Received: 16 October 2022 | Accepted: 9 April 2023

DOI: 10.1111/1365-2745.14114

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Herbivory and warming have opposing short-term effects on plant-community nutrient levels across high-Arctic tundra habitats

Matteo Petit Bon[1,2,3] | Kari Anne Bråthen[2] | Virve Tuulia Ravolainen[4] | Gianluigi Ottaviani[5,6] | Hanna Böhner[1,2] | Ingibjörg Svala Jónsdóttir[1,7]

[1]Department of Arctic Biology, University Centre in Svalbard, Longyearbyen, Norway; [2]Department of Arctic and Marine Biology | Faculty of Biosciences, Fisheries, and Economics, The Arctic University of Norway, Tromsø, Norway; [3]Department of Wildland Resources | Quinney College of Natural Resources and Ecology Centre, Utah State University, Logan, Utah, USA; [4]Norwegian Polar Institute, Fram Centre, Tromsø, Norway; [5]Department of Botany and Zoology | Faculty of Science, Masaryk University, Brno, Czech Republic; [6]Institute of Botany of the Czech Academy of Sciences, Třeboň, Czech Republic and [7]Institute of Life and Environmental Sciences, University of Iceland, Reykjavik, Iceland

Correspondence
Matteo Petit Bon
Email: matteo.petitbon@gmail.com

Funding information
Czech Science Foundation, Grant/Award Number: 19-28491X and 20-13637S; Governor of Svalbard; Svalbard Environmental Protection Fund, Grant/Award Number: 15/128; Long-term research development project of the Czech Academy of Sciences, Grant/Award Number: RVO-67985939; National Science Foundation, Grant/Award Number: ANS-2113641; Research Council of Norway; Arctic Field Grant, Grant/Award Number: 269957

Handling Editor: Robert G. Björk

[Correction added on 11 September 2023, after first online publication: The copyright line was changed.]

Abstract

1. Environmental changes can rapidly alter standing biomass in tundra plant communities; yet, to what extent can they modify plant-community nutrient levels? Nutrient levels and their changes can affect biomass production, nutrient cycling rates and nutrient availability to herbivores. We examined how environmental perturbations alter Arctic plant-community leaf nutrient concentrations (percentage of dry mass, i.e. resource quality) and nutrient pools (absolute mass per unit area, i.e. resource quantity).
2. We experimentally imposed two different types of environmental perturbations in a high-Arctic ecosystem in Svalbard, spanning three habitats differing in soil moisture and plant-community composition. We mimicked both a pulse perturbation (a grubbing event by geese in spring) and a press perturbation (a constant level of summer warming).
3. After 2 years of perturbations, we quantified peak-season nitrogen and phosphorus concentrations in 1268 leaf samples from the most abundant vascular plant species. We derived community-weighted nutrient concentrations and total amount of nutrients (pools) for whole plant communities and individual plant functional types (PFTs).
4. Spring grubbing increased plant-community nutrient concentrations in mesic (+13%) and wet (+8%), but not moist, habitats, and reduced nutrient pools in all habitats (moist: −49%; wet, mesic: −31% to −37%). Conversely, summer warming reduced plant-community nutrient concentrations in mesic and moist (−10% to −12%), but not wet, habitats and increased nutrient pools in moist habitats (+50%).

5. Fast-growing PFTs exhibited nutrient-concentration responses, while slow-growing PFTs generally did not. Grubbing enhanced nutrient concentrations of forbs and grasses in wet habitats (+20%) and of horsetails and grasses in mesic habitats (+19–23%). Conversely, warming decreased nutrient concentrations of horsetails in wet habitats (−15%) and of grasses, horsetails and forbs in moist habitats (−12% to −15%). Nutrient pools held by each PFT were less affected, although the most abundant PFTs responded to perturbations.

6. *Synthesis*. Arctic plant-community nutrient levels can be rapidly altered by environmental changes, with consequences for short-term process rates and plant-herbivore interactions. Community-level responses in nutrient concentrations and pools were opposing and differed among habitats and PFTs. Our findings have implications for how we understand herbivory- and warming-induced shifts in the fine-scaled distribution of resource quality and quantity within and across tundra habitats.

KEYWORDS

international tundra experiment (ITEX), near-infrared reflectance spectroscopy (NIRS), nitrogen (N) and phosphorus (P), nutrient concentrations and pools, pink-footed geese (grubbing), plant functional types (PFTs), plant–herbivore interactions, pulse and press perturbations

1 | INTRODUCTION

The consequence of environmental changes for the nutrient dynamics (primarily nitrogen [N] and phosphorus [P]) of terrestrial plant communities is a crucial facet of environmental change studies (Vitousek et al., 2010; Yue et al., 2019). Plant-community nutrient levels—both concentrations (relative level of nutrients per unit of leaf dry mass) and pools (absolute amount of nutrients in leaf dry mass per unit area)—underpin multiple ecological processes and functions. Alterations in plant-community nutrient concentrations can modify the rates of carbon assimilation and litter decomposition (Cornwell et al., 2008), thus biomass production and nutrient cycling rates, as well as the palatability of forage for herbivores (resource quality; Grime et al., 1996). At the same time, alterations in plant-community nutrient pools can affect nutrient fluxes (Chapin et al., 2012), such as the input to the soil nutrient pools, as well as the amount of nutrients available to herbivores (resource quantity; Sterner & Elser, 2002). A key ramification of changes in resource quality and quantity is that they can alter the linkages between above-ground (vegetation) and below-ground (soil) compartments, influencing a range of ecosystem processes and functions simultaneously (Wardle et al., 2004).

In the Arctic, cold temperatures and short growing seasons constrain decomposition rates, hence the release of nutrients from soil organic matter, rendering tundra ecosystems notably nutrient-limited (Hobbie et al., 2002). Numerous field experiments have demonstrated that N availability exerts strong controls on tundra plant-community productivity and composition, soil microbial activity, and ecosystem carbon storage. Yet, these same experiments have also identified a prominent role of P availability in modulating N controls on ecosystem structure and processes (Gignac et al., 2022; Sitters et al., 2019; Street et al., 2017; Sundqvist et al., 2014). Moreover, from an herbivore perspective, N is fundamental for protein synthesis and thus growth, while P is crucial for bony structures and the synthesis of ATP (Sterner & Elser, 2002). Hence, perturbations that cause modifications in N and P levels of plant communities are likely to have large impacts on tundra ecosystem functioning.

Arctic ecosystems are affected by diverse environmental perturbations. The tundra hosts large populations of relatively few vertebrate herbivore species (Speed et al., 2019), with migratory geese being abundant in many regions. Arctic-breeding goose populations have considerably increased in size over the past few decades (Fox & Madsen, 2017; but see Weegman et al., 2022). This was caused by enhanced conservation measures and decreased hunting pressure (Fox & Madsen, 2017), shifts in agricultural practices in temperate overwintering areas (Fox & Abraham, 2017), and climate warming (Jensen et al., 2008). Increasing numbers of geese and higher temperatures are having marked impacts on tundra plant-community structure and productivity (Madsen et al., 2011). Yet, whether and how these impacts may be paralleled by similarly fast changes in plant-community nutrient levels remains poorly explored (but see Petit Bon et al., 2021).

After arrival and throughout the pre-breeding period in spring, goose species from the genera *Anser* and *Chen* forage for subterranean plant material through grubbing (Fox et al., 2006). Grubbing, which often occurs in the upper 2–8 cm of thawed soil, causes uprooting and fragmentation of the moss layer and vascular plants (Fox et al., 2006; Figure S1a,b). As a sudden and relatively short-in-time disturbance at the onset of the growing season (a pulse perturbation in the system; Ravolainen et al., 2020), goose grubbing can drastically reduce the standing biomass of tundra plant communities (Jefferies et al., 2006; Speed et al., 2009), thus decreasing their N and P pools. However, goose activities in spring might increase plant-community N and P concentrations by promoting nutrient leaching from decomposing roots and rhizomes through grubbing, defecating unassimilated nutrients back into the soil, or stimulating the regrowth of highly nutritious plant tissues (Beard et al., 2019; Beaulieu et al., 1996), potentially offsetting, at least in part, the reduction in nutrient pools.

The Arctic is warming nearly four times faster than the rest of the planet (Rantanen et al., 2022), and there is ample evidence that tundra plant communities are changing in ways that may affect their nutrient levels (Bjorkman et al., 2018). Studies that simulated an average temperature rise in summer (a constant, press perturbation in the system) have shown that Arctic plant communities can respond rapidly, although often heterogeneously, with an increase in aboveground plant cover and abundance (Bjorkman et al., 2020; Elmendorf et al., 2012; Walker et al., 2006; but see Hudson & Henry, 2010). Therefore, one could expect warmer temperatures to generally enhance plant-community N and P pools. However, in the short-term, elevated temperatures can lower plant N and P concentrations by speeding up the seasonal decline in plant quality or diluting nutrients within the larger plant biomass (Doiron et al., 2014; Flint & Meixell, 2021; Lameris et al., 2017), potentially offsetting, at least in part, the increase in nutrient pools.

Arctic ecosystems host various vascular plant species belonging to several plant functional types (PFTs; sensu Chapin et al., 1996), which shift their abundance according to prevailing environmental factors. Fine-scaled variations in topography and soil moisture conditions in the Arctic create a mosaic of different habitats (Sjögersten et al., 2006). Habitats are characterized by different plant communities, with a composition of PFTs that differ in their standing biomass, thus in their N and P pools (Arndal et al., 2009). Because PFTs often vary consistently in their N and P concentrations (forbs > graminoids > deciduous shrubs > evergreen shrubs; Thomas et al., 2018), they can further increase the spatial heterogeneity in nutrient levels among and within plant communities. Such heterogeneity not only suggests that tundra plant communities are likely to differ in their short-term nutrient responses to environmental changes but also that PFTs in these communities may display distinct responses. For example, meta-analyses of circum-Arctic experiments indicate that short-term warming (Walker et al., 2006) and fertilization (Dormann & Woodin, 2002) often promote the abundance of graminoids and shrubs, generally at the expense of the inherently less abundant, but more nutrient-rich, forbs (Bråthen et al., 2021). This suggests that nutrient-pool responses to perturbations might be larger for those PFTs that are more abundant in the community (mass ratio hypothesis; Grime, 1998). Concurrently, studies that examined changes in tundra-plant nutrient concentrations found that fast-growing PFTs, such as forbs and graminoids, tend to show faster responses compared to slow-growing PFTs, such as shrubs (Aerts et al., 2009; Petit Bon, Inga, et al., 2020), possibly because of their greater ability to readily exploit available nutrients. The composition of PFTs in plant communities affects key ecological processes, such as biomass accumulation, litter decomposition and herbivory (Dorrepaal, 2007; Wookey et al., 2009). Current knowledge of climate change effects on tundra ecosystems is largely based on PFT abundance responses, whereas a lack of fine-scaled nutrient data at the community level has hampered studies of PFT nutrient responses (Petit Bon, Böhner, et al., 2020).

Here, we quantified responses in leaf N and P concentrations (resource quality) and pools (resource quantity) at the whole community level and in most abundant PFTs, to goose activity (grubbing and faeces deposition) and higher temperatures in high-Arctic Svalbard. We simulated pink-footed goose activity in spring (a pulse perturbation) and raised average summer temperatures (a press perturbation) over 2 years in a full-factorial field experiment across three habitats that differ in soil moisture, and hence plant-community composition. We hypothesized goose activity to increase plant-community nutrient concentrations and decrease nutrient pools, while warming to have opposite effects. We also expected plant communities in the three habitats to vary in their nutrient responses, reflecting those of most abundant PFTs. We anticipated fast-growing PFTs to exhibit stronger nutrient-concentration responses compared to slow-growing PFTs, and abundant PFTs to show the largest nutrient-pool responses. Previous findings from the tundra suggest that geese and warmer summers can drive vegetation composition to change in opposite directions (Choi et al., 2022). Hence, we also explored whether interactive effects between them may drive PFT nutrient responses.

2 | MATERIALS AND METHODS

2.1 | Study system

The archipelago of Svalbard (62,700 km^2), in the European high-Arctic, is mainly covered by glaciers or rocky and sparsely vegetated ground, while only 15% of the land area is vegetated (Johansen et al., 2012). This study was conducted in Adventdalen (78°10′N, 16°05′E), a well-vegetated valley on Spitsbergen, the largest island of the archipelago, and experiments were carried out during the summers of 2016 and 2017. Over the 2 years, average annual and summer (June to August) temperatures were −1.2°C and 6.3°C, respectively, while the mean annual precipitation was 258 mm. Linear trends in average annual and summer temperature for the period 1988–2017 indicate an increase by approximately 1.7°C per decade and 0.7°C per decade, respectively, thus making Svalbard one of the World's most rapidly warming regions (data from Svalbard airport, ca. 10 km from the study area, http://met.no; Nordli et al., 2020).

There are only three resident vertebrate herbivores in Svalbard, the wild Svalbard reindeer *Rangifer tarandus platyrhynchus*, the Svalbard rock ptarmigan *Lagopus muta hyperborea*, and the sibling vole *Microtus levis*. While reindeer and ptarmigan are widely distributed across the archipelago, the sibling vole is an introduced species found in a small bird cliff area (Fauteux et al., 2021), and only occasionally occurs near our study sites in population-peak years (Fuglei et al., 2008). Adventdalen is an important pre-breeding staging area for two migratory goose species, the pink-footed goose *Anser brachyrhynchus* and the barnacle goose *Branta leucopsis*. After arrival in spring (mid-to-late May) and for approximately 2–3 weeks, pink-footed geese almost exclusively forage through grubbing, while barnacle geese mostly feed by grazing above-ground vegetation (Fox & Bergersen, 2005); see for example Zacheis et al. (2001) for similarities with other high-latitude systems in North America. In this study, spring goose herbivory was modelled on grubbing disturbance (including faeces deposition) by pink-footed geese.

The Svalbard pink-footed goose population has increased from 15,000 individuals in 1965 up to 90,000 individuals in 2017 (Madsen et al., 2017). In an assessment of the distribution of goose grubbing in Svalbard, pink-footed geese were shown to prefer wet habitats (Speed et al., 2009). Though less preferred, they also use drier habitats early in the spring when the still frozen soil does not permit grubbing in wet habitats (Fox et al., 2006). Due to the increase in population size, the utilization of drier habitats has also increased (Pedersen et al., 2013), indicating that most plant communities in Svalbard can be exposed to some degree of spring goose grubbing.

2.2 | Experimental design and perturbations

Seven replicate sites (300–1500 m apart), each comprising three habitats (30–100 m apart) differing in soil moisture (wet > moist > mesic), were marked within a 5-km^2 area in Adventdalen in late summer 2015, at an altitude of 15–60 m a.s.l. Habitats were selected following descriptions by Rønning (1996) and represent important pink-footed goose habitats in Svalbard (Fox et al., 2006). Wet habitats are characterized by wetland vegetation, dominated by grasses (predominantly *Dupontia fisheri* and *Calamagrostis neglecta*), the sedge *Eriophorum scheuchzeri* and the horsetail *Equisetum arvense*. Moist habitats are characterized by moss meadow vegetation, with *E. arvense*, the deciduous dwarf-shrub *Salix polaris*, the grass *Alopecurus ovatus* and the forb *Bistorta vivipara* being abundant species. Mesic habitats are characterized by heath vegetation, dominated by the rush *Luzula confusa* and co-occurring evergreen and deciduous dwarf-shrubs, grasses and forbs (main species are *Dryas octopetala*, *S. polaris*, *A. ovatus*, *Poa arctica* and *B. vivipara*). Species nomenclature follows the Svalbard flora (https://svalbardflora.no). Besides species composition, the three habitats also differ in abiotic conditions (Table 1).

After snowmelt in spring 2016, an experimental block constituted by four plots (80 × 80 cm) was established in all three habitats at each site (Figure 1a). One of the selected experimental blocks for wet habitats was discarded due to a flooding event (*n* plots = 80; *N* replicated blocks = 7 [moist and mesic habitats] and 6 [wet habitats]). Plots within blocks (2–10 m apart) were featured by homogeneous vascular-plant cover (at least 80% of the plot surface should be vegetated) and plant-community composition, and by similar microtopographical features. Two treatments with two levels in each were randomly allocated to the plots at each block in a full-factorial arrangement: (i) a simulated pulse perturbation mimicking the spring activity by pink-footed geese (disturbed and undisturbed plots) and (ii) a simulated press perturbation based on a constant level of summer warming (warmed and ambient plots).

Spring goose activity was applied once both years at the peak of the grubbing season (early-to-mid June). Grubbing was simulated in a regular fashion to ca. 33% of the plot surface (Figure S1c) by using a steel tube (20 mm diameter) that was inserted to a depth of about 50 mm and twisted to remove and export both above-ground and below-ground plant material from the plot, following Speed et al. (2010). We then fertilized disturbed plots by adding 120 g of fresh goose faeces collected each spring within the study area. The intensity of our treatment (hereafter referred to as grubbing) reflected what we observed in naturally grubbed areas typically found in moist habitats. As previously reported (Speed et al., 2009), we also observed somewhat higher intensity of goose grubbing in wet habitats and lower intensity in mesic habitats. Nevertheless, a consistent disturbance intensity made it possible to compare plant-community nutrient responses across habitats (cf. Speed et al., 2010).

Summer warming was achieved by hexagonal open-top chambers (OTCs, made of LEXAN© polycarbonate; 1.4 m base diameter), following the International Tundra Experiment (ITEX) protocol (Henry & Molau, 1997; Molau & Mølgaard, 1996). OTCs are passive warming devices (Hollister et al., 2022) that have been used in several ecological studies to increase plot-scale temperatures experienced by plants (see e.g. Elmendorf et al., 2012). Overall, our OTCs increased mean (~0.9°C) and maximum (~3.5°C) July air temperature (measured at +5 cm from the moss surface) and mean (~1.0°C) and maximum (~1.5°C) July moss-mat temperature (−2 cm) compared to

TABLE 1 Summary of the abiotic characteristics of the three studied habitats. Data collected from un-manipulated control plots at the peak of the growing season (20–28 of July 2017). Soil moisture averaged from five recordings at each plot (measured using a ML3 Theta Probe and HH2 Moisture Meter Logger; Delta-T Devices Ltd.). Soil N-content averaged from three sub-samples at each plot (measured using a Vario EL Cube Elementar analyser; GmbH). Mean ± standard deviation is shown.

Environmental characteristics	Wet habitats—wetland (*n* = 6)	Moist habitats—moss meadow (*n* = 7)	Mesic habitats—mesic heath (*n* = 7)
Soil moisture (% volume)	94.8 ± 12.7	64.2 ± 11.5	41.1 ± 7.8
Soil N-content (% dry weight)	0.28 ± 0.09	0.37 ± 0.15	0.54 ± 0.27

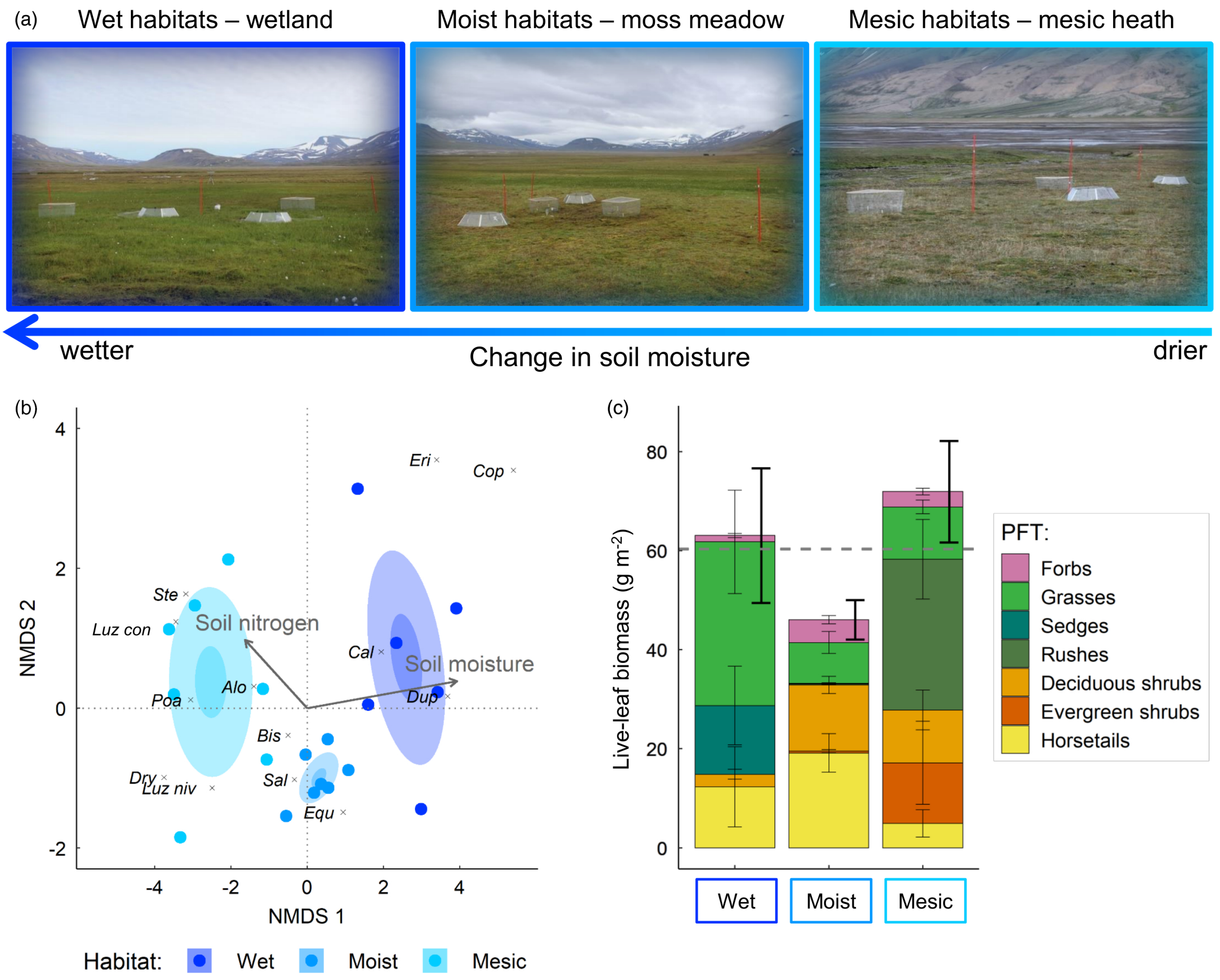

FIGURE 1 Overview of the three habitats and associated plant communities. (a) Example of experimental blocks established in wet, moist, and mesic habitats; photos: July 2016. (b) Two-dimensional NMDS ordination of plant species live-leaf biomass in un-manipulated control plots of the three habitats ($n=20$, stress$\,=0.089$, Non-metric fit $r^2=0.99$, Linear fit $r^2=0.96$). The ordination shows only the 14 species for which we collected leaf samples (species abbreviations are reported in Table 2). Ellipses represent the 95% confidence interval for the mean (i.e. plant-community centroids—bold ellipses) and for the standard deviation of the mean (shaded ellipses); plant-community: $R^2=0.53$, $p=0.001$. Fit of the environmental parameters (Table 1) when a posteriori regressed on the two axes of the bi-plot: Soil moisture: $r^2=0.77$, $p=0.0001$; Soil N-content: $r^2=0.18$, $p=0.003$. (c) Average plant-community live-leaf biomass in un-manipulated control plots of the three habitats, sorted according to PFTs. Thick and thin bars are the standard error of the means for the whole plant community and for each PFT, respectively. The grey-dashed line shows the average plant-community live-leaf biomass across habitats.

ambient conditions; further details can be found in Table S1. OTCs were deployed soon after snowmelt (early June) during both years and were kept throughout the summer.

To avoid natural herbivory, all plots were caged off 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 herbivores from 'ambient' plots. In 'warmed' plots, a piece of metal net was used to close the open-top part of each OTC, which then acted as an herbivore exclosure. Both OTCs and cages were removed in early October, when geese had long left the archipelago, and during the winter period, to prevent changes in snow accumulation patterns. For further details on the experimental design, refer to Petit Bon et al. (2021).

2.3 | Plant-community nutrient concentrations and pools: Sample collection and processing

We collected leaves from all most abundant vascular plants within each plot and quantified their N and P concentrations (as % dry weight, hereafter %dwt). All leaves were collected at peak summer in 2017 (period 20–28 of July), following 2 years of perturbations. By using relative and absolute contribution of each species to the live-leaf biomass at each plot, we then calculated community-weighted means of leaf N- and P-concentration (%dwt) and N- and P-pool (as g [dwt] m^{-2}, hereafter g m^{-2}) at the whole community level, as well as for plant functional types (PFTs). Community-weighted means (sensu Garnier et al., 2004) have proved to be a simple, yet reliable, metric to characterize the functional structure of plant communities and its relationship with the environment, and further link it to ecosystem functioning (Lavorel et al., 2011; Myers-Smith et al., 2019).

Leaf sampling was performed randomly within each plot by positioning a metal frame (50 × 50 cm) with 25 evenly distributed intercepts in the centre of each plot. Nine sticks (3 mm Ø—numbered from 1 to 9) were dropped down vertically from 9 randomly selected intercepts within the frame. From sticks 1 to 9, the species for which the uppermost leaf had touched the stick was registered. Since we aimed at sampling the plant species (and PFTs) that built up most of the above-ground biomass within each plot, the same species was not recorded twice. Hence, the second closest species to a stick was registered when the stick would provide a species already recorded. Three to five fresh leaves of each registered species were collected at each plot (on average 5.6 [range: 3–9] species per plot), starting from the stick at which the species was first recorded and continuing with the subsequent sticks. Across habitats, we harvested a total of 1493 leaves from 14 species belonging to seven broadly classified PFTs (Table 2). Their combined live-leaf biomass encompassed in average over 99% of the live-leaf biomass within plots (own data, see below).

During fieldwork, leaves were stored in separate tea-filter bags and flattened with a plant press within maximum 10 h after collection. After 72 h, all leaves were oven-dried at 60°C for 48 h. Whenever a single leaf was not large enough for nutrient analysis (leaf area of 4 mm Ø; Petit Bon, Böhner, et al., 2020), more leaves from the same species and plot were merged, leading to a total of 1268 independent leaf samples (Table 2). Each leaf-sample was analysed with near-infrared reflectance spectroscopy (NIRS FieldSpec 3; ASD Inc.) in 350–2500 nm range and equipped with a 4-mm light-adapter for full-leaf scanning (Petit Bon, Böhner, et al., 2020). For each leaf sample, 3-to-8 measures were taken, depending on leaf size, for a total of 4387 measures. Each measure was converted to both N and P concentrations (%dwt) by using prediction models based on milled and tableted plant samples (Ancin-Murguzur et al., 2019) and correction coefficients for full leaves (Petit Bon, Böhner, et al., 2020). We computed the median of the replicate measures for each leaf sample and then averaged the medians of the samples to obtain mean N and P concentrations for each species within a plot. We obtained nutrient data for a total of 450 independent species samples (Table 2). For a similar approach, refer to Petit Bon, Inga, et al. (2020) and Petit Bon et al. (2022).

We determined live-leaf biomass in each plot using the point intercept frequency method (PIM; Bråthen & Hagberg, 2004; Molau & Mølgaard, 1996). To incorporate some of the within-plot spatial variation, two subplots (25 × 25 cm) were randomly selected within each plot and PIM was performed within these at peak season in 2017 by using a sampling frame (25 × 25 cm area × 35 cm height) with 25 evenly distributed points. Within each subplot, we vertically lowered a stick (3 mm Ø) at all points and counted the number of hits with each vascular plant live-leaf. Point intercept data for each species were averaged between the two subplots within a plot and

TABLE 2 Vascular plant species and corresponding plant functional type (PFT) considered in this study, and from which we collected leaves for nutrient analyses (species are listed in alphabetical order in relation to their PFT).

Species	Abbreviation[a]	Sample size[b]	Plant functional type (PFT)	Habitat[c]
Bistorta vivipara	*Bis*	262, (251), [72]	Forbs	Wet, moist, mesic
Coptidium lapponicum	*Cop*	12, (12), [4]		
Oxyria digyna	*Oxy*	6, (4), [2]		
Stellaria longipes	*Ste*	51, (17), [17]		
Alopecurus ovatus	*Alo*	191, (190), [59]	Grasses	Wet, moist, mesic
Calamagrostis neglecta	*Cal*	56, (56), [20]		
Dupontia fisheri	*Dup*	114, (114), [36]		
Poa arctica	*Poa*	77, (63), [25]		
Eriophorum scheuchzeri	*Eri*	63, (63), [20]	Sedges	Wet
Luzula confusa	*Luz con*	90, (88), [27]	Rushes	Mesic
Luzula nivalis	*Luz niv*	22, (22), [7]		
Salix polaris	*Sal*	269, (266), [76]	Deciduous dwarf-shrubs	Wet, moist, mesic
Dryas octopetala	*Dry*	91, (59), [22]	Evergreen dwarf-shrubs	Mesic
Equisetum arvense	*Equ*	189, (63), [63]	Horsetails	Wet, moist, mesic

[a] Abbreviations used in Figure 1b.

[b] For each species, the number of harvested leaves (in total, $n = 1493$), the number of independent leaf samples analysed (round brackets; in total, $n = 1268$) and the number of independent species samples obtained and from which community-weighted nutrient concentrations and pools were calculated (square brackets; in total, $N = 450$) are reported (see Section 2.3 for details). Note that [N] also represents the number of experimental plots out of the total, that is 80, in which each species was found.

[c] Habitats in which each PFT was abundant enough (cf. Figure 1c) to allow the assessment of PFT nutrient responses to environmental perturbations (see *Data Analysis* for details).

converted into live-leaf biomass (g m^{-2}) using the correlation coefficients in Petit Bon et al. (2021). Briefly, correlation coefficients were obtained by calculating the relationship between PIM data and live-leaf biomass data, separately for each PFT (Table 2), collected from 17 external plots selected for destructive harvesting across the three studied habitats. Relative and absolute biomass data are presented in Figures S2 and S3, respectively.

Community-weighted means of N- and P-concentration (relative level of nutrients per unit of leaf dry mass) and N- and P-pool (absolute amount of nutrients in leaf dry mass per unit area) were calculated for each plot:

$$\text{Plant–community nutrient concentrations } (\%\text{dwt}): \sum_{i=1}^{n} = p_i \times (\text{nutrient concentration})_i,$$

$$\text{Plant–community nutrient pools } (\text{g m}^{-2}): \sum_{i=1}^{n} = \frac{bi \times (\text{nutrient concentration})i}{100},$$

where *n* represents the number of species in a plot, p_i is the relative contribution of the species *i* to the overall plot live-leaf biomass, b_i is the absolute contribution of the species *i* to the overall plot live-leaf biomass, and *nutrient concentration* is the N- and P-concentration (%dwt) of the species *i*. Both p_i and b_i for each species at each plot were derived using live-leaf biomass (g m^{-2}) data obtained through conversion of the initial PIM data (see above). The same formulae were used to obtain N- and P-concentration and N- and P-pool for each PFT, where *n* represents the number of species belonging to the PFT in a plot.

Some PFTs encompassed a single plant species (Table 2), which is inherent to high-Arctic, species-poor communities. This only happened when a species was the unique representative of the PFT at our sites. Because of their circumpolar distribution, these species (e.g. *Dryas octopetala*; Welker et al., 1997) and genera (e.g. *Salix* spp.; Jones et al., 1997) have been widely studied in terms of their responses to environmental perturbations. Therefore, we refer to 'PFT' throughout the Article and for comparisons with other Arctic studies.

2.4 | Data analysis

A non-metric multidimensional scaling (NMDS; Legendre & Legendre, 2012) was run to confirm differences in plant-community composition among the three habitats (wet, moist, and mesic). The NMDS was based on Euclidean distances of the species *log-transformed* + 1 live-leaf biomass (g m^{-2}) in un-manipulated control plots. We assessed differences in plant-community composition between habitats with permutational multivariate analysis of variance (PERMANOVA). PERMANOVA used the Euclidean distance matrix and consisted of restricted permutations ($n = 10{,}000$) to account for the hierarchical spatial structure of the study design (permutations of 'plots' were constrained within their 'site').

Plant-community and PFT nutrient responses to spring goose grubbing (two-level factor: undisturbed and disturbed) and summer warming (two-level factor: ambient and warming) were studied using a generalized linear mixed-effects model (GLMM) framework.

Plant-community nutrient responses: For each response variable, we fitted a GLMM with Gaussian distribution and either identity-link (for N- and P-concentration) or log-link (for N- and P-pool) function, for a total of four models. In each model, the initial full fixed-effects structure included the three-way interaction between 'habitat', 'spring grubbing' and 'summer warming'. To account for the hierarchical study design, 'site' and 'habitat-within-site' were specified as nested random-effects.

PFT nutrient responses: Species (and PFT) composition differed between plant communities (see NMDS *Results*), and thus PFT nutrient responses were studied separately at each habitat. N- and P-concentration responses were quantified using GLMMs with Gaussian distribution and identity-link function, as done for plant-community responses (see above). N- and P-pool responses in moist habitats were also quantified as for whole plant-community nutrient-pool responses, using GLMMs with Gaussian distribution and log-link function. However, some zero N- and P-pool occurred at the PFT level in wet and mesic habitats (~15% of the data). These zeros, which refer to the absence of a PFT from a plot, correspond to NAs (i.e. absence of data) in PFT nutrient concentrations, which have thus no issues with zero observations. Therefore, PFT N- and P-pool responses in these habitats were addressed using GLMMs with compound Poisson-Gamma distribution and log-link function (Zhang, 2013). This distribution was particularly suitable because it allows observations being exact zeros (i.e. the absence of a PFT), but is otherwise a continuous, positively skewed distribution (for a similar approach, see e.g. Sitters et al., 2019). In each model (12 models in total; six models for both nutrient concentrations and pools), the initial full fixed-effects structure included the three-way interaction between 'PFT', 'spring grubbing' and 'summer warming'. The number of 'levels' for the categorical predictor 'PFT' differed between models fitted for the three habitats, reflecting differences in PFT composition between plant communities (Table 2). To account for the hierarchical study design and the repeated sampling within plots, we included 'site' and 'plot-within-site' as nested random-effects.

By using likelihood ratio test (Bolker et al., 2009) on full models (fitted using maximum likelihood—ML), we selected the most parsimonious, but common, fixed-effects structure for all the analyses, separately for plant-community and PFT nutrient responses. We retained a common model structure to be able to (i) compare effect sizes of nutrient concentration and pool responses as well as of N and P responses and (ii) quantify community-specific and PFT-specific responses to the imposed perturbations. The final model structure for plant-community nutrient responses included 'habitat', 'spring grubbing' and 'summer warming' as additive fixed-effects and 'habitat × spring grubbing' and 'habitat × summer warming' as interactive fixed-effects. The final model structure for PFT nutrient responses included 'PFT', 'spring grubbing' and 'summer warming' as additive fixed-effects and 'PFT × spring grubbing' and 'PFT × summer warming' as interactive fixed-effects. Parameter estimates of each final model (fitted using restricted-ML) are presented in Tables S2–S9. Final models were validated by extracting simulation-based scaled residuals, which were visually inspected for deviations from the expected distribution, homoscedasticity, presence of outliers, dispersion and zero-inflation.

In the graphical presentation of the results, we focus on the effect of spring goose grubbing and summer warming on nutrient concentrations and pools, separately for the three plant communities and for each PFT. We display the main effects of our experimental treatments (and how they compare to each other) since their interaction was not found to be statistically significant in any of the models. We largely focus on patterns in plant-community and PFT nutrient-concentration and nutrient-pool responses to perturbations, according to our study questions. To keep this focus, other results on how perturbations altered the differences in nutrient levels among plant communities and PFTs, that is, their nutrient hierarchies, are extensively presented in the Supporting Information (see Section 3).

All statistical analyses were performed in the R Statistical Program ver. 4.0.3 (https://www.r-project.org) using the 'VEGAN' package for NMDS and PERMANOVA (Oksanen et al., 2020), the 'GLMMTMB' package for GLMMs (Brooks et al., 2017), the 'EMMEANS' package to extract parameter estimates and their CI from GLMMs (Lenth, 2021), and the 'GGPLOT2' package for graphical displays (Wickham, 2016).

3 | RESULTS

3.1 | Plant-community characterization

Plant species and PFT composition differed between the three plant communities (Figure 1b; Figure S4), supporting our a priori selection of the three studied habitats. Accordingly, PFT live-leaf biomass differed between plant communities (Figure 1c). The variability in plant species and PFT composition was higher in mesic and wet habitats than moist habitats, as expressed by the wider confidence intervals around their centroids (Figure 1b; Figure S4; cf. standard errors in Figure 1c).

3.2 | Plant-community and PFT nutrient levels in absence of perturbations

Plant-community N and P concentrations (relative level of nutrients per unit of leaf dry mass; Figure 2a,b) and pools (absolute amount of nutrients in leaf dry mass per unit area; Figure 2c,d) varied to a different extent among habitats. Plant-community N-concentration in wet and moist habitats was similar (in average, 3.2%) and 13% higher than that in mesic habitats. Plant-community P-concentration was on average 0.28% and did not differ across habitats. Because nutrient pools positively correlated with live-leaf biomass (Figure S5), plant-community nutrient pools were similar in wet and mesic habitats (N: 2.0 g m^{-2}; P: 0.18 g m^{-2}), and overall larger there than in moist habitats (N: 1.4 g m^{-2}; P: 0.12 g m^{-2}).

Within habitats, leaf N and P concentrations (Figure 2a,b) and pools (Figure 2c,d) also varied among PFTs. In wet habitats, PFT nutrient concentrations followed the order: horsetails and sedges (in average, N: 3.7%; P: 0.36%) ≥ deciduous shrubs (N: 3.1%; P: 0.29%) ≥ forbs and grasses (N: 2.9%; P: 0.26%). Nutrient pools were larger in grasses, sedges and horsetails (94% of the total) than in deciduous shrubs and forbs. In moist habitats, nutrient-rich horsetails and forbs (N: 3.6%; P: 0.30%) opposed to the more nutrient-poor grasses and deciduous shrubs (N: 2.7%; P: 0.25%). Nutrient pools were the largest in horsetails (48% of the total), intermediate in deciduous shrubs and grasses (42% together), and the lowest in forbs. In mesic habitats, PFT N-concentration varied in the order: horsetails (3.7%) ≥ forbs and grasses (3.2%) ≥ deciduous shrubs (2.7%) ≥ rushes and evergreen shrubs (2.4%), while P-concentration was overall higher in horsetails, forbs and grasses (0.29%) compared to sedges and shrubs (0.24%). PFTs contributed more similarly to the plant-community nutrient pools, although rushes did so to the largest extent (38% of the total).

3.3 | Plant-community nutrient responses to perturbations

Overall, plant-community leaf N and P responses to perturbations were similar in relative magnitude (Figure 3), likely reflecting the tight positive correlations between N and P levels in plant communities (Figure S6).

Spring goose grubbing and summer warming had opposing effects on plant-community N and P concentrations (Figure 3a) and pools (Figure 3b), though the strength of responses differed among habitats. Grubbing raised plant-community nutrient concentrations in mesic habitats (+13%), P-concentration in wet habitats (+10%) and did not affect nutrient concentrations in moist habitats, whereas warming decreased nutrient concentrations in mesic and moist habitats (range: −10% to −12%) and did not affect those in wet habitats. Conversely, grubbing reduced plant-community N and P pools in all habitats (moist: −49 > wet and mesic: −31% to −37%), whereas warming tended to enhance nutrient pools, but significantly so (+50%) only in moist habitats. Plant communities under goose grubbing had 12%–23% higher N-concentration and 35%–65% lower N and P pools than those under warming, but higher P-concentration (+29%) only in mesic habitats.

3.4 | PFT nutrient responses to perturbations

Spring goose grubbing and summer warming also had opposing effects on PFT leaf N and P concentrations and pools (Figure 4), and the strength of nutrient responses also differed among PFTs.

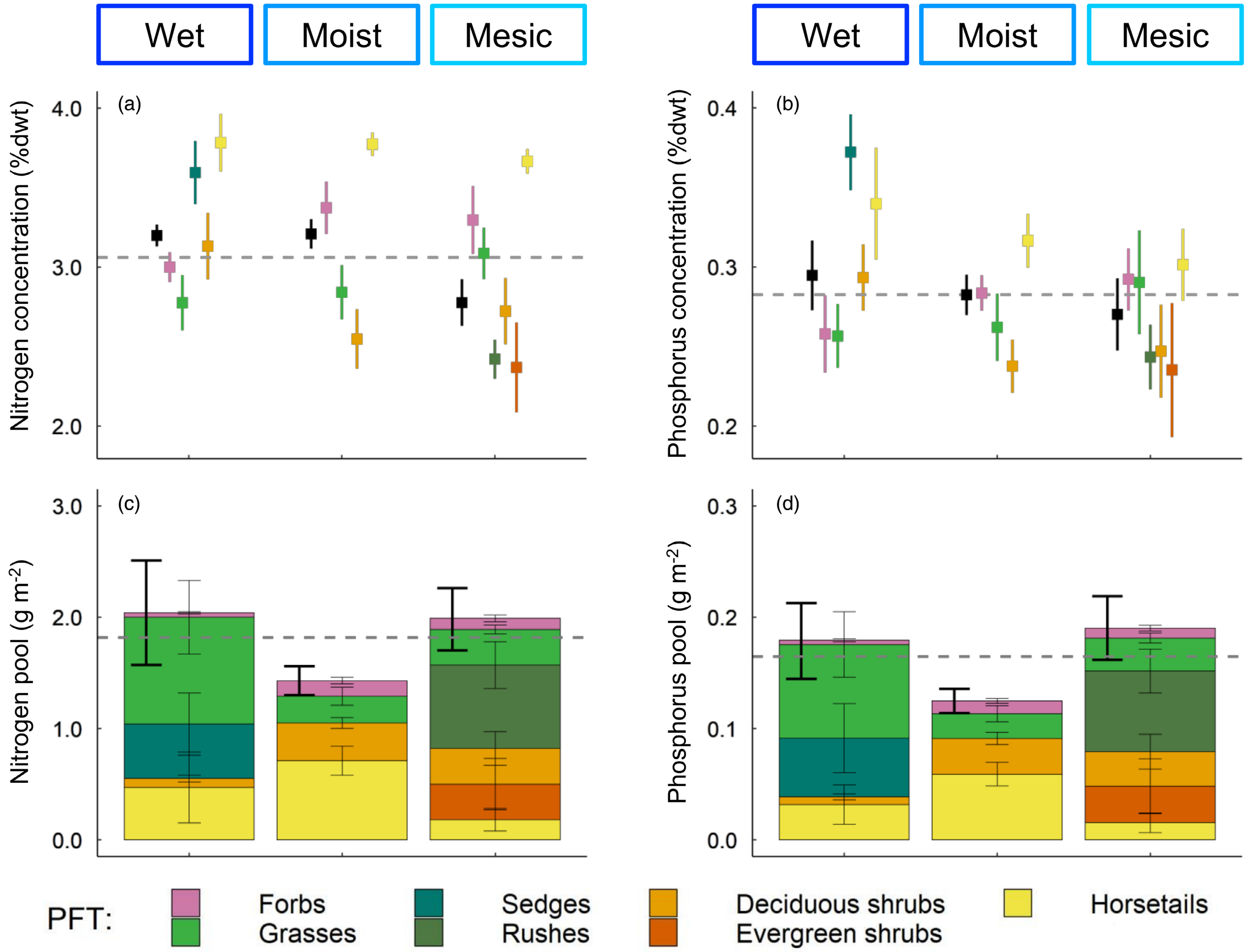

FIGURE 2 Plant-community leaf nutrient levels in absence of environmental perturbations. Plant-community and PFT (a) N- and (b) P-concentration and (c) N- and (d) P-pool in un-manipulated control plots of wet, moist, and mesic habitats. (a, b) Average plant-community (black) and PFT (coloured) N- and P-concentration. Bars are the standard error (SE) of the means. (c, d) Average plant-community N- and P-pool, sorted according to PFTs. Thick and thin bars are the SE of the means for the plant-community and for each PFT, respectively. The grey-dashed lines show the average plant-community nutrient levels across habitats.

In wet habitats (Figure 4a,d), grubbing increased N and P concentrations in forbs and grasses (+20%), whereas warming decreased N-concentration in horsetails (−15%). Forbs and grasses under grubbing had 25% higher nutrient concentrations than those under warming. None of the PFT nutrient pools were affected by perturbations in wet habitats.

In moist habitats (Figure 4b,e), grubbing did not alter nutrient concentrations of any PFTs, while warming decreased N and P concentrations in forbs, horsetails and grasses (range: −12% to −15%). Each of these PFTs under warming had 14%–18% lower N-concentration than that under grubbing. Conversely, only P-concentration in forbs was lower (−21%) under warming than that of forbs under grubbing. Though the only change in nutrient pools was a reduction of N and P in horsetails following grubbing (−64%), both these and the P-pool of grasses were 71% and 56% lower, respectively, under grubbing than under warming.

In mesic habitats (Figure 4c,f), grubbing increased N and P concentrations in grasses (+23%) and N-concentration in horsetails (+19%), while warming did not alter nutrient concentrations of any PFTs. Grasses and horsetails under grubbing had 25% higher N-concentration than those under warming. As well, grasses and deciduous shrubs in grubbed tundra had 29%–35% higher P-concentration than those in warmed tundra. The only change in nutrient pools was an increase of N and P in evergreen shrubs following warming (+150%), which translated to a 4-fold difference compared to pools under grubbing.

4 | DISCUSSION

We show that the spring grubbing activity by geese (a pulse perturbation) and a constant level of elevated summer temperatures (a

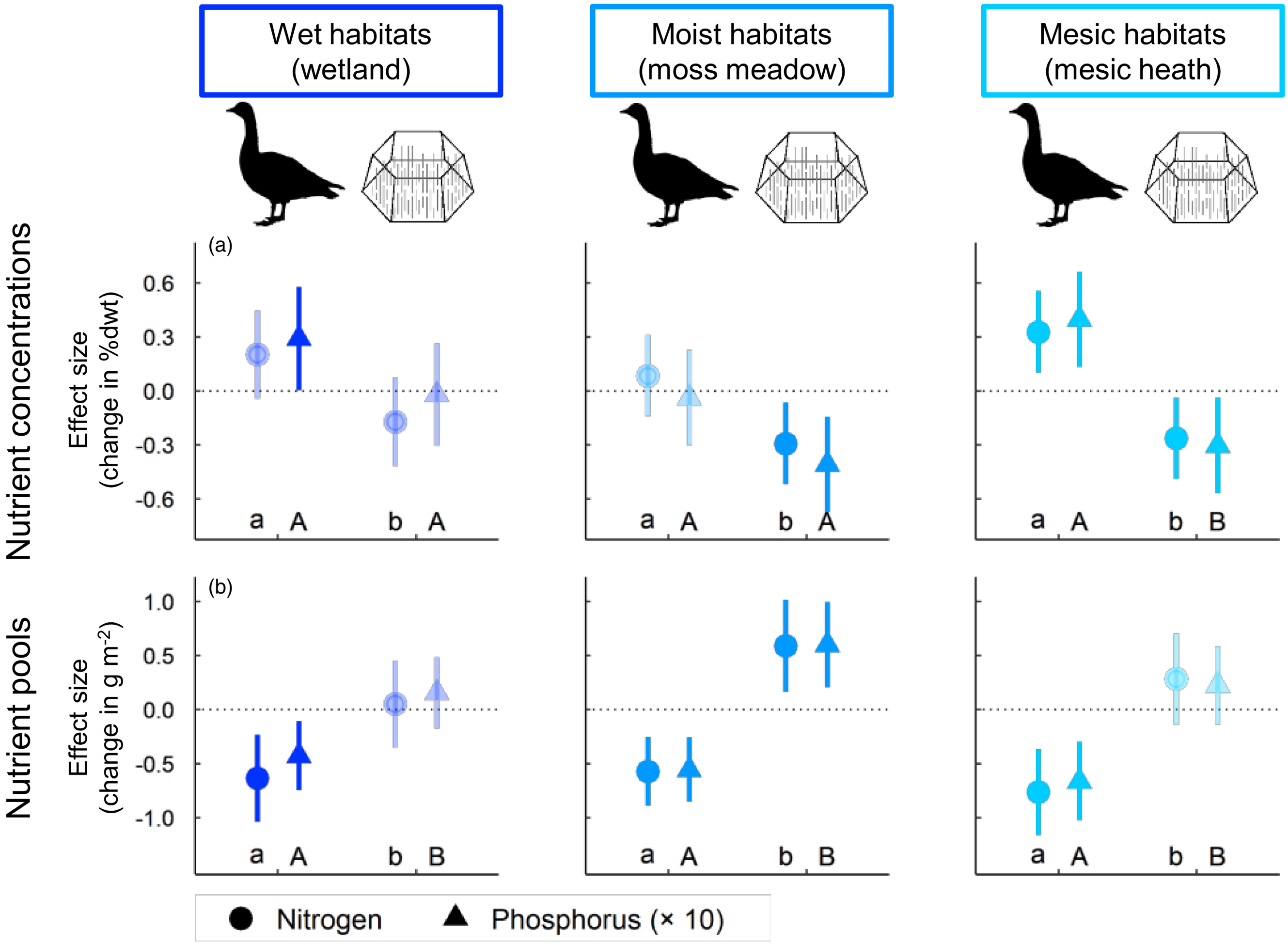

FIGURE 3 Plant-community leaf nutrient responses to environmental perturbations. Effects of spring goose grubbing (pulse perturbation) and summer warming (press perturbation) on plant-community (a) N- and P-concentration and (b) N- and P-pool in wet, moist and mesic habitats (results for nutrient pools were back-transformed on the response scale). Effect sizes and their 95% confidence interval (CI) of experimental treatments are expressed as contrasts to the un-manipulated control plots, that is the reference level denoted with the dotted line at 0 effect size (refer to Figure 2 for plant-community nutrient concentrations and pools in absence of perturbations). Effect sizes (and their CI) in bold colours underline statistically significant effects (i.e. 95% CI not overlapping zero), whereas effect sizes (and their CI) in shaded colours underline non-statistically significant effects. Different letters (lowercase for N levels, uppercase for P levels) at the base of each panel indicate that the difference between grubbing alone and warming alone was statistically significant, as inferred from the 95% CI around the model-estimated effect size. Notice that effect sizes and their CI for P levels have been increased of one order of magnitude (×10) for display purposes. To what extent perturbations altered the difference in nutrient levels among plant communities, that is their nutrient hierarchies, is shown in Figures S7 and S8.

press perturbation), two major global change drivers in the tundra, act as key, short-term modifiers of high-Arctic plant-community nutrient levels. Consistent with our hypotheses, grubbing increased N and P concentrations (relative level of nutrients per unit of leaf dry mass) and decreased N and P pools (absolute amount of nutrients in leaf dry mass per unit area) in plant communities, while warming had the opposite effects. No signs of interactive effects were found. However, nutrient responses to environmental perturbations differed among the three plant communities, as well as across the seven PFTs. Combined, these findings demonstrate that environmental changes have the potential to rapidly, yet differentially, alter plant-community and PFT nutrient concentrations (resource quality) and pools (resource quantity) within and among tundra habitats.

4.1 | Plant-community nutrient responses to perturbations

The observed changes in plant-community leaf nutrient concentrations align with those from studies assessing the short-term effect of goose herbivory (generally positive; Beard et al., 2019; Beaulieu et al., 1996) and warming (generally negative; Doiron et al., 2014; Tolvanen & Henry, 2001) on individual tundra species. Similarly, observed changes in plant-community nutrient pools reflect expectations of a negative effect of herbivores and a positive effect of elevated temperatures on the total amount of nutrients in tundra plants. For example, in a 5-year exclosure experiment in a Canadian low-Arctic ecosystem, caribou decreased the leaf N-pool of the shrub *Betula glandulosa* (Zamin &

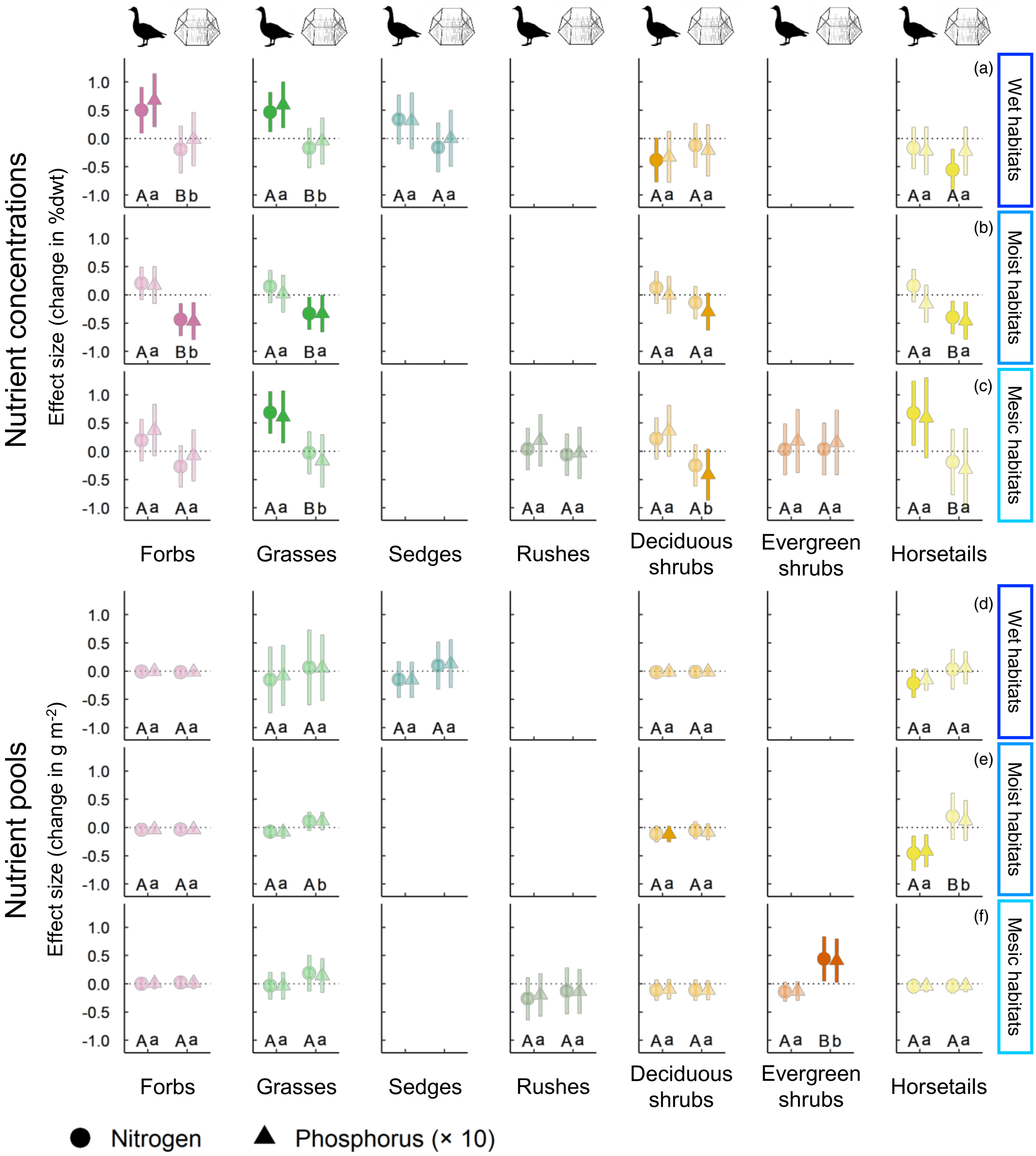

FIGURE 4 Plant functional type leaf nutrient responses to environmental perturbations. Effects of spring goose grubbing and summer warming on PFT (a–c) N- and P-concentration and (d–f) N- and P-pool, separately for wet, moist and mesic habitats. Effect sizes and their 95% confidence interval of experimental treatments are expressed as contrasts to the un-manipulated control plots, that is the reference level at 0 effect size. Effect sizes (and their CI) in bold colours underline either statistically significant (i.e. 95% CI not overlapping zero) or biologically meaningful, close-to-significant (i.e. 90% CI not overlapping zero) effects, whereas effect sizes (and their CI) in shaded colours underline non-statistically significant effects. Different letters at the base of each panel indicate that the difference between grubbing alone and warming alone was statistically significant. Empty panels denote that the PFT was not represented in the plant-community (cf. Table 2). Full interpretation of graph content is provided in the caption of Figure 3. To what extent perturbations altered the difference in nutrient levels among PFTs is shown in Figures S9 and S10.

Grogan, 2013). Doiron et al. (2014) showed that, in high-Arctic Canada, 2 years of experimental warming increased the overall N-pool of five graminoid species grazed by geese, four of which were also found at our sites: *Dupontia fisheri* (grass in wet habitats), *Eriophorum scheuchzeri* (sedge in wet habitats), and *Luzula confusa* and *L. nivalis* (rushes in mesic habitats). Our results expand these earlier findings by showing that the effects of perturbations on nutrient levels of single tundra species can propagate at the community level.

At the community level, the two perturbations elicited peak-summer nutrient-concentration responses of similar magnitude, but with opposite directions. Increases in plant-community N and P concentrations in response to grubbing show that even a short pulse of goose-plant interactions at the onset of the brief high-Arctic summer could provide summer-long, positive effects on resource quality for goslings and other herbivores (e.g. reindeer). This aligns with previous findings from coastal sub-Arctic grazing lawns, where geese can establish positive nutritional legacies for offspring (Beard et al., 2019; Ruess et al., 2019), and from alpine/low-Arctic tundra grasslands, where small-rodent activities in winter can raise plant-community N and P concentrations throughout the following summer (Petit Bon et al., 2022; Petit Bon, Inga, et al., 2020). Conversely, summer warming generally reduced plant-community nutrient concentrations, suggesting potential short-term negative effects of elevated temperatures on resource quality (Doiron et al., 2014), and eventually herbivore fitness (Doiron et al., 2015). Importantly, these opposing effects of grubbing and warming, if maintained until the end of the summer (see e.g. Beard et al., 2019; Welker et al., 1997 for single tundra species), would drive nutrient cycling rates in opposite directions.

Plant-community nutrient-pool responses were larger following grubbing than warming. By removing the moss layer from grubbing holes and the vascular plants growing within them, grubbing caused reductions in the bulk of nutrients held by the three plant communities. This indicates that pulse perturbations in the Arctic tundra (see Ravolainen et al., 2020), such as rodent population peaks (Olofsson et al., 2012) or insect outbreaks (Lund et al., 2017), are important drivers of amount of N and P available to herbivores (Ims & Fuglei, 2005; Petit Bon, Inga, et al., 2020). The fact that, in our study, warming caused overall weaker nutrient-pool responses suggests that the reduction in plant-community nutrient concentrations potentially overrides the positive effects of elevated temperatures on plant biomass (cf. Doiron et al., 2014). Yet, in moss meadows (moist habitats), the warming-induced increase in plant biomass was pronounced enough to promote larger N and P pools despite a negative effect of elevated temperatures on N and P concentrations, as recently shown in *Carex subspathacea* meadows in Northern Alaska (Flint & Meixell, 2021). Therefore, our findings illustrate that tundra plant communities can differ in their immediate nutrient pool responses to perturbations, and that these responses, at least to warming (press perturbation), might or might not be influenced by changes in nutrient concentrations.

Nutrient responses of the three plant communities differed in their magnitude, with wetlands (wet habitats) being the least responsive to perturbations. Several reasons may explain this pattern. First, the water-saturated soil throughout the summer was likely responsible for the only slight increase in soil temperatures within OTCs, which plausibly was too weak to affect the phenological development and productivity of wetlands. Second, the soil in wet habitats had the lowest N concentration, which may constrain the extent to which plant communities respond to herbivory (Bråthen et al., 2007) and higher temperatures (Shaver et al., 2000). Finally, the thick moss layer in these wetlands (Speed et al., 2010) may have provided an efficient protection of the below-ground vascular-plant component from grubbing (Gornall et al., 2009; Petit Bon et al., 2021). These observations underscore the importance of designing field experiments to explicitly account for habitat differences to better understand variations in the effects of perturbations on resource quality and quantity in tundra ecosystems.

4.2 | PFT nutrient responses to perturbations

At the PFT level, the direction of leaf nutrient-concentration responses to goose grubbing and warming was generally consistent with that of whole plant-community responses. However, as predicted, fast-growing PFTs, such as forbs and grasses, displayed overall stronger responses compared to slow-growing PFTs, such as shrubs. These findings generally match with previous studies showing faster responses to perturbations by species and PFTs with a more acquisitive strategy, that is, fast rates of resource acquisition and use, compared to PFTs with a more conservative strategy, that is, slow rates of resource acquisition and use (Freschet et al., 2010; Reich, 2014; Sitters et al., 2019; Wang et al., 2017). This emphasizes the need to untangle individual PFT nutrient responses to better predict their consequences for ecosystem functioning (Myers-Smith et al., 2019).

Our results still revealed a considerable variability in nutrient responses of both fast-growing and most abundant PFTs. The effect of either perturbation on the same fast-growing PFT often differed across habitats. For example, N and P concentrations of grasses were increased by grubbing in wet habitats, but not in moist habitats, while warming reduced grass nutrient concentrations in moist habitats, but not in wet habitats. As for nutrient pools, despite most abundant PFTs (e.g. horsetails and deciduous shrubs in moss meadows and evergreen shrubs in mesic heaths) were typically more responsive than least abundant PFTs (cf. mass ratio hypothesis; Grime, 1998), a consistent response pattern did not emerge. Other responses of PFTs (e.g. their abundance) are known to be spatially variable, as for example it is the case for warming effects mediated by habitat soil moisture (Elmendorf et al., 2012) and reindeer effects varying across tundra sites and vegetation types (Bernes et al., 2015; Sundqvist et al., 2019). Our study shows that there is also conspicuous small-scale spatial variability in PFT nutrient responses to perturbations, which warrants further studies in other Arctic regions.

We illustrate that field data gathered at the level of individual PFTs is a critical tool for quantifying the effects of environmental perturbations on nutrient distribution within plant communities. Both sedges and rushes, which together with grasses are often grouped as 'graminoids', were largely unresponsive to perturbations compared to the more responsive grasses. This stresses the importance of breaking down the frequently used 'graminoids' PFT into its sub-groups when addressing shifts in the nutrient structure of plant communities. In this study, we also considered horsetails separately, which are often merged with herbaceous vegetation when investigating PFT abundance responses. Horsetails, which are an important food source for northern-breeding geese (Fox et al., 2006; Thomas & Prevett, 1982), clearly differed from other PFTs in their N and P levels, as well as in their responses to grubbing and warming. This suggests that their inclusion as a separate PFT can improve our understanding of alterations in resource quality and quantity in tundra following perturbations.

4.3 | Evaluation of methods and results

Results from our field experiment might be more conservative than those expected when addressing naturally occurring goose grubbing and warming. As one of our goals was to compare nutrient responses to environmental perturbations among plant communities, we simulated grubbing with the same intensity across habitats. Our experimental grubbing did not consider possible herbivore patch choices (Van der Wal et al., 2000), as well as it did not account for trampling effects, which generally enhance nutrient availability by favouring the incorporation of litter and faeces into the soil (Tuomi et al., 2021). Further, the increase in air temperature induced by our OTCs (~1°C throughout the warmest month—July) was smaller than the whole-summer average increase of ~1.5°C obtained with OTCs across 35 globally distributed tundra sites (Elmendorf et al., 2012). Thus, the magnitude of warming observed in our study falls within the lower half of the warming intensity achieved through OTCs across tundra ecosystems (Hollister et al., 2022).

We calculated community-weighted means (Garnier et al., 2004) of N and P by including nutrient levels measured on all most abundant species (~99% of the live-leaf biomass within plots). We acknowledge that the below-ground compartment, which in tundra can account for a large part of the whole plant-community biomass (Ottaviani et al., 2020), remains to be explored. We also incorporated intraspecific variability, here obtained by averaging N and P concentrations from 3 to 5 different individuals sampled at each plot, which can increase accuracy and reduce biases when describing the functional structure of plant communities (Carmona et al., 2015). The three plant communities studied here cover together approx. 45% of the Middle Arctic tundra subzone (Subzone C, ~23% of the non-glaciated Arctic; Walker et al., 2005), stressing the potential generality of our findings and their applicability to a wide range of tundra ecosystems.

5 | CONCLUSIONS

We conclude by outlining three take-home messages stemming from the short-term changes in plant-community N and P concentrations (resource quality) and pools (resource quantity) observed in this study. First, spring goose grubbing (a pulse perturbation) and summer warming (a press perturbation) generally had opposing effects on nutrient levels. These have implications as to how resource quality and quantity might be impacted by changing goose populations in a warmer Arctic. Second, we found that different tundra plant communities differ in the magnitude of their N and P responses. This calls for caution when extrapolating nutrient responses to perturbations across habitats, and further suggests that investigating community-specific responses is pivotal to widen our knowledge of the fine-scaled spatial distribution of resource quality and quantity. Third, we revealed that, within communities, PFTs also exhibit different N and P responses, indicating that the variability often observed when addressing PFT abundance responses to perturbations is paralleled by variable nutrient responses.

AUTHOR CONTRIBUTIONS

Matteo Petit Bon, Ingibjörg S. Jónsdóttir, Kari Anne Bråthen and Virve T. Ravolainen conceived the idea and designed methodology. Matteo Petit Bon collected the data, analysed the data and led the writing of the manuscript, for which all authors contributed critically and gave final approval for publication.

ACKNOWLEDGEMENTS

We are grateful to UNIS and its Logistic Department for providing funding, facilities and technical support. Funding for field assistance and material was provided by the Governor of Svalbard (Svalbard Environmental Protection Fund, grant 15/128) and the Research Council of Norway (Arctic Field Grant 269957) (both to Matteo Petit Bon). At a later stage, Matteo Petit Bon was supported by the Czech Science Foundation (grant number 20-13637S) and the National Science Foundation (grant ANS-2113641). Gianluigi Ottaviani was supported by the long-term research development project of the Czech Academy of Sciences (grant RVO-67985939) and by the Czech Science Foundation (grant number 19-28491X). We thank Anton Hochmuth, Calum Bachell and numerous other students for field assistance. The Governor of Svalbard gave permit for fieldwork and sample collection (RiS-ID 10346).

CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest to declare.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14114.

DATA AVAILABILITY STATEMENT

Data are available via DataverseNO UiT Open Research Data Repository https://doi.org/10.18710/KVALRH (Petit Bon et al., 2023).

ORCID

Matteo Petit Bon https://orcid.org/0000-0001-9829-8324
Kari Anne Bråthen https://orcid.org/0000-0003-0942-1074
Virve Tuulia Ravolainen https://orcid.org/0000-0001-8411-7238
Gianluigi Ottaviani https://orcid.org/0000-0003-3027-4638
Hanna Böhner https://orcid.org/0000-0001-7356-5457
Ingibjörg Svala Jónsdóttir https://orcid.org/0000-0003-3804-7077

REFERENCES

Aerts, R., Callaghan, T. V., Dorrepaal, E., Van Logtestijn, R. S. P., & Cornelissen, J. H. C. (2009). Seasonal climate manipulations result in species-specific changes in leaf nutrient levels and isotopic composition in a sub-arctic bog. *Functional Ecology*, *23*(4), 680–688. https://doi.org/10.1111/j.1365-2435.2009.01566.x

Ancin-Murguzur, F. J., Bison, M., Smis, A., Böhner, H., Struyf, E., Meire, P., & Bråthen, K. A. (2019). Towards a global arctic-alpine model for near-infrared reflectance spectroscopy (NIRS) predictions of foliar nitrogen, phosphorus and carbon content. *Scientific Reports*, *9*(1), 8259. https://doi.org/10.1038/s41598-019-44558-9

Arndal, M. F., Illeris, L., Michelsen, A., Albert, K., Tamstorf, M., & Hansen, B. U. (2009). Seasonal variation in gross ecosystem production, plant biomass, and carbon and nitrogen pools in five high Arctic vegetation types. *Arctic, Antarctic, and Alpine Research*, *41*(2), 164–173. https://doi.org/10.1657/1938-4246-41.2.164

Beard, K. H., Choi, R. T., Leffler, A. J., Carlson, L. G., Kelsey, K. C., Schmutz, J. A., & Welker, J. M. (2019). Migratory goose arrival time plays a larger role in influencing forage quality than advancing springs in an Arctic coastal wetland. *PLoS ONE*, *14*, e0213037. https://doi.org/10.1371/journal.pone.0213037

Beaulieu, J., Gauthier, G., & Rochefort, L. (1996). The growth response of graminoid plants to goose grazing in a high Arctic environment. *Journal of Ecology*, *84*(6), 905–914. https://doi.org/10.2307/2960561

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*, 4. https://doi.org/10.1186/s13750-014-0030-3

Bjorkman, A. D., Criado, M. G., Myers-Smith, I. H., Ravolainen, V. T., Jónsdóttir, I. S., Westergaard, K. B., Lawler, J. P., Aronsson, M., Bennett, B., Gardfjell, H., Heiðmarsson, S., Stewart, L., & Normand, S. (2020). Status and trends in Arctic vegetation: Evidence from experimental warming and long-term monitoring. *Ambio*, *49*(3), 678–692. https://doi.org/10.1007/s13280-019-01161-6

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Georges, D., Goetz, S. J., Guay, K. C., Henry, G. H. R., HilleRisLambers, J., Hollister, R. D., Karger, D. N., Kattge, J., Manning, P., … Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, *562*, 57–62. https://doi.org/10.1038/s41586-018-0563-7

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Bråthen, K. A., & Hagberg, O. (2004). More efficient estimation of plant biomass. *Journal of Vegetation Science*, *15*(5), 653–660. https://doi.org/10.1111/j.1654-1103.2004.tb02307.x

Bråthen, K. A., Ims, R. A., Yoccoz, N. G., Fauchald, P., Tveraa, T., & Hausner, V. H. (2007). Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems*, *10*, 773–789. https://doi.org/10.1007/s10021-007-9058-3

Bråthen, K. A., Pugnaire, F. I., & Bardgett, R. D. (2021). The paradox of forbs in grasslands and the legacy of the mammoth steppe. *Frontiers in Ecology and the Environment*, *19*(10), 584–592. https://doi.org/10.1002/fee.2405

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.3929/ethz-b-000240890

Carmona, C. P., Rota, C., Azcárate, F. M., & Peco, B. (2015). More for less: Sampling strategies of plant functional traits across local environmental gradients. *Functional Ecology*, *29*(4), 579–588. https://doi.org/10.1111/1365-2435.12366

Chapin, F. S., Bret-Harte, M. S., Hobbie, S. E., & Zhong, H. (1996). Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science*, *7*(3), 347–358. https://doi.org/10.2307/3236278

Chapin, F. S., Matson, P. A., Mooney, H. A., & Vitousek, P. M. (2012). *Principles of terrestrial ecosystem ecology* (2nd ed.). SpringerLink.

Choi, R. T., Petit Bon, M., Leffler, A. J., Kelsey, K. C., Welker, J. M., & Beard, K. H. (2022). Short-term effects of experimental goose grazing and warming differ in three low-Arctic coastal wetland plant communities. *Journal of Vegetation Science*, *33*(3), e13139. https://doi.org/10.1111/jvs.13139

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., Van Bodegom, P., Brovkin, V., Chatain, A., … Westoby, M. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, *11*(10), 1065–1071. https://doi.org/10.1111/j.1461-0248.2008.01219.x

Doiron, M., Gauthier, G., & Lévesque, E. (2014). Effects of experimental warming on nitrogen concentration and biomass of forage plants for an arctic herbivore. *Journal of Ecology*, *102*(2), 508–517. https://doi.org/10.1111/1365-2745.12213

Doiron, M., Gauthier, G., & Lévesque, E. (2015). Trophic mismatch and its effects on the growth of young in an Arctic herbivore. *Global Change Biology*, *21*(12), 4364–4376. https://doi.org/10.1111/gcb.13057

Dormann, C. F., & Woodin, S. J. (2002). Climate change in the Arctic: Using plant functional types in a meta-analysis of field experiments. *Functional Ecology*, *16*(1), 4–17. https://doi.org/10.1046/j.0269-8463.2001.00596.x

Dorrepaal, E. (2007). Are plant growth-form-based classifications useful in predicting northern ecosystem carbon cycling feedbacks to climate change? *Journal of Ecology*, *95*(6), 1167–1180. https://doi.org/10.1111/j.1365-2745.2007.01294.x

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., Collier, L. S., Cooper, E. J., Cornelissen, J. H. C., Day, T. A., Fosaa, A. M., Gould, W. A., Grétarsdóttir, J., Harte, J., Hermanutz, L., Hik, D. S., Hofgaard, A., Jarrad, F., Jónsdóttir, I. S., … Wookey, P. A. (2012). Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. *Ecology Letters*, *15*(2), 164–175. https://doi.org/10.1111/j.1461-0248.2011.01716.x

Fauteux, D., Stien, A., Yoccoz, N. G., Fuglei, E., & Ims, R. A. (2021). Climate variability and density-dependent population dynamics: Lessons from a simple high Arctic ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(37), e2106635118. https://doi.org/10.1073/pnas.2106635118

Flint, P. L., & Meixell, B. (2021). Response of forage plants to alteration of temperature and spring thaw date: Implications for geese in a warming Arctic. *Ecosphere*, *12*(7), e03627. https://doi.org/10.1002/ecs2.3627

Fox, T. A. D., & Abraham, K. F. (2017). Why geese benefit from the transition from natural vegetation to agriculture. *Ambio*, *46*, 188–197. https://doi.org/10.1007/s13280-016-0879-1

Fox, T. A. D., & Bergersen, E. (2005). Lack of competition between barnacle geese *Branta leucopsis* and pink-footed geese *Anser brachyrhynchus* during the pre-breeding period in Svalbard. *Journal of Avian Biology*, *36*(3), 173–178. https://doi.org/10.1111/j.0908-8857.2005.03540.x

Fox, T. A. D., Francis, I. S., & Bergersen, E. (2006). Diet and habitat use of Svalbard pink-footed geese *Anser brachyrhynchus* during arrival and pre-breeding periods in Adventdalen. *Ardea*, *94*, 691–699.

Fox, T. A. D., & Madsen, J. (2017). Threatened species to super-abundance: The unexpected international implications of successful goose conservation. *Ambio*, *46*, 179–187. https://doi.org/10.1007/s13280-016-0878-2

Freschet, G. T., Cornelissen, J. H. C., Van Logtestijn, R. S. P., & Aerts, R. (2010). Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology*, *98*(2), 362–373. https://doi.org/10.1111/j.1365-2745.2009.01615.x

Fuglei, E., Stien, A., Yoccoz, N. G., Ims, R. A., Eide, N. E., Prestrud, P., Deplazes, P., & Oksanen, A. (2008). Spatial distribution of *Echinococcus multilocularis*, Svalbard, Norway. *Emerging Infectious Diseases*, *14*(1), 73–75. https://doi.org/10.3201/eid1401.070565

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., & Toussaint, J.-P. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, *85*(9), 2630–2637. https://doi.org/10.1890/03-0799

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., 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*, 747–758. https://doi.org/10.1007/s00442-009-1427-5

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, *86*(6), 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Grime, J. P., Cornelissen, J. H. C., Thompson, K., & Hodgson, J. G. (1996). Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. *Oikos*, *77*(3), 489–494. https://doi.org/10.2307/3545938

Henry, G. H. R., & Molau, U. (1997). Tundra plants and climate change: The international tundra experiment (ITEX). *Global Change Biology*, *3*(S1), 1–9. https://doi.org/10.1111/j.1365-2486.1997.gcb132.x

Hobbie, S. E., Nadelhoffer, K. J., & Högberg, P. (2002). A synthesis: The role of nutrients as constraints on carbon balances in boreal and arctic regions. *Plant and Soil*, *242*, 163–170. https://doi.org/10.1023/A:1019670731128

Hollister, R. D., Elphinstone, C., Henry, G. H. R., Bjorkman, A. D., Klanderud, K., Björk, R. G., Björkman, M. P., Bokhorst, S., Carbognani, M., Cooper, E. J., Dorrepaal, E., Elmendorf, S. C., Fetcher, N., Gallois, E. C., Guðmundsson, J., Healey, N. C., Jónsdóttir, I. S., Klarenberg, I. J., Oberbauer, S. F., … Wookey, P. A. (2022). A review of open top chamber (OTC) performance across the ITEX network. *Arctic Science*, e-First, 1–14. https://doi.org/10.1139/as-2022-0030

Hudson, J. M., & Henry, G. H. R. (2010). High Arctic plant community resists 15 years of experimental warming. *Journal of Ecology*, *98*(5), 1035–1041. https://doi.org/10.1111/j.1365-2745.2010.01690.x

Ims, R. A., & Fuglei, E. (2005). Trophic interaction cycles in tundra ecosystems and the impact of climate change. *BioScience*, *55*(4), 311–322. https://doi.org/10.1641/0006-3568(2005)055%5B0311:TICITE%5D2.0.CO;2

Jefferies, R. L., Jano, A. P., & Abraham, K. F. (2006). A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology*, *94*(1), 234–242.

Jensen, R. A., Madsen, J., O'Connell, M., Wisz, M. S., Tømmervik, H., & Mehlum, F. (2008). Prediction of the distribution of Arctic-nesting pink-footed geese under a warmer climate scenario. *Global Change Biology*, *14*(1), 1–10. https://doi.org/10.1111/j.1365-2486.2007.01461.x

Johansen, B. E., Karlsen, S. R., & Tømmervik, H. (2012). Vegetation mapping of Svalbard utilising Landsat TM/ETM+ data. *Polar Record*, *48*(S1), 47–63. https://doi.org/10.1017/S0032247411000647

Jones, M. H., Bay, C., & Nordenhäll, U. (1997). Effects of experimental warming on arctic willows (*Salix* spp.): A comparison of responses from the Canadian high Arctic, Alaskan Arctic, and Swedish subarctic. *Global Change Biology*, *3*(S1), 55–60. https://doi.org/10.1111/j.1365-2486.1997.gcb135.x

Lameris, T. K., Jochems, F., van der Graaf, A. J., Andersson, M., Limpens, J., & Nolet, B. A. (2017). Forage plants of an Arctic-nesting herbivore show larger warming response in breeding than wintering grounds, potentially disrupting migration phenology. *Ecology and Evolution*, *7*(8), 2652–2660. https://doi.org/10.1002/ece3.2859

Lavorel, S., Grigulis, K., Lamarque, P., Colace, M. P., Garden, D., Girel, J., Pellet, G., & Douzet, R. (2011). Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology*, *99*(1), 135–147. https://doi.org/10.1111/j.1365-2745.2010.01753.x

Legendre, P., & Legendre, L. (2012). *Numerical ecology* (2nd ed.). Elsevier.

Lenth, R. V. (2021). *Emmeans: Estimated marginal means, aka least-squares means*. R package version 1.5-4. https://CRAN.R-project.org/package=emmeans

Lund, M., Raundrup, K., Westergaard-Nielsen, A., López-Blanco, E., Nymand, J., & Aastrup, P. (2017). Larval outbreaks in West Greenland: Instant and subsequent effects on tundra ecosystem productivity and CO_2 exchange. *Ambio*, *46*, 26–38. https://doi.org/10.1007/s13280-016-0863-9

Madsen, J., Jaspers, C., Tamstorf, M., Mortensen, C. E., & Rigét, F. (2011). Long-term effects of grazing and global warming on the composition and carrying capacity of graminoid marshes for moulting geese in East Greenland. *Ambio*, *40*, 638–649. https://doi.org/10.1007/s13280-011-0170-4

Madsen, J., Jensen, G. H., Cottaar, F., Amstrup, O., Asferg, T., Bak, M., Bakken, J., Balsby, T. J. S., Christensen, T. K., Clausen, K. K., Frikke, J., Gundersen, O. M., Günther, K., Kjeldsen, J. P., Koffijberg, K., Kruckenberg, H., Kuijken, E., Månsson, J., Nicolaisen, P. I., … Verscheure, C. (2017). *Svalbard pink-footed goose. Population status report 2016–2017.* Danish Centre for Environment and Energy (Aarhus University).

Molau, U., & Mølgaard, P. E. (1996). *ITEX manual*. Danish Polar Center.

Myers-Smith, I. H., Thomas, H. J. D., & Bjorkman, A. D. (2019). Plant traits inform predictions of tundra responses to global change. *New Phytologist*, *221*(4), 1742–1748. https://doi.org/10.1111/nph.15592

Nordli, Ø., Wyszyński, P., Gjelten, H., Isaksen, K., Łupikasza, E., Niedźwiedź, T., & Przybylak, R. (2020). Revisiting the extended Svalbard airport monthly temperature series, and the compiled corresponding daily series 1898–2018. *Polar Research*, *39*, 3614.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens,

M. H. H., Szoecs, E., & Wagner, H. (2020). *Vegan: Community ecology package*. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Olofsson, J., Tømmervik, H., & Callaghan, T. V. (2012). Vole and lemming activity observed from space. *Nature Climate Change*, *2*, 880–883. https://doi.org/10.1038/nclimate1537

Ottaviani, G., Molina-Venegas, R., Charles-Dominique, T., Chelli, S., Campetella, G., Canullo, R., & Klimešová, J. (2020). The neglected belowground dimension of plant dominance. *Trends in Ecology & Evolution*, *35*(9), 763–766. https://doi.org/10.1016/j.tree.2020.06.006

Pedersen, Å. Ø., Speed, J. D. M., & Tombre, I. M. (2013). Prevalence of pink-footed goose grubbing in the arctic tundra increases with population expansion. *Polar Biology*, *36*, 1569–1575. https://doi.org/10.1007/s00300-013-1374-9

Petit Bon, M., Böhner, H., Bråthen, K. A., Ravolainen, V. T., & Jónsdóttir, I. S. (2021). Variable responses of carbon and nitrogen contents in vegetation and soil to herbivory and warming in high-Arctic tundra. *Ecosphere*, *12*(9), e03746. https://doi.org/10.1002/ecs2.3746

Petit Bon, M., Böhner, H., Kaino, S., Moe, T., & Bråthen, K. A. (2020). One leaf for all: Chemical traits of single leaves measured at the leaf surface using near-infrared reflectance spectroscopy. *Methods in Ecology and Evolution*, *11*(9), 1061–1071. https://doi.org/10.1111/2041-210X.13432

Petit Bon, M., Bråthen, K. A., Ravolainen, V. T., Böhner, H., & Jónsdóttir, I. S. (2023). Replication data for: Herbivory and warming have opposing short-term effects on plant-community nutrient levels across high-Arctic tundra habitats. *DataverseNO UiT Open Research Data Repository*, https://doi.org/10.18710/KVALRH

Petit Bon, M., Inga, K. G., Jónsdóttir, I. S., Utsi, T. A., Soininen, E. M., & Bråthen, K. A. (2020). Interactions between winter and summer herbivory affect spatial and temporal plant nutrient dynamics in tundra grassland communities. *Oikos*, *129*(8), 1229–1242. https://doi.org/10.1111/oik.07074

Petit Bon, M., Inga, K. G., Utsi, T. A., Jónsdóttir, I. S., & Bråthen, K. A. (2022). Forage quality in tundra grasslands under herbivory: Silicon-based defences, nutrients and their ratios in grasses. *Journal of Ecology*, *110*(1), 129–143. https://doi.org/10.1111/1365-2745.13790

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, *3*, 168. https://doi.org/10.1038/s43247-022-00498-3

Ravolainen, V. T., Soininen, E. M., Jónsdóttir, I. S., Eischeid, I., Forchhammer, M., Van der Wal, R., & Pedersen, Å. Ø. (2020). High Arctic ecosystem states: Conceptual models of vegetation change to guide long-term monitoring and research. *Ambio*, *49*, 666–677. https://doi.org/10.1007/s13280-019-01310-x

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211

Rønning, O. I. (1996). *The Flora of Svalbard*. Norwegian Polar Institute.

Ruess, R. W., McFarland, J., Person, B., & Sedinger, J. S. (2019). Geese mediate vegetation state changes with parallel effects on N cycling that leave nutritional legacies for offspring. *Ecosphere*, *10*(8), e02850. https://doi.org/10.1002/ecs2.2850

Shaver, G. R., Canadell, J., Chapin, F. S., Gurevitch, J., Harte, J., Henry, G. H. R., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L., & Rustad, L. (2000). Global warming and terrestrial ecosystems: A conceptual framework for analysis. *BioScience*, *50*(10), 871–882. https://doi.org/10.1641/0006-3568(2000)050%5B0871:GWATEA%5D2.0.CO;2

Sitters, J., Cherif, M., Egelkraut, D., Giesler, R., & Olofsson, J. (2019). Long-term heavy reindeer grazing promotes plant phosphorus limitation in arctic tundra. *Functional Ecology*, *33*(7), 1233–1242. https://doi.org/10.1111/1365-2435.13342

Sjögersten, S., Van der Wal, R., & Woodin, S. J. (2006). Small-scale hydrological variation determines landscape CO_2 fluxes in the high Arctic. *Biogeochemistry*, *80*, 205–216. https://doi.org/10.1007/s10533-006-9018-6

Speed, J. D. M., Cooper, E. J., Jónsdóttir, I. S., Van der Wal, R., & Woodin, S. J. (2010). Plant community properties predict vegetation resilience to herbivore disturbance in the Arctic. *Journal of Ecology*, *98*(5), 1002–1013. https://doi.org/10.1111/j.1365-2745.2010.01685.x

Speed, J. D. M., Skjelbred, I. Å., Barrio, I. C., Martin, M. D., Berteaux, D., Bueno, C. G., Christie, K. S., Forbes, B. C., Forbey, J., Fortin, D., Grytnes, J.-A., Hoset, K. S., Lecomte, N., Marteinsdóttir, B., Mosbacher, J. B., Pedersen, Å. Ø., Ravolainen, V. T., Rees, E. C., Skarin, A., … Soininen, E. M. (2019). Trophic interactions and abiotic factors drive functional and phylogenetic structure of vertebrate herbivore communities across the Arctic tundra biome. *Ecography*, *42*(6), 1152–1163. https://doi.org/10.1111/ecog.04347

Speed, J. D. M., Woodin, S. J., Tømmervik, H., Tamstorf, M. P., & Van der Wal, R. (2009). Predicting habitat utilization and extent of ecosystem disturbance by an increasing herbivore population. *Ecosystems*, *12*, 349–359. https://doi.org/10.1007/s10021-009-9227-7

Sterner, R. W., & Elser, J. J. (2002). *Ecological stoichiometry: The biology of elements from molecules to the biosphere*. Princeton University Press.

Street, L. E., Mielke, N., & Woodin, S. J. (2017). Phosphorus availability determines the response of tundra ecosystem carbon stocks to nitrogen enrichment. *Ecosystems*, *21*, 1155–1167. https://doi.org/10.1007/s10021-017-0209-x

Sundqvist, M. K., Liu, Z., Giesler, R., & Wardle, D. A. (2014). Plant and microbial responses to nitrogen and phosphorus addition across an elevational gradient in subarctic tundra. *Ecology*, *95*(7), 1819–1835. https://doi.org/10.1890/13-0869.1

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

Thomas, H. J. D., Myers-Smith, I. H., Bjorkman, A. D., Elmendorf, S. C., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Hollister, R. D., Normand, S., Prevéy, J. S., Rixen, C., Schaepman-Strub, G., Wilmking, M., Wipf, S., Cornwell, W. K., Kattge, J., Goetz, S. J., Guay, K. C., Alatalo, J. M., … van Bodegom, P. (2018). Traditional plant functional groups explain variation in economic but not size-related traits across the tundra biome. *Global Ecology and Biogeography*, *28*(2), 78–95. https://doi.org/10.1111/geb.12783

Thomas, V., & Prevett, J. (1982). The role of horsetails (Equisetaceae) in the nutrition of northern-breeding geese. *Oecologia*, *53*, 359–363. https://doi.org/10.1007/BF00389014

Tolvanen, A., & Henry, G. H. R. (2001). Responses of carbon and nitrogen concentrations in high arctic plants to experimental warming. *Canadian Journal of Botany*, *79*(6), 711–718. https://doi.org/10.1139/b01-052

Tuomi, M., Väisänen, M., Ylänne, H., Brearley, F. Q., Barrio, I. C., Bråthen, K. A., Eischeid, I., Forbes, B. C., Jónsdóttir, I. S., Kolstad, A. L., Macek, P., Petit Bon, M., Speed, J. D. M., Stark, S., Svavarsdóttir, K., Thórsson, J., & Bueno, C. G. (2021). Stomping in silence: Conceptualizing trampling effects on soils in polar tundra. *Functional Ecology*, *35*(2), 306–317. https://doi.org/10.1111/1365-2435.13719

Van der Wal, R., Madan, N., van Lieshout, S., Dormann, C., Langvatn, R., & Albon, S. D. (2000). Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. *Oecologia*, *123*, 108–115. https://doi.org/10.1007/s004420050995

Vitousek, P. M., Porder, S., Houlton, B. Z., & Chadwick, O. A. (2010). Terrestrial phosphorus limitation: Mechanisms, implications, and nitrogen–phosphorus interactions. *Ecological Applications*, *20*(1), 5–15. https://doi.org/10.1890/08-0127.1

Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov,

E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A., & The Other Members of the CAVM Team. (2005). The circumpolar Arctic vegetation map. *Journal of Vegetation Science*, *16*(3), 267–282. https://doi.org/10.1111/j.1654-1103.2005.tb02365.x

Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., Epstein, H. E., Jónsdóttir, I. S., Klein, J. A., Magnússon, B., Molau, U., Oberbauer, S. F., Rewa, S. P., Robinson, C. H., Shaver, G. R., … Wookey, P. A. (2006). Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(5), 1342–1346. https://doi.org/10.1073/pnas.0503198103

Wang, P., Limpens, J., Mommer, L., van Ruijven, J., Nauta, A. L., Berendse, F., Schaepman-Strub, G., Blok, D., Maximov, T. C., & Heijmans, M. M. (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

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., van der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, *304*(5677), 1629–1633. https://doi.org/10.1126/science.1094875

Weegman, M. D., Alisauskas, R. T., Kellett, D. K., Zhao, Q., Wilson, S., & Telenský, T. (2022). Local population collapse of Ross's and lesser snow geese driven by failing recruitment and diminished philopatry. *Oikos*, *2022*(5), e09184. https://doi.org/10.1111/oik.09184

Welker, J. M., Molau, U., Parsons, A. N., Robinson, C. H., & Wookey, P. (1997). Responses of *Dryas octopetala* to ITEX environmental manipulations: A synthesis with circumpolar comparisons. *Global Change Biology*, *3*(S1), 61–73. https://doi.org/10.1111/j.1365-2486.1997.gcb143.x

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. SpringerLink.

Wookey, P. A., Aerts, R., Bardgett, R. D., Baptist, F., Bråthen, K. A., Cornelissen, J. H. C., Gough, L., Hartley, I. P., Hopkins, D. W., Lavorel, S., & Shaver, G. R. (2009). Ecosystem feedbacks and cascade processes: Understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology*, *15*(5), 1153–1172. https://doi.org/10.1111/j.1365-2486.2008.01801.x

Yue, K., Peng, Y., Fornara, D. A., Van Meerbeek, K., Vesterdal, L., Yang, W., Peng, C., Tan, B., Zhou, W., Xu, Z., Ni, X., Zhang, L., Wu, F., & Svenning, J.-C. (2019). Responses of nitrogen concentrations and pools to multiple environmental change drivers: A meta-analysis across terrestrial ecosystems. *Global Ecology and Biogeography*, *28*(5), 690–724. https://doi.org/10.1111/geb.12884

Zacheis, A., Hupp, J. W., & Ruess, R. W. (2001). Effects of migratory geese on plant communities of an Alaskan salt marsh. *Journal of Ecology*, *89*(1), 57–71. https://doi.org/10.1046/j.1365-2745.2001.00515.x

Zamin, T. J., & Grogan, P. (2013). Caribou exclusion during a population low increases deciduous and evergreen shrub species biomass and nitrogen pools in low Arctic tundra. *Journal of Ecology*, *101*(3), 671–683. https://doi.org/10.1111/1365-2745.12082

Zhang, Y. (2013). Likelihood-based and Bayesian methods for Tweedie compound Poisson linear mixed models. *Statistics and Computing*, *23*, 743–757. https://doi.org/10.1007/s11222-012-9343-7

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Effects of environmental perturbations on plot-scale July temperatures in 2017.

Table S2: Parameter estimates for the generalized linear mixed-effects models for the effects of environmental perturbations on plant-community leaf N- and P-concentration.

Table S3: Parameter estimates for the generalized linear mixed-effects models for the effects of environmental perturbations on plant-community leaf N- and P-pool.

Table S4: Parameter estimates for the generalized linear mixed-effects models for the effects of environmental perturbations on PFT leaf N- and P-concentration in wet habitats.

Table S5: Parameter estimates for the generalized linear mixed-effects models for the effects of environmental perturbations on PFT leaf N- and P-concentration in moist habitats.

Table S6: Parameter estimates for the generalized linear mixed-effects models for the effects of environmental perturbations on PFT leaf N- and P-concentration in mesic habitats.

Table S7: Parameter estimates for the generalized linear mixed-effects models for the effects of environmental perturbations on PFT leaf N- and P-pool in wet habitats.

Table S8: Parameter estimates for the generalized linear mixed-effects models for the effects of environmental perturbations on PFT leaf N- and P-pool in moist habitats.

Table S9: Parameter estimates for the generalized linear mixed-effects models for the effects of environmental perturbations on PFT leaf N- and P-pool in mesic habitats.

Figure S1: Natural and simulated spring grubbing by pink-footed geese.

Figure S2: Relative contribution of each PFT to plant-community live-leaf biomass in the three habitats.

Figure S3: Absolute contribution of each PFT to plant-community live-leaf biomass in the three habitats.

Figure S4: Differences in plant-community PFT composition between the three habitats.

Figure S5: Correlations between plant-community leaf nutrient pools and plant-community live-leaf biomass.

Figure S6: Correlations between plant-community leaf N and P levels.

Figure S7: Effects of environmental perturbations on the difference in leaf N-concentration and leaf N-pool among plant communities.

Figure S8: Effects of environmental perturbations on the difference in leaf P-concentration and leaf P-pool among plant communities.

Figure S9: Effects of environmental perturbations on the difference in leaf N-concentration and leaf N-pool among PFTs.

Figure S10: Effects of environmental perturbations on the difference in leaf P-concentration and leaf P-pool among PFTs.

How to cite this article: Petit Bon, M., Bråthen, K. A., Ravolainen, V. T., Ottaviani, G., Böhner, H., & Jónsdóttir, I. S. (2023). Herbivory and warming have opposing short-term effects on plant-community nutrient levels across high-Arctic tundra habitats. *Journal of Ecology*, *111*, 1514–1530. https://doi.org/10.1111/1365-2745.14114