

Grazing by abundant herbivore populations has the potential to increase thaw depth through their impact on vegetation. Grazing generally reduces living vascular plant biomass (Gauthier et al. 1995; Sjögersten *et al.*, 2011 for goose grazing, Falk *et al.*, 2015 for mammal grazing; but see Bernes *et al.*, 2015 for reindeer grazing), potentially reducing live LAI (Sundqvist *et al.*, 2019 for mammal grazing) and dead vascular plant accumulation (Speed et al., 2010; Sjögersten *et al.*, 2012 for goose grazing; Mosbacher et al., 2019 for mammal grazing). This results in an increase in the quantity of radiation reaching the ground (Juszak *et al.*, 2016 and 2017). Conversely, reduction of shrub cover by heavy mammalian grazing increases albedo, thereby decreasing the quantity of energy able to thaw the active layer (te Beest *et al.*, 2016). Goose feeding on below-ground parts (grubbing) is also known to disturb the moss mat, decreasing its insulative effect (van der Wal *et al.*, 2001, Gornall et al., 2009) with an unknown long-term effect on AL depth.

Arctic herbivores certainly have the potential to influence surface radiative transfer in Arctic terrestrial ecosystems, but their impact in the context of increased soil nutrient availability is poorly known.

Fertilization and grazing may affect active layer thaw through their impact on soil organic matter (SOM) accumulation. Long-term SOM accumulation causes the extension of syngenetic permafrost (the permafrost building upward after an addition of material at the surface, Vincent *et al.*, 2017). Relative to mineral topsoil, low thermal diffusivity of SOM at the top of the soil protects permafrost from thaw (Jorgenson *et al.*, 2010) and favors the creation of a thick, ice-rich transient layer at the top of the permafrost table (Shur *et al.*, 2005). Both fertilization and grazing have the potential to alter SOM quantity and structure by altering both the C fixation and decomposition rates in Arctic ecosystems. A long-term Alaskan study revealed increased SOM accumulation in the first 5 cm, and a decreased of SOM abundance below 5 cm in the soil of an experiment adding N and P simultaneously (Mack *et al.*, 2004). There is evidence that while fertilization increases C input and storage in the shallowest horizon, it may accelerate decomposition at depth (Nowinski *et al.*, 2008). Both goose grazing (Sjögersten *et al.*, 2012) and grubbing (van der Wal *et al.*, 2007) have been shown to reduce SOM stocks by reducing vascular plant growth and litter accumulation at Svalbard. Topsoil water content (SWC) has also been shown to be increased by goose grazing in Arctic wetlands (Sjögersten *et al.*, 2011 and 2012), potentially increasing topsoil thermal conductivity (O'Donnell *et al.*, 2009). Both grazing and increased nutrient availability may alter SOM accumulation at the top of the soil, but the consequences for active layer thaw and permafrost development are still to be explored.

178 The aim of this study is to reveal the potential long-term effects of surface fertilization and
179 grazing by greater snow geese [*Anser caerulescens caerulescens* (Linnaeus, 1758)], an
180 important grazer of the tundra (Gauthier et al. 2006), on active layer thaw in polygonal
181 wetlands of a Canadian High Arctic oasis (Bylot Island, Nunavut). To do so, we
182 characterized vegetation, surface properties, hydrology, and soil thermal properties in a 16-
183 year-old experiment of fertilization and grazing exclusion. Our hypotheses are:

184 H1) N and P fertilization will increase leaf area index and dead vascular plant biomass, and
185 consequently increase surface albedo by covering the wet and dark moss layer, while grazing is
186 expected to reduce LAI, dead vascular plant biomass and albedo.

187 H2) N and P fertilization will increase organic matter accumulation at the top of the soil,
188 while grazing will limit such accumulation.

189 H3) N and P fertilization will decrease seasonal thaw depth, while grazing will increase it.

190

Materials and methods

Site

The experiment took place in the Qarlikturvik valley, on Bylot Island, Nunavut, Canada (73°08'N, 80°00'W). The geomorphology of this glacial valley is characterized by a succession of glacio-fluvial outwash, proglacial river, alluvial fans, and aggradation terraces. The surface is almost continuously covered by vascular plants and mosses and may be considered as a polar oasis (Bliss & Matveyeva, 1992). About 23% of the 70 km^2 of the valley and surrounding upland is covered by wetlands located in low centered polygons (Hughes *et al.*, 1994a) dominated by sedges (*Carex aquatilis* Walhenb., *Eriophorum angustifolium* Honck, *E. scheuzerii* Hoppe), grasses (*Dupontia fischeri* R.Br., *Pleuropogon sabinei* R.Br., Gauthier *et al.*, 1995) and mosses (*Drepanocladus* spp., *Calliergon giganteum* (Schimp.) Kindb., Pouliot *et al.*, 2009). Mesic environments occur on polygonal rims, degraded and high centered polygons, in alluvial fans and in hummocky tundra on the gentle slopes on either side of the valley (Zoltai *et al.*, 1983). Abundant wetland vegetation allows the valley to be one of the most important brood-rearing sites for the Greater Snow Goose in the Canadian Arctic with about 20,000 nesting pairs (Reed *et al.*, 2002). Greater Snow Geese mostly feed on *D. fischeri* and *Eriophorum* spp. in wetlands and are known to impact wetland vegetation biomass and nutrients concentration (Gauthier *et al.*, 1995, Valéry *et al.*, 2010).

Experimental design

A long-term randomized block split-plot design with four block and four fertilization treatments plus a control were established in polygonal wetlands of the valley in 2003.

213 Blocks were selected with a distance of at least 500 m from one another to capture polygon
214 heterogeneity in terms of vegetation, substrate type and soil wetness. Within polygons,
215 fertilization treatments were randomly attributed to five 2 m x 2 m permanent plots and
216 fertilized yearly between 2003 and 2019. Half of each plot (thereafter referenced as a
217 subplot) was protected with a permanent 50-cm tall chicken wire fence with ropes criss-
218 crossing the top since 2005, the protected part being randomly selected. During the
219 installation, plots were placed in homogeneous environment, characterized by a well-
220 developed moss-carpet and a good cover of graminoids typically grazed by geese. Plots
221 were at least 5 m apart to prevent cross-contamination of added nutrients (verified by
222 Pouliot *et al.*, 2009).

223 Fertilization treatments were selected to mimic both the range of potential nutrient release
224 associated with higher mineralization rates in the shallowest horizons of the soil (Gignac
225 *et al.*, 2022, Wang *et al.*, 2017), in addition to the possible nutrient addition via goose
226 faeces and atmospheric deposition. A low N treatment plot received 1 $g \cdot m^{-2}$ of N, whereas
227 the High N plot treatment received 5 $g \cdot m^{-2}$ of N. High P treatment was fertilized with 3
228 $g \cdot m^{-2}$ of P and the High N+P treatment with 5 $g \cdot m^{-2}$ of N and 1 $g \cdot m^{-2}$ of P. Control treatment
229 received the same quantity of water as other treatments. Fertilization treatments exceeded
230 the maximal amount of nutrients added by goose faeces (maximum of 29 $faeces \cdot m^{-2}$
231 recorded on a single plot, equivalent to 0.6-1 $g \cdot m^{-2}$ of N and 0.03-0.06 $g \cdot m^{-2}$ of P, G.
232 Gauthier, unpublished data), but was lower than many other Arctic fertilization
233 experiments (*e.g.,* Shaver & Chapin 1995; Gough and Hobbie, 2003; Ylänne *et al.*, 2020).
234 The complete fertilization protocol, applied each year, is available in Pouliot et al. (2009).

235 **Field sampling**

Field sampling took place during the summer months (primarily July-August) of 2017, 2018 and 2019. Fences were deployed over the usually unprotected part of the plot during the sampling year to avoid grazing between the emergence of the vegetation and sampling. Therefore, we measured the long-term impact of fertilization and grazing on ecosystem properties, without capturing the signal of annual disturbance due to goose presence. Temporary fences were removed after sampling to allow late-summer grazing and early season grubbing to resume normally.

Vegetation

We harvested vascular plants and mosses in grazed and ungrazed subplots at the peak of the 2018 growing season (between July 25, 2018 and August 3, 2018). Using a knife, we extracted four 10 cm x 10 cm x 10 cm clods randomly chosen in an 80 cm x 80 cm grid covering half of each subplot. We counted the number of vascular ramets of each species in each clod and summed them to obtain total vascular plant density per subplot in $ind \cdot m^{-2}$. Vascular plant biomass ($g \cdot m^{-2}$) was obtained by weighing green parts of plants sampled in a subplot after drying them 48 h in a furnace at 60° C. In each clod, a 19.6 cm^2 circular subsample was harvested using a cylinder with cutting edges to sample mosses through the 10 cm depth of the clod. Bryophytes of three out of four subsamples were sorted at the species level and weighed after drying to obtain green biomass per species. Again, species biomasses were summed to obtain a total green moss biomass per subplot, in $g \cdot m^{-2}$. We limited vegetation sampling within one half of the subplots, to let an undisturbed area for the 2019 measurements. All the subplots in a block were harvested the same day and treated in the two following days.

Leaf area index (LAI) and dead vascular plant biomass were measured in 2018 and 2019, respectively. LAI was estimated per subplot using the mean leaf area of each species, their density in the plot and their mean number of leaves (Appendix A). For dead vascular plant biomass, two or three 10 cm x 10 cm x 10 cm clods were selected arbitrarily in every subplot to represent standing vegetation. Standing dead parts of plant individuals and dead parts on the ground were separated from green parts and weighted dry to obtain a dead biomass for each subplot, in $g \cdot cm^2$.

Thaw depth and soil volumetric water content

Thaw depth and soil water content were measured repeatedly during the 2017, 2018 and 2019 summer. Thaw depth was measured physically using a graduated steel probe driven into the soil down to the frozen part. Because of different sampling period length allowed in the field, we measured thaw depth two times in 2017, four times in 2018 and six times in 2019, from early June to mid-August. At each visit, we measured thaw depth at two to four locations in each subplot depending upon the year. Soil volumetric water content (SWC) was measured one, three and four times in 2017, 2018 and 2019, respectively. In 2017 and 2018, we measured SWC at three and four locations per subplot using a WET-2 WET sensor coupled to a HH2 moisture meter (Delta T Devices Ltd), respectively. In 2019, SWC was measured at a unique location, using an Hydraprobe (Stevens). To ensure compatibility of the results, we used raw permittivity (ε) of both machine and converted it back to SWC using default HH2 calibration such as $SWC=\sqrt{(\sqrt{\varepsilon}-1.6)/8.4}$. Each subplot within a block was measured within 2 h on the same day, and measurements taken in a subplot were averaged to give a value per subplot per date.

Distance between surface and water table

Distance between soil surface and water table was measured four times in each subplot during the 2019 growing season. About 8.25 cm diameter and 1 m deep holes were drilled in each plot early in June 2019. At each subplot visit, the distance was measured in cm using a graduated probe. If there was no liquid water, the distance between surface and ice was used.

Albedo

We measured repeatedly incident and reflected radiations during the 2018 (three times) and 2019 (four times) summers using a radiometer (SKR 1850/S light sensor, coupled to a SpectroSense2+ logger, Skye). Measurements were made around four wavelengths: blue (466±19 nm), green (556±22 nm), red (644±51nm) and Near Infra-Red (NIR, 860±37 nm). Incident radiations were captured with a cosine-corrected sensor. Sensors were placed on a handheld pole keeping the reflected light sensor 150 cm above the soil surface, representing a $0.35m^2$ surface of measurement for reflected radiation. We measured radiations at four (2018) or two (2019) different locations within each subplot and averaged them per subplot per date. Horizontality of sensors was checked with a level. We calibrated reflectance (the ratio between incident and reflected radiations) per band against six Spectralon® standards of known reflectance (2%, 5%, 10%, 20%, 40% and 50% reflectance). We then computed albedo using the *albedo* function in the *microclima* R package (Maclean *et al.*, 2019), weighting corrected reflectance of each band by its relative energy contribution along all the measured bands. Each treatment of a block was measured during a 1 h interval.

Soil physical properties

Soil cores (10 cm x 10 cm) were harvested in each subplot at the beginning of August 2019 (except for one lost sample in one grazed control). Soil was sampled down to approximately 20 cm. After bringing refrigerated samples to the University of Quebec at Trois-Rivières, thermal conductivity was measured at 5, 10 and 15 cm (when possible) using a TP08 non-steady-state probe (Hukseflux), inserted into a copper made insertion guide, coupled to a Campbell CR1000 datalogger (Appendix B). Valid measurements (as defined in appendix B) were averaged to obtain a mean value per sample per depth.

After thermal conductivity measurements, soil samples were photographed and separated by visually homogeneous horizons. For each horizon, we determined the organic matter content as the Loss-On-Ignition (LOI, $g \cdot g^{-1}$), calculated using the dry weight (W_d) and the burned weight (W_b) as $(W_d - W_b)/W_d$. Soil LOI is linearly related to soil C content in highly organic peat (Bhatti & Bauer, 2002; Klingenfuß *et al.*, 2014). We then computed dry density and porosity using the equations and the compiled values in Balland and Arp (2005, details in appendix B). These three variables link the biological processes driving SOM accumulation to the thermal conductivity of soil. For example, we expect less decomposed SOM to form a soil less dense and more porous, than in case of more decomposed SOM. This high soil porosity could lead to low conductivity if pores are filled with air, or to high conductivity if pores are filled with water.

Data analysis

Statistical analysis

We used linear mixed effect models and generalized additive mixed models (GAMMs) to estimate interactive effects of fertilization and grazing. Each model contained discrete fertilization treatments (with levels Control, Low N, High P, High N, High N+P), grazing status and the interaction between fertilization and grazing as fixed effects. Details of models' structure and transformation are presented in Table 1.

Following Amrhein *et al.* (2019), we avoided discrete thinking by not choosing a *p-value* threshold guiding statistical inference. Instead, we highlighted a statistically supported effect by analysing both the *p-value* of the factor continuously and considering the magnitude and 95 % confidence interval of the post-hoc differences between the control and other experimental treatments.

All statistical analyses were calculated with R 4.0.3 (R Core Team, 2020). Mixed effects models were fitted using the *lme4* package (Bates *et al.*, 2014) and inferences were made using functions in *lmerTest* (Kuznetsova *et al.*, 2017). GAMMs were fitted using the *gam* function and in the *mgcv* package (Wood, 2011), random effects being represented as penalized regression terms. Treatment marginal means and inferences about contrasts were estimated using the *emmeans* package (Lenth, 2021).

Table 1 : Description of data, model structure and transformation (Transf.) for each variable analysed in this study. Transformations were selected to ensure normality of residuals. Each model contained fertilization (F, five levels), grazing (G) status and their interaction as fixed effects. Random effects structure was determined following Gumpertz and Brownie (1992).

Variable	Transf.	Measurements	Fixed effects	Random effects
Vascular plant biomass	*none*	Unique value per subplot (2018)	Block	Plot
Leaf area index	*logit*	*n = 40*		
Bryophyte biomass	*log*			
Dead vascular plant biomass	*log*			
Soil Loss-on-Ignition	*logit*	Unique value for each horizon of each subplot, weighted by the relative thickness of the horizon (2019) *n = 39 × number of horizons in each soil column*	Block	Plot Subplot Third order cubic spline along depth for each F x G level (GAMM)
Soil dry density	*log*			
Soil porosity	*logit*			
Soil thermal conductivity	*log*	Mean value at 5 and 10 cm depth for each subplot (2019) *n = 39 × 2 depths*	Block Depth (two levels) Depth x Fertilization Depth x Grazing Depth x F x G	Plot Subplot
Water table depth	none	Mean value per subplot (2019) *n = 40*	Block	Plot
Albedo	*logit*	Mean value per subplot per year (2017, 2018, 2019) *n = 40 × 3 years*	Block Year Year x Block Year x Fertilization Year x Grazing Year x F x G	Plot Subplot Year x Plot
Soil Volumetric Water Content	none			
Thaw depth	none			

Numerical modelling

We used a numerical heat transfer model with phase change to disentangle the effect of changes in surface and soil properties on active layer thaw. Using marginal means of soil parameters of the grazed and ungrazed Control and High N+P treatments, we examined what part of the observed variation in thaw depth may be attributed to change in soil properties. We explored two scenarios: the “Soil scenario” reproduced the differences among treatments in term of soil properties only, with fixed albedo. The “Soil+Albedo

scenario" implemented the observed differences in both soil properties and albedo. Developing a complete radiative and land-surface modelling was beyond the scope of the study, so we evaluated the impact of surface properties by interpreting the difference between observed and modelled thaw depth. Preliminary results showed that thaw depth was unsensitive to variation in snow depth or depth hoar formation during the five year of the modelling experiment, max snow depth ranging from 0.10 to 0.36 m. We thus used the observed snow depth with similar snow properties for all scenario and treatments. Complete model specification is available in Appendix C and Chen *et al*. (2021).

Results

Fertilization increased vascular plant biomass, but grazing had no effect (Table 2, Fig. S1), whereas neither fertilization nor grazing impacted bryophyte biomass (Table 2, Fig. S2). Vascular plant biomass of High N+P plots was 318% higher than biomass of Control plots [mean effect (95% confidence interval, ci): 69.8 (45.0;94.6) $g \cdot m^{-2}$].

S*urface properties*

Fertilization increased green Leaf Area Index (LAI), but grazing had no effect (Fig. 1b, Table 2), whereas grazing reduced dead vascular plant biomass with little effect of fertilization (Fig.1c, Table 2). LAI of High N+P plots was 345% higher than LAI of Control plots [mean effect (95% ci): 0.54 (0.34;0.73) $m^2 \cdot m^{-2}$]. Grazed subplots had a dead vascular plant biomass 60.0% lower than ungrazed subplots [mean effect (95% ci): -15.6 (-7.69;-23.4) $g \cdot m^{-2}$].

Fertilization increased surface albedo whereas grazing decreased it (Fig. 1a, Table 3). For example, albedo of High N+P plots was higher by 79% [mean effect (95% ci): 0.05 (0.03;0.08)] than albedo of Control plots. Grazed subplots had a 25% lower albedo [mean effect (95% ci): 0.03 (0.02;0.03)] than ungrazed ones. Grazing effect was slightly reduced in more fertilized plots. For example, grazed Control had a 32% lower albedo than the respective ungrazed subplots [mean effect (95% ci): -0.03 (-0.02;-0.04)] whereas ungrazed High N+P had a 10.8% lower albedo than High N+P ungrazed subplots [mean effect (95% ci): -0.02 (-0.03;0.01)].

Table 2: Results of the linear mixed models and generalized additive mixed models fitted to estimate the impact of fertilization (F) and goose grazing (G) on Leaf Area Index (LAI); dead vascular plant biomass;

bryophyte biomass; soil Loss-on-Ignition, dry bulk density and porosity; distance between soil surface and water table and soil thermal conductivity in wetlands of Bylot Island, Nunavut, Canada.

	Fertilization			Grazing			Block			FxG		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Vascular biomass	4,23	30.2	<0.001	1,23	0.273	0.606	3,23	7.12	0.002	4,23	1.25	0.317
Bryophyte biomass	4,10	1.15	0.388	1,13	0.03	0.858	3,10	8.35	0.005	4,13	2.82	0.069
Leaf Area Index	4,10	12.7	0.001	1,13	0.01	0.912	3,10	1.47	0.230	4,13	1.7	0.268
Dead vascular biomass	4,12	3.17	0.054	1,15	29,0	<0.001	3,12	2.63	0.098	4,15	0.97	0.455
Soil Loss-On-Ignition	4,145	10.2	<0.001	1,145	1.05	0.307	3,145	70.4	<0.001	4,145	2.49	0.046
Soil dry density	4,139	6.66	<0.001	1,139	1.62	0.206	3,139	24.8	<0.001	4,139	1.82	0.128
Soil Porosity	4,137	5.16	0.001	1,137	1.41	0.238	3,137	18.2	<0.001	4,137	1.5	0.218
Distance to water table	4,27	10.7	<0.001	1,27	11.9	0.002	3,27	7.84	0.001	4,27	0.40	0.810
Soil thermal conductivity	4,24	2.88	0.044	1,24	11.7	0.002	3,24	1.42	0.262	4,24	1.00	0.432

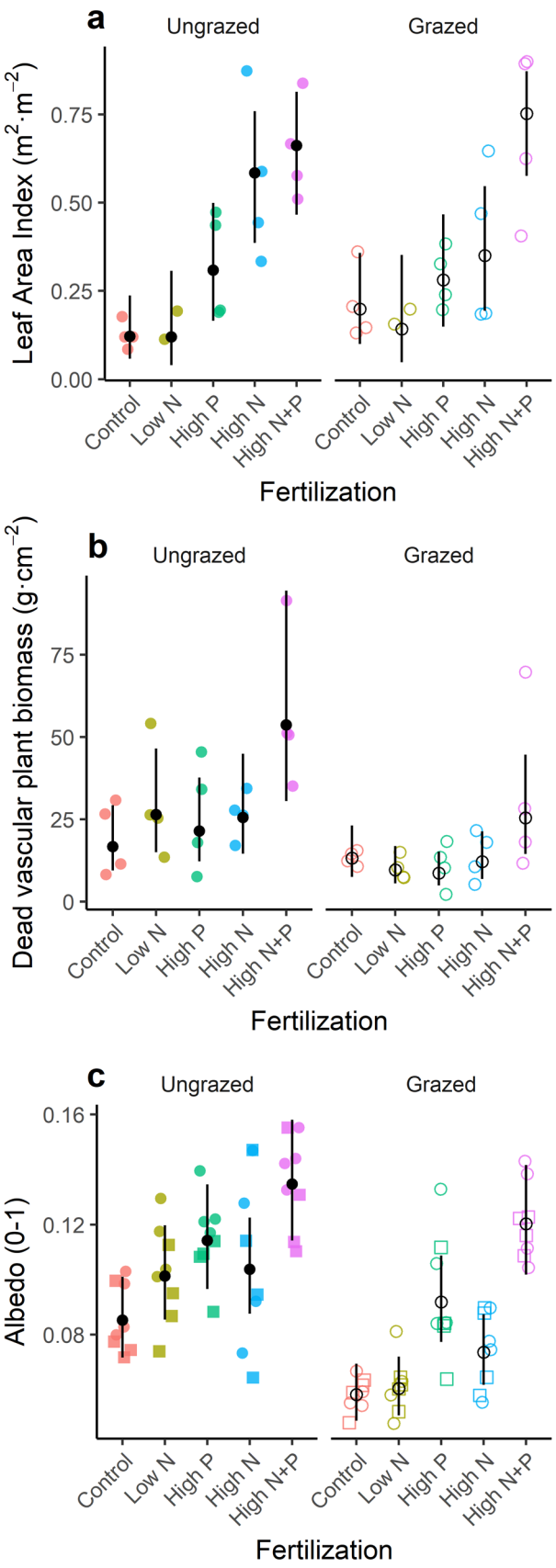

Figure 1: Effect of fertilization treatments and goose grazing on a) albedo, b) green leaf area index (LAI) and c) dead vascular plant biomass in wetlands of Bylot Island, Nunavut, Canada. Colored points are measured values. Plain and open symbols represent ungrazed and grazed treatments, respectively. Colored circles and squares represent measurements made in 2018 and 2019, respectively. Black points represent each treatment marginal mean, and the line the 95% confidence interval.

Table 3: Results of the linear mixed models fitted to estimate the impact of fertilization and grazing on albedo; topsoil volumetric water content (0-5cm depth, SWC) and thaw depth in wetlands of Bylot Island, Nunavut, Canada.

	Albedo			**SWC**			**Thaw depth**		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Fertilization	4,12	10.7	0.001	4,11	4.91	0.015	4,12	1.87	0.180
Grazing	1,14	79.4	<0.001	1,15	22.9	0.001	1,15	9.70	0.007
FxG	4,14	3.65	0.029	4,15	2.06	0.138	4,15	0.65	0.633
Block	3,12	0.81	0.510	3,11	0.93	0.456	3,12	1.12	0.380
Year	1,12	12.8	0.004	2,24	15.2	<0.001	2,23	35.8	<0.001
YxB	3,12	0.87	0.482	6,24	2.09	0.092	6,23	1.47	0.233
YxF	4,12	0.90	0.496	8,24	0.61	0.765	8,23	0.75	0.648
YxG	1,15	2.87	0.111	2,30	1.72	0.197	2,29	0.66	0.524
YxFxG	4,15	0.31	0.865	8,30	0.49	0.852	8,29	0.47	0.868

Soil organic matter accumulation and properties

By adding new barely decomposed organic horizons at the top of the soil column (Fig. S3, S4), fertilization increased the distance between the surface and the water table, whereas grazing decreased it (Fig. 2, Table 2). For example, the land surface was 486% further from the water table in High N+P plots than in Control plots [mean effect (95% ci): 7.16 (3.99;10.3) cm]. On average, the surface of grazed subplots was 50% closer to the water table than the surface of ungrazed ones [mean effect (95% ci): -2.62 (-1.05;-4.2) cm].

Fertilization favored dry topsoil conditions (Fig. 3a, Table 3, topsoil referring approximately to the shallowest 5 cm of the soil column), creating soil characterized by low dry bulk density, high LOI and high porosity (Table 3, Fig. S4-6) whereas grazing maintained the soil wetter (Fig. 3a, Table 3). For example, SWC was 37% lower in the High N+P plots than in the Control [mean effect (95% ci): -0.31 (-0.52;-0.1) $m^3 \cdot m^{-3}$], whereas it was 20% higher in grazed subplots than in ungrazed ones [mean effect (95% ci): 0.1 (0.07;0.19) $m^3 \cdot m^{-3}$].

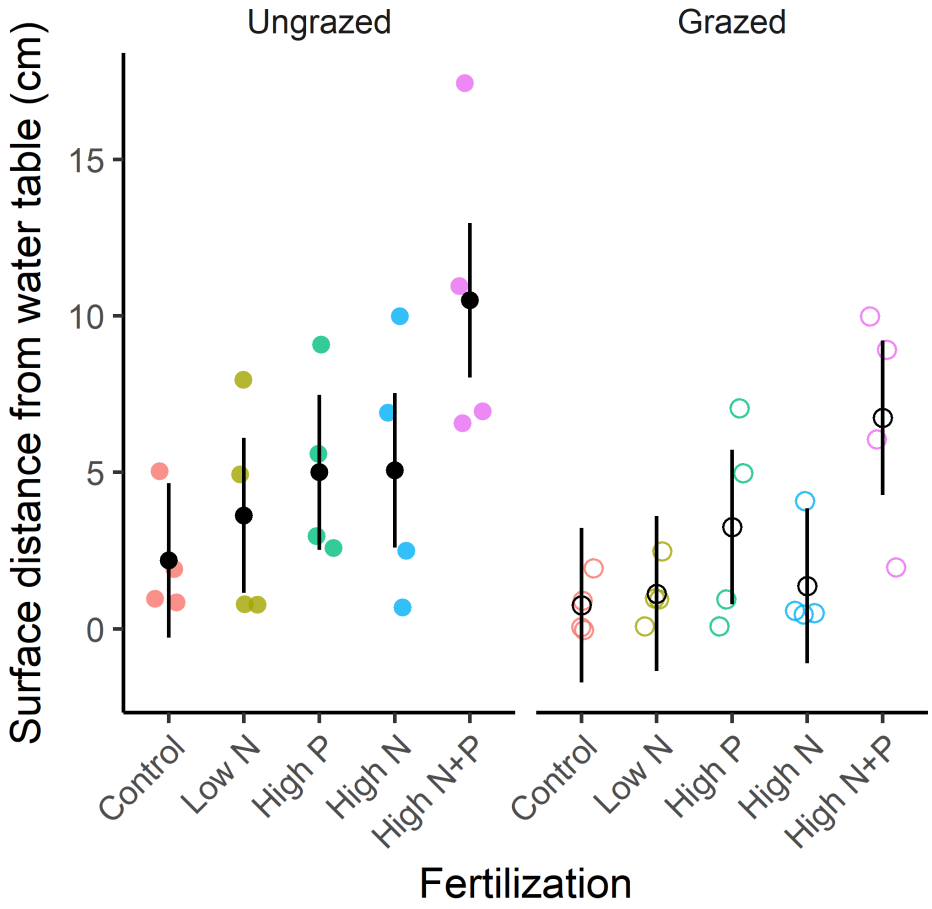

Figure 2: Effect of fertilization and grazing treatments on distance between soil surface and the water table in wetlands of Bylot Island, Nunavut, Canada. Colored points are measured values. Plain and open symbols represent ungrazed and grazed treatments, respectively. Black points represent each treatment marginal mean, and the line the 95% confidence interval.

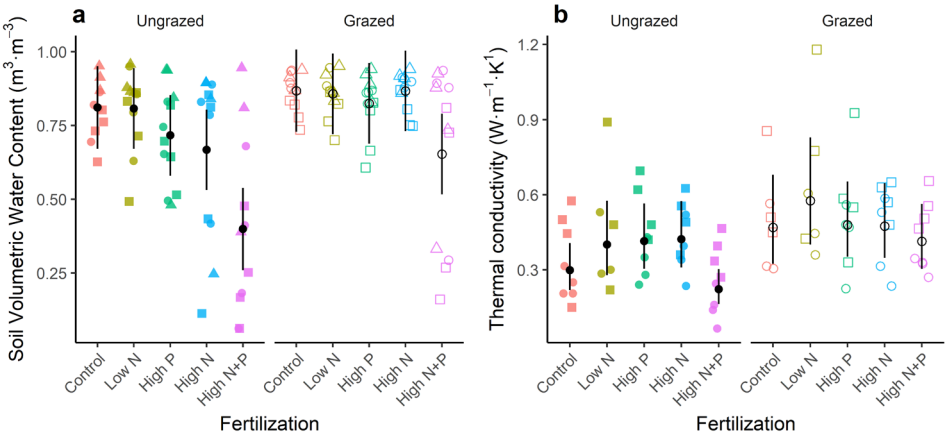

Figure 3: Effect of fertilization and grazing treatments on a) topsoil volumetric water content and b) soil thermal conductivity in wetlands of Bylot Island, Nunavut, Canada. Colored points are measured values. In panel a), colored triangles, circles and squares represent measurements made in 2017, 2018 and 2019,

respectively. In panel b), colored circles and squares represent measurements made at 5 and 10 cm depth, respectively. Black points represent each treatment marginal mean, and the line the 95% confidence interval.

Grazing increased thermal conductivity (Table 2, Fig. 3b), whereas the fertilization effect was weak and too uncertain to be interpreted [e.g., High N+P – Control = -0.05 (-0.22;0.11) $W \cdot m^{-1} \cdot K^{-1}$, mean (95% ci)]. Grazed subplots had a thermal conductivity 38% higher than ungrazed ones [mean effect (95% ci): 0.131 (0.03;0.22) $W \cdot m^{-1} \cdot K^{-1}$]. Thermal conductivity increased with depth (*p-value* < 0.001, Fig. S7). The higher thermal conductivity in grazed treatment was caused by the higher SWC in these subplots. Adding SWC as a covariate in the linear mixed model predicting thermal conductivity canceled the effect of grazing (Fertilization: *p-value* = 0.510; Grazing: *p-value* = 0.730, Fig. S8). Computed frozen thermal conductivity showed a similar pattern, with soil of High N+P being less conductive than soil of Control plots and the soil of grazed subplots being more conductive than the soil of ungrazed subplots (Appendix C, table C6).

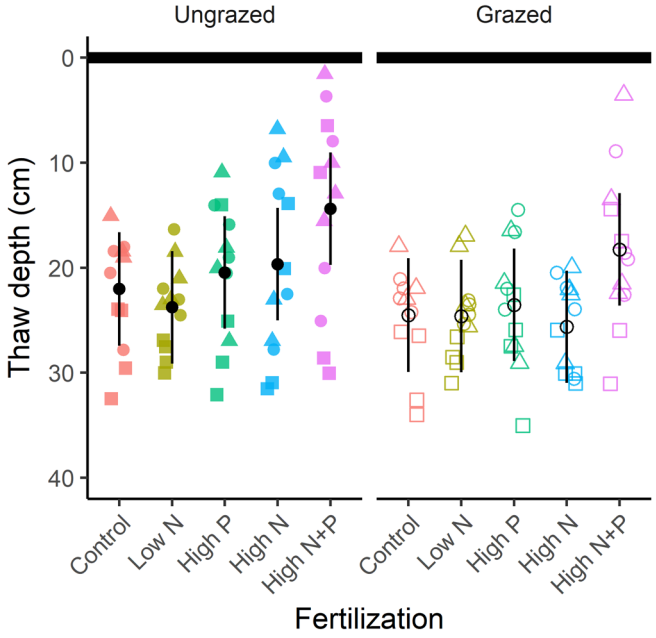

Figure 4: Effect of fertilization and grazing treatments on thaw depth. Colored points are measured values in wetlands of Bylot Island, Nunavut, Canada. Black horizontal line represents soil surface. Plain and open symbols represent ungrazed and grazed treatments, respectively. Colored triangles, circles and squares

represent measurements made in 2017, 2018 and 2019, respectively. Black points represent each treatment marginal mean, and the line the 95% confidence interval. Note the inverted y-axis, zero representing soil surface.

Thaw depth

Grazing increased thaw depth, with strong variations of average thaw depth among years (Tab. 3, Fig. 4). Grazed subplots had a 16% lower thaw depth than ungrazed ones [mean effect (95% ci): 3.25 (1.10;5.40) cm].

Modelling of thaw depth dynamics supported the effect of grazing on thaw depth (Fig. 5), mainly driven by an increase of topsoil thermal conductivity ("Soil" scenario in Fig. 5a). Increasing albedo from 0.06 (grazed Control) to 0.14 (ungrazed High N+P) had a negligible effect on thaw depth ("Soil + Albedo" scenario in Fig. 5a). Modelling results suggested an interaction between fertilization and grazing, grazing effect being greater in the High N+P treatment than in the Control (Fig. 5a, b). Maximum difference among treatments arose at the end of the thawing season (beginning of September), suggesting that empirical results based on measured July thaw depth are conservative (Fig. 5b).

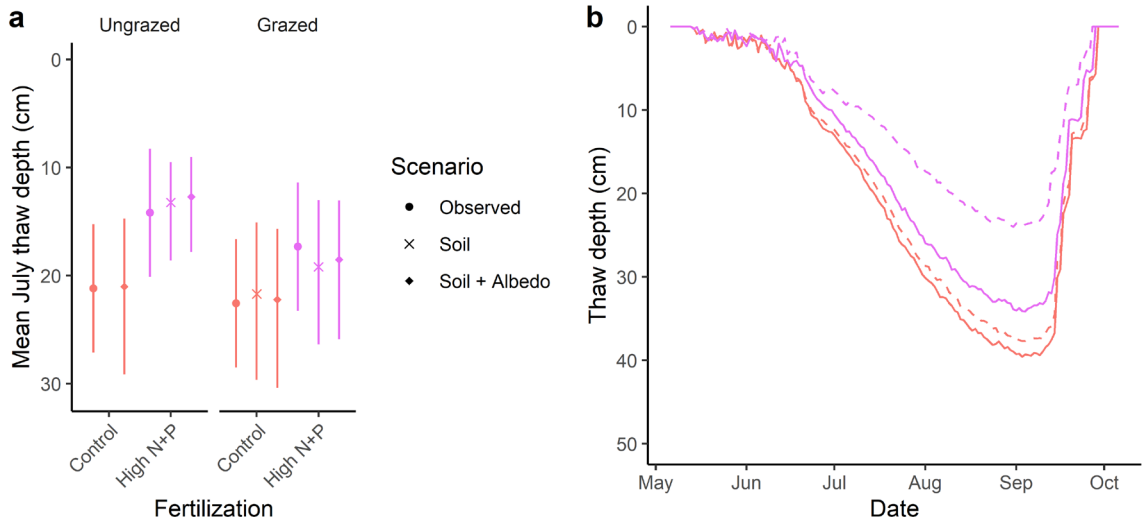

Figure 5: Modelled effect of fertilization and grazing on thaw depth. a) observed and modeled mean July thaw depth in 2018, and b) modelled dynamic of thaw depth along the thawing season in the "Soil + Albedo" scenario, averaged over all the modelling years. Only differences in soil properties among treatments were

implemented in the "Soil scenario", whereas the "Soil + Albedo" scenario implemented both differences in soil properties and albedo. "Soil" scenario is absent from the ungrazed Control, as it represents the reference from which parameters are modified. Red and purple colors represent Control and High N+P treatments, respectively. Plain and dashed lines represent grazed and ungrazed situations, respectively. Note the reversed *y-axis*.

Discussion

Our results reveal that both N and P availability and grazing impact active layer and permafrost dynamics in High Arctic polygonal wetlands. Fertilization increased live vascular plant cover and albedo, decreasing the radiative energy entering the plant-soil system. Therefore, enhanced herbaceous tundra growth following higher nutrient availability may attenuate the increase of surface temperature due to global warming. Fertilization also increased SOM accumulation at the top of the soil column, changing soil physical structure and composition and increasing permafrost aggradation rate. This suggests that increased topsoil nutrient availability speeds up upward permafrost development rate. Goose grazing reduced albedo and dead vascular plant biomass, increasing the energy entering the plant-soil system. In addition, grazing reduced SOM accumulation and soil thermal conductivity, deepening the active layer. These last results point toward a novel and important perspective, which suggests that grazers may limit syngenetic permafrost development.

The decrease in thaw depth and SWC accelerated the transition from *Cyperaceae* to grasses following increased topsoil nutrient availability whereas grazing slowed down such changes and maintained species preferred by geese. Increased topsoil nutrient availability may limit the availability of nutrient at depth by limiting thaw depth. Therefore, reduction of thaw depth may cause a negative feedback disadvantaging the growth of deep-rooting plants, such as plants from the *Cyperaceae* family (Wang *et al.*, 2017). Favored *Poaceae*

489 growth (Wang *et al.,* 2017), soil drying, and shallower thaw depth may all concur to the
490 competitive exclusion of sedges (*Carex aquatilis*) and cotton grasses (*Eriophorum spp.*) in
491 case of increased subsurface nutrient availability (as shown by Gignac *et al.*, 2022 and
492 Nishizawa *et al.*, 2021 in the present experiment). Conversely, goose grazing increases
493 topsoil water content and deepens thaw depth. Thus, grazing indirectly favor the growth of
494 plants preferred by geese, such as *Eriophorum scheuzeri* (as shown by Nishizawa *et al.*,
495 2021 in the present experiment). This suggests that geese can concur to maintain polygonal
496 wetlands in a state favorable for their feeding, despite marked increase in nutrient
497 availability.

498 *Surface properties*

499 As expected in H1, fertilization increased live LAI due to an increase in primary production
500 (the impact of fertilization on live biomass is discussed in Gignac *et al.*, 2022), whereas
501 grazing diminished dead biomass, probably decreasing and increasing the quantity of
502 shortwave radiations reaching the soil surface, respectively. Similar to our results, Prager
503 *et al.* (2017) found that fertilization increased LAI in a moist acidic tundra. Grazing did not
504 impact vascular plant biomass nor LAI. Because grazed subplots were protected during the
505 sampling year, we measured undisturbed growth from the below-ground parts. Therefore,
506 vascular plant communities seem to be resilient to long-term grazing, which is coherent
507 with the demonstrated regrowth ability of dominant grasses (Mattheis & Tieszen 1976, Bakker
508 & Loonen 1998) and sedges (Archer & Tieszen 1983, Raillard & Svodoba 1999) in Arctic wetlands
509 (Beaulieu *et al.*, 1996).

510 A sensitivity analysis considering multiple parameters of tundra surface energy budget
511 (Beringer *et al.*, 2002) showed LAI having a non-linear impact on ground heat flux, with

512 greatest reduction when LAI was around one. Measured live LAI was lower than one, but
513 total cover including dead biomass should reach this threshold. Similarly, Juszak *et al.*
514 (2016, 2017) described sedge dominated tundra with a total LAI of 1.4, dead vascular
515 leaves representing half of the total leaf area. Therefore, both live and dead leaf area index
516 influence tundra radiation budget. Overall, our results suggest that nutrient availability may
517 decrease and grazing increase transmission of radiation to the ground in herbaceous tundra.

518 As expected in H1, fertilization increased surface albedo, whereas grazing decreased it.
519 Higher albedo resulted from greater LAI (Juszak *et al.*, 2014) and light-colored litter cover
520 (Juszak *et al.*, 2017), but also possibly from the lower moss water content in the more
521 fertilized plots (Kim & Verma, 1996). The switch from dark mosses (*Drepanocladus spp.*
522 being dominant in Control plots) to light green mosses (*Aulacomnium spp.* being dominant
523 in N+P plots, Gignac *et al.*, 2022) may also have contributed to increase albedo.
524 Conversely, grazing reduced albedo mostly by increasing topsoil water content and
525 reducing light-colored dead vascular plant biomass accumulation. Our results clearly show
526 N and P availability and grazing respectively increase and decrease summer albedo in a
527 High Arctic system even without deciduous shrubs, which had not yet invaded our
528 experimental plots after 16 years. However, surface albedo may not be the most
529 determinant parameter for ground heat flux and active layer thaw, as higher transmission
530 of shortwave radiations through the canopy to the ground may counteract an increase in
531 albedo (Blok *et al.*, 2010). Modelling experiment suggested a negligible effect of albedo
532 on thaw depth.

533 Even if our results suggested diminished shortwave radiation input to the ground in
534 response to fertilization, the consequences for net radiation budget and ground heat flux

are hard to estimate. Cooler vegetation and soil surface may emit less longwave radiations than warmer vegetation and soil, leading to similar budget even with differences in net shortwave input (Juszak *et al.*, 2016).

The observed change in vegetation and SWC may have impacted heat flux partitioning. Eugster *et al.* (2005) reported that tundra with lower LAI has a smoother surface (lower roughness length) than tundra with higher LAI, but it did not impact latent and sensible heat fluxes. Increased LAI may increase latent heat flux (McFadden *et al.*, 1998), but surface drying following fertilization and protection from grazing likely resulted in lower evaporation (Liljedhal *et al.*, 2011). It is however uncertain whether a change in surface resistance at this scale would impact the soil heat flux, or if latent and sensible heat fluxes would change at the expense of one another (McFadden *et al.*, 1998).

Organic matter accumulation

As expected in H2, fertilization increased SOM accumulation at the top of the soil column, whereas grazing decreased it. SOM accumulation followed a substantial increase in vascular plant primary productivity in fertilized treatments, especially when N and P were added together (Gignac *et al.*, 2022). Topsoil SOM accumulation after long-term fertilization has been measured by Mack et al. (2004) in a moist acidic Arctic tundra, but the effect is not general (see *e.g.,* Koyama *et al.,* 2013 and Ylänne *et al.* 2020). The impact of goose grazing and grubbing on soil OM is not clear either, with both negative (*e.g.,* Sjögersten *et al.,* 2012; van der Wal et al., 2007) and null effects (*e.g.,* Speed et al., 2010) being reported in similar systems.

Because fertilization increased surface aggradation without impacting thaw depth, it implies permafrost table shall have migrated upward at a greater rate in fertilized plots than in control ones. Considering the historical aggradation rate of 0.7 mm·year^{-1} measured at our study site (Fortier *et al.*, 2006), the surface of Control plots should have risen by approximately 11 mm in 16 years. Assuming that the water table is homogeneous in a polygon, we consider that a higher distance between the soil surface and the water table implies higher surface aggradation. Therefore, the surface of High N+P plots had on average risen 72 mm above the surface of Control plots (Fig. S9). Fertilization had thus multiplied the aggradation rate by up to seven times relative to the historical rate (5 mm·year^{-1} in the High N+P plots). However, grazing slowed down surface aggradation, grazed subplots being on average 26 mm closer to the water table than ungrazed ones. Therefore, grazing limited the uplifting related to fertilization, surface of grazed High N+P plots having risen by approximately 57 mm only during the 16 years of the experiment (for an aggradation rate of 3.6 mm·year^{-1}). These results point toward an important role of grazers in limiting both polygon development and permafrost carbon storage in productive polygonal tundra, especially in presence of increased nutrient availability.

Soil thermal properties

SOM accumulation and disconnection from the water table decreased topsoil thermal conductivity. SWC is known to be an important factor controlling thermal conductivity in Arctic soils (Hinzman *et al.*, 1991), a wetter organic soil often leading to higher ground heat flux and deeper thaw depth (see *e.g.,* Liljedahl *et al.*, 2011, Juszak *et al.*, 2016). However, Eugster *et al.* (2005) noted a covariation between heat capacity and thermal conductivity in moist acidic and non-acidic Arctic tundra, high soil temperature being

associated with low soil heat flux. Similarly, McFadden *et al.* (1998) noted that the energy stored in soil water was released at night, countering higher midday soil thermal conductivity in wet Arctic tundra.

Our results suggested SOM content and porosity alone had little impact on thermal conductivity. SOM content has been recognized as an important driver of thermal diffusivity and active layer thickness across the Arctic (Zhu *et al.*, 2019). Because the present experiment took place at the top of an accumulation of approximately three meters of a mix of peat and loess (Fortier *et al.* 2006) with already high OM content and high porosity (0.20 $g \cdot g^{-1}$ and 0.8 $cm^3 \cdot cm^{-3}$ on average at the bottom of the sampled soil column), fertilization caused little contrast.

Transportation may have partly dried samples prior to measurements, causing a decrease in thermal conductivity. Yet, since we would expect the decrease in SWC and thermal conductivity to be greater in wet samples than in already dry soils, the differences in thermal conductivity may have been reduced by transport, implying that our results are conservative. Because thermal conductivity computation based on soil LOI and field SWC measurements led to qualitatively similar conclusions, and because the modeling experiment reproduced observed thaw depth well, we consider our conclusion to be robust to sample disturbance.

Thaw depth

As hypothesized in H3, grazing increased thaw depth, but contrary to our expectation, fertilization did not impact it. The effect of grazing on thaw depth has been little explored in the literature. Grazing by Muskox has been shown to both decrease (Falk *et al.*, 2015)

and increase (Mosbacher *et al.*, 2019) thaw depth in Northeastern Greenland, depending upon the year of measurement. The conservative 3.3 cm average difference we observed between grazed and ungrazed subplots is comparable to what has been measured in several fertilization (6 cm on average in Gough *et al.*, 2016; 4 cm on average in Wang *et al.*, 2017) and surface warming experiments (3 cm on average in Natali *et al.*, 2011; higher thaw rate in Leffler *et al.*, 2016; not supported statistically in Hollister *et al.*, 2006 and Voigt *et al.*, 2017). Grazing thus restricted permafrost development by limiting surface aggradation and deepening the active layer. Considering the 3.3 cm increase in active layer depth, grazing reduced permafrost aggradation rate to 1.5 $mm \cdot year^{-1}$ in grazed High N+P subplots compared to 5 $mm \cdot year^{-1}$ without grazing.

Modelling results suggested the decrease of thermal conductivity following fertilization made thaw depth shallower, whereas grazing deepened thaw depth by increasing topsoil thermal conductivity. Thaw depth showed little sensitivity to a decrease of incoming radiation following a more reflective vegetation (similar to Juszak *et al.*, 2016). Previous studies showed that topsoil water content tends to increase thaw depth, especially if deep water and ice content remains constant (Kwon *et al.*, 2016; Clayton *et al.*, 2021). Fertilization effect on thaw depth and the interaction between fertilization and grazing was not supported by our statistical analysis. This may be because of low statistical power, and because plot positioning in the polygon was masking the effect of fertilization, thaw depth being lower in plots close to rims and higher in plots in the vicinity of a water body. Fertilization effects inferred from modelling results were robust to such spatial noise because they represent the addition of a dry organic layer at the top of the soil column, maintain deep soil water and ice content constant and assume no lateral energy transfer.

Habitat type deserves consideration when prospecting the effect of increased nutrients availability and varying herbivore population on Arctic ecosystems. We are not aware of studies measuring thaw depth in response to these factors in mesic uplands (e.g. tundra heath and shrub tundra), such as the ones surrounding the studied wetland area. This lack in literature may be related with the physical difficulty encountered with thaw depth measurements in rocky soils (Gough *et al.*, 2016). In such mesic uplands, vascular plant biomass also increases following fertilization (*e.g.,* Grellman, 2002; van Wijk *et al.*, 2004). However, it is uncertain if greater primary productivity would lead to aggradation and drying of the surface (Ola *et al.*, 2022). Uplands are often well drained and characterized by epigenetic permafrost, in which case permafrost does not form by the aggradation of the base of the active layer (French, 2017). Finally, uplands are less intensively grazed by geese compared with wetlands (Hughes *et al.*, 2014), with a presumably lower impact of grazing on permafrost dynamic.

Conclusion

We showed in this study that increase of tundra nutrient availability and grazing can create feedback to the active layer dynamic of High Arctic herbaceous tundra. Fertilization caused OM accumulation at the surface, increasing permafrost aggradation rate, suggesting that the growth of vegetation resulting from higher nutrient mineralization may hinder the degradation of permafrost caused by global warming in herbaceous polygonal tundra. Grazing reduced surface aggradation and deepened the active layer, primarily because of increased topsoil water content. Grazers seem therefore to be a major determinant of the future of permafrost in herbaceous polygonal wetlands, especially while nutrient availability increases in this system. Therefore, population management and resource

availability in the south, which can cause strong increase in herbivorous populations migrating to the Arctic in summer (Lefebvre *et al.*, 2017), may indirectly slow down permafrost development in the North. However, the net effect of grazing on polygonal wetlands carbon budget remains unclear, as water saturation of the shallowest soil horizons may limit decomposition (Boye *et al.*, 2017) and concurs to SOM accumulation in Arctic peatlands (Grosse *et al.*, 2011). Overall, our results point toward the importance of understanding impact of biotic drivers when examining potential consequences of climate change on the permafrost of High-Arctic wetlands.

Supplementary materials

Appendix A: Details on the measurement of leaf area index.

Appendix B: Details on the measurement of soil physical and thermal properties.

Appendix C: Detail of the set-up of the modeling experiment.

Fig. S1: Impact of fertilization and grazing on vascular plant biomass.

Fig. S2: Impact of fertilization and grazing on bryophytes biomass.

Fig S3: Pictures of the soil columns of contrasted treatments.

Fig. S4: Impact of fertilization and grazing on soil Loss-On-Ignition.

Fig. S5: Impact of fertilization and grazing on soil dry density.

Fig. S6: Impact of fertilization and grazing on soil porosity.

Fig. S7: Impact of fertilization, grazing and depth on soil thermal conductivity.

Fig. S8: Marginal impact of soil volumetric water content, fertilization and grazing on soil thermal conductivity.

Fig S9: Pictures of plots showing organic accumulation at the surface.

Acknowledgement

We are grateful to the many people who permit the access to the Sirmilik National Park and the long-term ecological monitoring on Bylot Island, including the Mittimatalik community and Parks Canada's staff, with a special thanks to Maryse Mahy. We thank Riika Rinnan and two anonymous reviewers for having contributed to improve the quality

and clarity of the paper. This study was supported by the Fonds de Recherche du Québec-Nature et technologies (FRQNT-2018-PR- 208107), the Natural Sciences and Engineering Research Council of Canada (Discovery program), the Network of Centers of Excellence of Canada Arctic Net Northern Scientific Training Program (Polar Knowledge), Université Laval and Université du Québec à Trois-Rivières with the UQTR Chair in Functional Arctic Ecology (2019-2022), the RIVE research center and GRBV research group. Logistical support for fieldwork was provided and organized by the Polar Continental Shelf Program (Natural Resources Canada) and the Centre d'Études Nordiques (CEN) with a special thanks to M.-C. Cadieux and C. Boismenu.

Conflicts of interest

The authors have no conflicts of interest.

Author contributions

Lucas Deschamps conceptualized the study; realized field, soil and vascular plant measurements; compiled data; designed and realized statistical analysis; designed modeling experiment; wrote the manuscript.

Vincent Maire conceptualized and funded the study; organized and realized field sampling; revised the manuscript at all stages.

Lin Chen designed and realized modeling experiments; revised the final version of the manuscript.

Daniel Fortier conceptualized the study; revised modeling parameters; revised the final version of the manuscript.

Gilles Gauthier initiated and maintained the experiment; funded the study; revised the manuscript at multiple stages.

Amélie Morneault realized field and bryophyte measurements; revised the final version of the manuscript.

Elizabeth Hardy-Lachance realized field measurements; revised the final version of the manuscript.

Isabelle Dalcher-Gosselin realized field measurements; revised the final version of the manuscript.

François Tanguay realized field measurements; revised the final version of the manuscript.

Charles Gignac realized field and dead biomass measurements; revised the final version of the manuscript.

Jeffrey McKenzie conceptualized numerical code with Lin Chen; revised the final version of the manuscript.

Line Rochefort initiated the experiment; funded the study; revised the final version of the manuscript.

Esther Lévesque maintained the experiment; conceptualized and funded the study; organized field sampling; revised the manuscript at all stages.

Data availability

Data and codes will be available as a Figshare repository at the publication of the manuscript.

References

Amrhein, V., Greenland, S., & McShane, B. (2019). Scientists rise up against statistical significance. *Nature*, *567*, 305–307. https://doi.org/10.1038/d41586-019-00857-9

Archer, S., & Tieszen, L. L. (1983). Effects of simulated grazing on foliage and root production and biomass allocation in an arctic tundra sedge (*Eriophorum vaginatum*). *Oecologia*, *58*, 92–102. https://doi.org/10.1007/BF00384547

Bakker, C., & Loonen, M. J. J. E. (1998). The Influence of Goose Grazing on the Growth of *Poa arctica* : Overestimation of Overcompensation. *Oikos*, *82*(3), 459–466. https://doi.org/10.2307/3546367

Balland, V., & Arp, P. A. (2005). Modeling soil thermal conductivities over a wide range of conditions. *Journal of Environmental Engineering and Science*, *4*(6), 549–558. https://doi.org/10.1139/s05-007

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1-48. https://doi.org/10.18637/jss.v067.i01

Beringer, J., McIlwaine, S., Lynch, A., Chapin, F., & Bonan, G. (2002). The use of a reduced form model to assess the sensitivity of a land surface model to biotic surface parameters. *Climate Dynamics*, *19*(5–6), 455–466. https://doi.org/10.1007/s00382-002-0237-9

Bernes, C., Bråthen, K. A., Forbes, B. C., Speed, J. D. M., & Moen, J. (2015). What are the impacts of reindeer/caribou (*Rangifer tarandus* L.) on arctic and alpine vegetation? A systematic review. *Environmental Evidence*, *4*(1), 1–26. https://doi.org/10.1186/s13750-014-0030-3

Beaulieu, J., Gauthier, G., & Rochefort, L. (1996). The growth response of graminoid plants to goose grazing in a High Arctic environment. Journal of Ecology, 905-914. https://doi.org/10.2307/2960561

Bhatti, J. S., & Bauer, I. E. (2002). Comparing loss-on-ignition with dry combustion as a method for determining carbon content in upland and lowland forest ecosystems. *Communications in Soil Science and Plant Analysis*, *33*(15–18), 3419–3430. https://doi.org/10.1081/CSS-120014535

Bliss, L. C., & Matveyeva, N. V. (1992). Circumpolar arctic vegetation. In F. S. Chapin III, R. L. Jefferies, J. F. Reynolds, G. R. Shaver, J. Svoboda, & E. W. Chu (Eds.), *Arctic ecosystems in a changing climate: an ecophysiological perspective* (Vol. 59, p. 89). Academic Press San Diego.

Blok, D., Heijmans, M. M. P. D., Schaepman-Strub, G., Kononov, A. V., Maximov, T. C., & Berendse, F. (2010). Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Global Change Biology*, *16*(4), 1296–1305. https://doi.org/10.1111/j.1365-2486.2009.02110.x

Boye, K., Noël, V., Tfaily, M. M., Bone, S. E., Williams, K. H., Bargar, J. R., & Fendorf, S. (2017). Thermodynamically controlled preservation of organic carbon in floodplains. *Nature Geoscience*, *10* (6), 415–419. https://doi.org/10.1038/ngeo2940

Chen, L., Voss, C. I., Fortier D., & McKenzie, J. M. (2021). Surface energy balance of sub-Arctic roads and highways in permafrost regions. *Permafrost and Periglacial Processes*, 32(4): 681-701. https://doi.org/10.1002/ppp.2129.

Clayton, L. K., Schaefer, K., Battaglia, M. J., Bourgeau-Chavez, L., Chen, J., Chen, R. H., ... & Zhao, Y. (2021). Active layer thickness as a function of soil water content. *Environmental Research Letters*, *16*(5), 055028.

Eugster, W., McFadden, J. P., & Stuart Chapin, F. (2005). Differences in Surface Roughness, Energy, and CO_2 Fluxes in Two Moist Tundra Vegetation Types, Kuparuk Watershed, Alaska, U.S.A. *Arctic, Antarctic, and Alpine Research*, *37*(1), 61–67. https://doi.org/10.1657/1523-0430(2005)037[0061:DISREA]2.0.CO;2

Falk, J. M., Schmidt, N. M., Christensen, T. R., & Ström, L. (2015). Large herbivore grazing affects the vegetation structure and greenhouse gas balance in a high arctic mire. *Environmental Research Letters*, *10*(4). https://doi.org/10.1088/1748-9326/10/4/045001

Fortier, D., Allard, M., & Pivot, F. (2006). A late-Holocene record of loess deposition in ice-wedge polygons reflecting wind activity and ground moisture conditions, Bylot Island, eastern Canadian Arctic. *Holocene*, *16* (5), 635–646. https://doi.org/10.1191/0959683606hl960rp

French, H. M. (2017). The Periglacial Environment. John Wiley & Sons: Hoboken, NJ, USA. https://doi.org/10.1002/9781119132820

Gauthier, G., Hughes, R. J., Reed, A., Beaulieu, J., & Rochefort, L. (1995). Effect of Grazing by Greater Snow Geese on the Production of Graminoids at an Arctic Site. *Journal of Ecology*, *83*(4), 653–664. https://doi.org/10.2307/2261633

Gauthier, G., Giroux J. F. & Rochefort., L. (2006). The impact of goose grazing on arctic and temperate wetlands. *Acta Zoologica Sinica*, 52(supplement):108-111.

Gignac, C., Rochefort, L., Gauthier, G., Lévesque, E., Maire, V., Deschamps, L., Pouliot, R., & Marchand-Roy, M. (2022). N/P Addition Is More Likely Than N Addition Alone to Promote a Transition from Moss-Dominated to Graminoid-Dominated

Tundra in the High-Arctic. *Atmosphere*, *13*(5), 676. https://doi.org/10.3390/atmos13050676

Gornall, J. L., Jónsdóttir, I. S., Woodin, S. J., & Van der Wal, R. (2007). Arctic mosses govern below-ground environment and ecosystem processes. *Oecologia*, *153*(4), 931–941. https://doi.org/10.1007/s00442-007-0785-0

Gornall, J. L., Woodin, S. J., Jónsdóttir, I. S., & van der Wal, R. (2009). Herbivore impacts to the moss layer determine tundra ecosystem response to grazing and warming. *Oecologia*, *161*(4), 747–758. https://doi.org/10.1007/s00442-009-1427-5

Gough, L., & Hobbie, S. E. (2003). Responses of Moist Non-Acidic Arctic Tundra to Altered Environment : Productivity , Biomass , and Species Richness. *Oikos*, *103*(1), 204–216. https://doi.org/10.1034/j.1600-0706.2003.12363.x

Gough, L., Bettez, N. D., Slavik, K. A., Bowden, W. B., Giblin, A. E., Kling, G. W., … Shaver, G. R. (2016). Effects of long-term nutrient additions on Arctic tundra, stream, and lake ecosystems: beyond NPP. *Oecologia*, *182*(3), 653–665. https://doi.org/10.1007/s00442-016-3716-0

Grellmann, D. (2002). Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. *Oikos*, *98*(2), 190–204. https://doi.org/10.1034/j.1600-0706.2002.980202.x

Grosse, G., Harden, J., Turetsky, M., McGuire, A. D., Camill, P., Tarnocai, C., Frolking, S., Schuur, E. A. G., Jorgenson, T., Marchenko, S., Romanovsky, V., Wickland, K. P., French, N., Waldrop, M., Bourgeau-Chavez, L., & Striegl, R. G. (2011). Vulnerability of high-latitude soil organic carbon in North America to disturbance. *Journal of Geophysical Research: Biogeosciences*, *116* (3). https://doi.org/10.1029/2010JG001507

Gu, Q., & Grogan, P. (2020). Responses of low Arctic tundra plant species to experimental manipulations: Differences between abiotic and biotic factors and between short- and long-term effects. *Arctic, Antarctic, and Alpine Research*, *52* (1), 524–540. https://doi.org/10.1080/15230430.2020.1815360

Gumpertz, M. L., & Brownie, C. (1992). Repeated measures in randomized block and split-splot experiments. *Canadian Journal of Forest Research*, *23*, 625–639. https://doi.org/10.1139/x93-083

Hartley, A. E., Neill, C., Melillo, J. M., Crabtree, R., & Bowles, F. P. (1999). Plant Performance and Soil Nitrogen Mineralization in Response to Simulated Climate Change in Subarctic Dwarf Shrub Heath. *Oikos*, *86*(2), 331. https://doi.org/10.2307/3546450

Hinzman, L. D., Kane, D. L., Gieck, R. E., & Everett, K. R. (1991). Hydrologic and thermal properties of the active layer in the Alaskan Arctic. *Cold Regions Science and Technology*, *19*(2), 95–110. https://doi.org/10.1016/0165-232X(91)90001-W

Hodkinson, I. D., Webb, N. R., Bale, J. S., & Block, W. (1999). Hydrology, water availability and tundra ecosystem function in a changing climate: The need for a closer integration of ideas? *Global Change Biology*, *5*(3), 359–369. https://doi.org/10.1046/j.1365-2486.1999.00229.x

Hollister, R. D., Webber, P. J., Nelson, F. E., & Tweedie, C. E. (2006). Soil thaw and temperature response to air warming varies by plant community: Results from an open-top chamber experiment in northern Alaska. *Arctic, Antarctic, and Alpine Research*, *38*(2), 206–215. https://doi.org/10.1657/1523-0430(2006)38[206:STATRT]2.0.CO;2

Hughes, R. J., Reed, A., & Gauthier, G. (1994a). Space and Habitat Use by Greater Snow Goose Broods on Bylot Island , Northwest Territories. *The Journal of Wildlife Management*, *58*(3), 536–545. https://doi.org/10.2307/3809326

Hughes, R. J., Gauthier, G., &; Reed, A. (1994b). Summer habitat use and behaviour of Greater Snow Geese *Anser caerulescens*. *Wildfowl*, *45* 49–64.

Jorgenson, M. T., Romanovsky, V., Harden, J., Shur, Y., O'Donnell, J., Schuur, E. A. G., … & Marchenko, S. (2010). Resilience and vulnerability of permafrost to climate change. *Canadian Journal of Forest Research*, *40*(7), 1219–1236. https://doi.org/10.1139/X10-060

Juszak, I., Erb, A. M., Maximov, T. C., & Schaepman-Strub, G. (2014). Arctic shrub effects on NDVI, summer albedo and soil shading. *Remote Sensing of Environment*, *153*, 79–89. https://doi.org/10.1016/j.rse.2014.07.021

Juszak, I., Eugster, W., Heijmans, M. M. P. D., & Schaepman-Strub, G. (2016). Contrasting radiation and soil heat fluxes in Arctic shrub and wet sedge tundra. *Biogeosciences*, *13*(13), 4049–4064. https://doi.org/10.5194/bg-13-4049-2016

Juszak, I., Iturrate-Garcia, M., Gastellu-Etchegorry, J. P., Schaepman, M. E., Maximov, T. C., & Schaepman-Strub, G. (2017). Drivers of shortwave radiation fluxes in Arctic tundra across scales. *Remote Sensing of Environment*, *193*, 86–102. https://doi.org/10.1016/j.rse.2017.02.017

Kim, J., & Verma, S. B. (1996). Surface exchange of water vapour between an open sphagnum fen and the atmosphere. *Boundary-Layer Meteorology*, *79*(3), 243–264. https://doi.org/10.1007/bf00119440

Klingenfuß, C., Roßkopf, N., Walter, J., Heller, C., Zeitz, J. (2014). Soil organic matter to soil organic carbon ratios of peatland soil substrates. *Geoderma*, *235–236*, 410–417. https://doi.org/10.1016/j.geoderma.2014.07.010

Koven, C. D., Ringeval, B., Friedlingstein, P., Ciais, P., Cadule, P., Khvorostyanov, D., … Tarnocai, C. (2011). Permafrost carbon-climate feedbacks accelerate global warming. *Proceedings of the National Academy of Sciences*, *108*(36), 14769–14774. https://doi.org/10.1073/pnas.1103910108

Koven, C. D., Lawrence, D. M., & Riley, W. J. (2015). Permafrost carbon−climate feedback is sensitive to deep soil carbon decomposability but not deep soil nitrogen dynamics. *Proceedings of the National Academy of Sciences*, 112(12), 3752–3757. https://doi.org/10.1073/pnas.1415123112

Koyama, A., Wallenstein, M. D., Simpson, R. T., & Moore, J. C. (2013). Carbon-Degrading Enzyme Activities Stimulated by Increased Nutrient Availability in Arctic Tundra Soils. *PLoS ONE*, *8*(10).https://doi.org/10.1371/journal.pone.0077212

Kwon, M. J., Heimann, M., Kolle, O., Luus, K. A., Schuur, E. A., Zimov, N., ... & Göckede, M. (2016). Long-term drainage reduces CO_2 uptake and increases CO_2 emission on a Siberian floodplain due to shifts in vegetation community and soil thermal characteristics. *Biogeosciences*, 13(14), 4219-4235. https://doi.org/10.5194/bg-13-4219-2016

Kuznetsova A., Brockhoff P. B. and Christensen R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, 82(13), 1–26. https://doi.org/10.18637/jss.v082.i13

Lefebvre, J., Gauthier, G., Giroux, J. F., Reed, A., Reed, E. T., & Bélanger, L. (2017). The greater snow goose *Anser caerulescens atlanticus*: Managing an overabundant population. *Ambio*, 46(2), 262-274. https://doi.org/10.1007/s13280-016-0887-1

Leffler, A. J., Klein, E. S., Oberbauer, S. F., & Welker, J. M. (2016). Coupled long-term summer warming and deeper snow alters species composition and stimulates gross primary productivity in tussock tundra. *Oecologia*, *181*(1), 287–297. https://doi.org/10.1007/s00442-015-3543-8

Lenth, R. V. (2021). *emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.6.2-1.* Retrieved from https://cran.r-project.org/package=emmeans

Liljedahl, A. K., Hinzman, L. D., Harazono, Y., Zona, D., Tweedie, C. E., Hollister, R. D., … & Oechel, W. C. (2011). Nonlinear controls on evapotranspiration in Arctic coastal wetlands. *Biogeosciences*, *8*(11), 3375–3389. https://doi.org/10.5194/bg-8-3375-2011

Liu, N., Michelsen, A., & Rinnan, R. (2020). Vegetation and soil responses to added carbon and nutrients remain six years after discontinuation of long-term treatments. *Science of the Total Environment*, *722*, 137885. https://doi.org/10.1016/j.scitotenv.2020.137885

Mack, M. C., Schuur, E. A. G., Bret-Harte, M. S., Shaver, G. R., & Chapin III, F. S. (2004). Ecosystem carbon storage in arctic tundra reduce by long-term nutrient fertilization. *Nature*, *431*(7007), 440–443. https://doi.org/10.1038/nature02887

Maclean, I. M. D., Mosedale, J. R., & Bennie, J. J. (2019). Microclima: An r package for modelling meso- and microclimate. *Methods in Ecology and Evolution*, *10*(2), 280–290. https://doi.org/10.1111/2041-210X.13093

Mattheis, P. J., & Tieszen, L. L. (1976). Responses of *Dupontia fischeri* to Simulated Lemming Grazing in an Alaskan Arctic Tundra. *Annals of Botany*, *40* (166), 179–197. https://doi.org/10.1093/oxfordjournals.aob.a085121

McFadden, J. P., Chapin, F. S., & Hollinger, D. Y. (1998). Subgrid-scale variability in the surface energy balance of arctic tundra. *Journal of Geophysical Research Atmospheres*, *103*(D22), 28947–28961. https://doi.org/10.1029/98jd02400

Miner, K. R., Turetsky, M. R., Malina, E., Bartsch, A., Tamminen, J., McGuire, A. D., Fix, A., Sweeney, C., Elder, C. D., & Miller, C. E. (2022). Permafrost carbon emissions in a changing Arctic. *Nature Reviews Earth and Environment*, *3*(1), 55–67. https://doi.org/10.1038/s43017-021-00230-3

Mosbacher, J. B., Michelsen, A., Stelvig, M., Hjermstad-Sollerud, H., & Schmidt, N. M. (2019). Muskoxen Modify Plant Abundance, Phenology, and Nitrogen Dynamics in a High Arctic Fen. *Ecosystems*, *22*(5), 1095–1107. https://doi.org/10.1007/s10021-018-0323-4

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., … Hik, D. S. (2011). Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters*, *6*(4). https://doi.org/10.1088/1748-9326/6/4/045509

Natali, S. M., Schuur, E. A. G., Trucco, C., Hicks Pries, C. E., Crummer, K. G., & Baron Lopez, A. F. (2011). Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra. *Global Change Biology*, *17*(3), 1394–1407. https://doi.org/10.1111/j.1365-2486.2010.02303.x

Nishizawa, K., Deschamps, L., Maire, V., Bêty, J., Lévesque, E., Kitagawa, R., Masumoto, S., Gosselin, I., Morneault, A., Rochefort, L., Gauthier, G., Tanabe, Y., Uchida, M., & Mori, A. S. (2021). Long-term consequences of goose exclusion on nutrient cycles and plant communities in the High-Arctic. *Polar Science*, *27* (December 2020). https://doi.org/10.1016/j.polar.2020.100631

927 Nowinski, N. S., Trumbore, S. E., Schuur, E. A. G., MacK, M. C., & Shaver, G. R.
928 (2008). Nutrient addition prompts rapid destabilization of organic matter in an arctic
929 tundra ecosystem. *Ecosystems*, *11*(1), 16–25. https://doi.org/10.1007/s10021-007-
930 9104-1

931 O'Donnell, J. A., Romanovsky, V. E., Harden, J. W., & Mcguire, A. D. (2009). The
932 Effect of Moisture Content on the Thermal Conductivity of Moss and Organic Soil
933 Horizons from Black Spruce Ecosystems in Interior Alaska. *Soil Science*, *174* (12),
934 646–651. https://doi.org/10.1097/SS.0b013e3181c4a7f8

935 Ola, A., Fortier, D., Coulombe, S., Comte, J., & Domine, F. (2022). The Distribution of
936 Soil Carbon and Nitrogen Stocks Among Dominant Geomorphological Terrain
937 Units in Qarlikturvik Valley, Bylot Island, Arctic Canada. *Journal of Geophysical*
938 *Research: Biogeosciences*, *127*(7). https://doi.org/10.1029/2021JG006750

939 Pouliot, R., Rochefort, L., & Gauthier, G. (2009). Moss carpets constrain the fertilizing
940 effects of herbivores on graminoid plants in arctic polygon fens. *Botany*, *87*, 1209–
941 1222. https://doi.org/10.1139/B09-069

942 Prager, C. M., Naeem, S., Boelman, N. T., Eitel, J. U. H., Greaves, H. E., Heskel, M. A.,
943 … & Griffin, K. L. (2017). A gradient of nutrient enrichment reveals nonlinear
944 impacts of fertilization on Arctic plant diversity and ecosystem function. *Ecology and*
945 *Evolution*, *7*(7), 2449–2460. https://doi.org/10.1002/ece3.2863

946 Raillard, M. C., & Svoboda, J. (1999). Exact Growth and Increased Nitrogen
947 Compensation by the Arctic Sedge *Carex aquatilis* var. *stans* after Simulated Grazing.
948 *Arctic, Antarctic, and Alpine Research*, *31*(1), 21–26.
949 https://doi.org/10.1080/15230430.1999.12003277

950 Reed, A., Hughes, R. J., & Boyd, H. (2002). Patterns of distribution and abundance of
951 Greater Snow Geese on Bylot Island, Nunavut, Canada 1983-1998. *Wildfowl*, *53*,
952 53–65.

953 Schädel, C., Koven, C. D., Lawrence, D. M., Celis, G., Garnello, A. J., Hutchings, J.,
954 Mauritz, M., Natali, S. M., Pegoraro, E., Rodenhizer, H., Salmon, V. G., Taylor, M.
955 A., Webb, E. E., Wieder, W. R., & Schuur, E. A. (2018). Divergent patterns of
956 experimental and model-derived permafrost ecosystem carbon dynamics in response
957 to Arctic warming. *Environmental Research Letters*, *13* (10), 105002.
958 https://doi.org/10.1088/1748-9326/aae0ff

959 Schuur, E. A. G., Vogel, J. G., Crummer, K. G., Lee, H., Sickman, J. O., & Osterkamp,
960 T. E. (2009). The effect of permafrost thaw on old carbon release and net carbon
961 exchange from tundra. *Nature*, *459*(7246), 556–559.
962 https://doi.org/10.1038/nature08031

963 Shaver, G. R., & Chapin, F. S. (1995). Long–term responses to factorial, NPK fertilizer
964 treatment by Alaskan wet and moist tundra sedge species. *Ecography*, *18*(3), 259–
965 275. https://doi.org/10.1111/j.1600-0587.1995.tb00129.x

966 Shaver, G. R., Syndonia Bret-Harte, M., Jones, M. H., Johnstone, J., Gough, L., Laundre,
967 J., & Stuart Chapin, F. (2001). Species composition interacts with fertilizer to
968 control long-term change in tundra productivity. *Ecology*, *82*(11), 3163–3181.
969 https://doi.org/10.1890/0012-9658(2001)082[3163:SCIWFT]2.0.CO;2

970 Shur, Y., Hinkel, K. M., & Nelson, F. E. (2005). The transient layer: Implications for
971 geocryology and climate-change science. *Permafrost and Periglacial Processes*,
972 *16*(1), 5–17. https://doi.org/10.1002/ppp.518

973 Sjögersten, S., van der Wal, R., Loonen, M. J. J. E., & Woodin, S. J. (2011). Recovery of
974 ecosystem carbon fluxes and storage from herbivory. *Biogeochemistry*, *106*(3), 357–
975 370. https://doi.org/10.1007/s10533-010-9516-4

976 Sjögersten, S., van der Wal, R., & Woodin, S. J. (2012). Impacts of Grazing and Climate
977 Warming on C Pools and Decomposition Rates in Arctic Environments. *Ecosystems*,
978 15(3), 349–362. https://doi.org/10.1007/s10021-011-9514-y

979 Soudzilovskaia, N. A., Bodegom, P. M. Van, & Cornelissen, J. H. C. (2013). Dominant
980 bryophyte control over high-latitude soil temperature fluctuations predicted by heat
981 transfer traits, field moisture regime and laws of thermal insulation. *Functional*
982 *Ecology*, *27*, 1442–1454. https://doi.org/10.1111/1365-2435.12127

983 Speed, J. D. M., Woodin, S. J., Tømmervik, H., & van der Wal, R. (2010). Extrapolating
984 herbivore-induced carbon loss across an arctic landscape. *Polar Biology*, *33*(6), 789–
985 797. https://doi.org/10.1007/s00300-009-0756-5

986 Sundqvist, M. K., Moen, J., Björk, R. G., Vowles, T., Kytöviita, M. M., Parsons, M. A.,
987 & Olofsson, J. (2019). Experimental evidence of the long-term effects of reindeer on
988 Arctic vegetation greenness and species richness at a larger landscape scale. *Journal*
989 *of Ecology*, *107*(6), 2724–2736. https://doi.org/10.1111/1365-2745.13201

990 te Beest, M., Sitters, J., Ménard, C. B., & Olofsson, J. (2016). Reindeer grazing increases
991 summer albedo by reducing shrub abundance in Arctic tundra. *Environmental*
992 *Research Letters*, *11*(12). https://doi.org/10.1088/1748-9326/aa5128

993 R Core Team (2020). *R: A language and environment for statistical computing.* Vienna,
994 Austria: R Foundation for Statistical Computing. Retrieved from https://www.r-
995 project.org/.

996 Valéry, L., Cadieux, M. C., & Gauthier, G. (2010). Spatial heterogeneity of primary
997 production as both cause and consequence of foraging patterns of an expanding

greater snow goose colony. *Ecoscience*, *17*(1), 9–19. https://doi.org/10.2980/17-1-3279

van der Wal, R., Van Lieshout, S. M. J., & Loonen, M. J. J. E. (2001). Herbivore impact on moss depth, soil temperature and arctic plant growth. *Polar Biology*, *24*(1), 29–32. https://doi.org/10.1007/s003000000170

van der Wal, R., Sjögersten, S., Woodin, S. J., Cooper, E. J., Jónsdóttir, I. S., Kuijper, D., … & Huiskes, A. D. (2007). Spring feeding by pink-footed geese reduces carbon stocks and sink strength in tundra ecosystems. *Global Change Biology*, *13*(2), 539–545. https://doi.org/10.1111/j.1365-2486.2006.01310.x

van Wijk, M. T., Clemmensen, K. E., Shaver, G. R., Williams, M., Callaghan, T. V., Chapin, F. S., … & Rueth, H. (2004). Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: Generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology*, *10*(1), 105–123. https://doi.org/10.1111/j.1365-2486.2003.00719.x

Vincent, W. F., Lemay, M., & Allard, M. (2017). Arctic permafrost landscapes in transition: towards an integrated Earth system approach. *Arctic Science*, *3*(2), 39–64. https://doi.org/10.1139/as-2016-0027

Voigt, C., Lamprecht, R. E., Marushchak, M. E., Lind, S. E., Novakovskiy, A., Aurela, M., … & Biasi, C. (2017). Warming of subarctic tundra increases emissions of all three important greenhouse gases – carbon dioxide, methane, and nitrous oxide. *Global Change Biology*, *23*(8), 3121–3138. https://doi.org/10.1111/gcb.13563

Wang, P., Limpens, J., Mommer, L., van Ruijven, J., Nauta, A. L., Berendse, F., … & Heijmans, M. M. P. D. (2017). Above- and below-ground responses of four tundra plant functional types to deep soil heating and surface soil fertilization. *Journal of Ecology*, *105*(4), 947–957. https://doi.org/10.1111/1365-2745.12718

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, *73*(1), 3-36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Yi, S., Woo, M. K., & Arain, M. A. (2007). Impacts of peat and vegetation on permafrost degradation under climate warming. *Geophysical Research Letters*, *34*(16), 1–5. https://doi.org/10.1029/2007GL030550

Ylänne, H., Kaarlejärvi, E., Väisänen, M., Männistö, M. K., Ahonen, S. H. K., Olofsson, J., & Stark, S. (2020). Removal of grazers alters the response of tundra soil carbon to warming and enhanced nitrogen availability. *Ecological Monographs*, *90*(1), 1–13. https://doi.org/10.1002/ecm.1396

1034 Zhu, D., Ciais, P., Krinner, G., Maignan, F., Jornet Puig, A., & Hugelius, G. (2019).
1035 Controls of soil organic matter on soil thermal dynamics in the northern high
1036 latitudes. *Nature Communications*, 10(1), 1–9. https://doi.org/10.1038/s41467-019-
1037 11103-1

1038 Zoltai, S. C., & McCormick, K. J. (1983). A natural resource survey of Bylot Island
1039 andadjacent Baffin Island, Northwest Territories. Parks Canada, Ottawa, Ontario,
1040 Canada