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Upslope release—Downslope receipt? Multi-year plant uptake of permafrost-released nitrogen along an arctic hillslope

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Abstract

1. As arctic permafrost continues to thaw, previously inaccessible nitrogen (N) becomes available to N-limited arctic plants. Increased N availability could enhance plant growth and thereby potentially offset climate-induced carbon release. Arctic plants can take up newly available permafrost-N locally upon release. However, in a topographically diverse arctic landscape, permafrost-N may be transported along hillslopes, away from the point-of-release. The extent to which topographical N transport can impact arctic vegetation change depends on whether N is retained locally, captured by downslope recipient plant communities, or transported away.

2. We used stable isotope labelling (15N) to simulate upslope release of ammonium (NH4+) and nitrate (NO3−) from thawing permafrost on an arctic hillslope, western Greenland. We tracked the plant species-specific uptake of simulated permafrost-released N from the upslope point-of-release to the bottom of the slope through 4 years.

3. We found that arctic tundra plants successfully acquired locally released permafrost-N, even in sloping terrain, and that N was strongly retained in the plant–soil system through multiple years. At the same time, we also importantly demonstrate that permafrost-N can be transported and taken up by plants up to 30 m downslope from the point-of-release. Especially NO3− was more easily redistributed vertically within the soil column compared to NH4+ and therefore potentially more accessible to plants. Specifically, plant species with fast N uptake capacity and deep-soil foraging strategies may have competitive advantages for capitalising on deep-soil released and topographically transported permafrost-N (here exemplified by Equisetum arvense and Salix glauca). Nevertheless, even mosses gained access to permafrost-N via vertical and lateral redistribution on the slope. Ultimately, the intricate balance between strong local N retention, downslope transport and plant species-specific uptake strategies may contribute to shaping arctic vegetation change.

4. Synthesis. Across spatially complex arctic ecosystems, arctic plants can take up permafrost-released N both at the local point-of-release and at a considerable distance downslope. The potential for arctic plants to take advantage...
INTRODUCTION

As arctic permafrost continues to thaw, N availability increases in the deep active layer soil, which may provide an important nutrient input to N-limited arctic plants (Beermann et al., 2017; Keuper et al., 2012; Salmon et al., 2018). This increased N availability is driven by both direct release of N in plant-available chemical forms and organic matter decomposition of newly thawed permafrost soil (Elberling et al., 2010; Keuper et al., 2012). Even though this N-release occurs in the deep soil, at the interface between permafrost and active layer soil, arctic plants have the capacity to take up this newly available N locally at the point-of-release (Blume-Werry et al., 2019; Hewitt et al., 2018; Keuper et al., 2017; Pedersen et al., 2020; Wang et al., 2018; Zhu et al., 2016). However, in an undulating arctic landscape, N may be transported downslope via topographical and hydrological pathways (Harms & Jones Jr, 2012; Harms & Ludwig, 2016; McNamara et al., 1999). The question therefore arises whether upslope-released permafrost-N can benefit downslope plant communities, and specifically where, when and which plant species acquire topographically transported N.

In permafrost ecosystems, plant N acquisition is restricted to the seasonally thawed active layer soil (Blume-Werry et al., 2019; Iversen et al., 2015), beneath which the permafrost table creates an impermeable barrier that results in downslope movement of water and dissolved nutrients (McNamara et al., 1999). The extent to which N is transported downslope depends on slope gradient (Yano et al., 2010), surface and subsurface hydrology (Harms & Ludwig, 2016), microtopography of the permafrost table (Wright et al., 2009), soil characteristics (Yano et al., 2010), timing and extent of snowmelt and summer precipitation events (Harms & Jones Jr, 2012; McNamara et al., 2008; Yano et al., 2010). Therefore, as a consequence of permafrost thaw, the combination of increased N-release and hydrological changes could accelerate deep-soil N transport (Harms & Jones Jr, 2012; McNamara et al., 2008; Petrone et al., 2006), potentially making these nutrients available to plants located at a distance from the point-of-release.

Transport and plant uptake of N along arctic hillslopes also depend on the form in which N is released. Among other N-ions, thawing permafrost soils release inorganic N in the form of ammonium (NH$_4^+$) (Beermann et al., 2017; Elberling et al., 2010; Keuper et al., 2012), which can be converted into nitrate (NO$_3^-$) via nitrification (Oulehle et al., 2016). While NH$_4^+$ has relatively low mobility and is commonly preferred by plants and thus immobilised (Clemmensen et al., 2008; Sorensen, Clemmensen, et al., 2008), NO$_3^-$ is more soluble and has a high potential for export (Harms & Jones Jr, 2012; McClelland et al., 2007; Petrone et al., 2006). Hence, the N-form upon release may contribute to determining both the transport potential of, but also plant access to N along arctic hillslopes.

The ecosystem implications of downslope N movement are intricately linked to plant access and uptake. Strong N-limitation renders arctic plants efficient at capturing and retaining available N (Andresen et al., 2008; Clemmensen et al., 2008; Pedersen et al., 2020; Yano et al., 2010). However, since permafrost-N is released at a depth where biological retention is reduced due to low root biomass, downslope-moving deep-soil N may bypass shallow-rooted plants (Blume-Werry et al., 2019; Harms & Jones Jr, 2012). Consequently, N may be lost from the ecosystem, unless plants gain access to this N via processes of vertical redistribution through palsa formation (Seppälä, 2011), mycelial networks (Hewitt et al., 2020), or vertical recycling via root and leaf litter inputs (Blume-Werry et al., 2019; DeMarco et al., 2014; Hobbie & Horton, 2007; Marsh et al., 2000; Pedersen et al., 2020). Furthermore, plant N uptake may be dictated by species-specific characteristics, including rooting depth (Blume-Werry et al., 2019; Hewitt et al., 2018; Iversen et al., 2015; Keuper et al., 2017), mycorrhizal associations (Andresen et al., 2008; Hewitt et al., 2018, 2020; Michelsen et al., 1998), N-form preference (Clemmensen et al., 2008; Liu et al., 2018; McKane et al., 2002; Sorensen, Clemmensen, et al., 2008) or growth form (Andresen et al., 2020; McKane et al., 2002; Oulehle et al., 2016; Sloan et al., 2016; Sorensen, Clemmensen, et al., 2008). Thus, the extent to which permafrost-released N may benefit arctic plant communities locally and downslope from the point-of-release depends on which plant species can capture and make use of the available N before potential export.

Hitherto, studies investigating plant uptake of permafrost-released N have focused on local N uptake in non-sloping terrain (Blume-Werry et al., 2019; Hewitt et al., 2018; Keuper et al., 2017; Pedersen et al., 2020; Wang et al., 2018; Zhu et al., 2016). Studies of N transport along arctic hillslopes have mostly been directed towards the physical mechanisms of export and delivery to downslope aquatic ecosystems (Frey et al., 2007; Harms & Jones Jr, 2012; Harms & Ludwig, 2016; Jones Jr. et al., 2005; Lynch et al., 2019; Petrone et al., 2006). So far, the connection between hillslope hydrology and shrub distribution has been modelled (Mekonnen et al., 2021), but the potential plant uptake of topographically transported N has only been examined in the context

**KEYWORDS**

arctic hillslope, climate change, permafrost thaw, plant species-specific N uptake, plant–soil (belowground) interactions, stable isotope labelling $^{15}$N, topographical N transport, tundra
of surface-released N (Yano et al., 2010) and climate-scenario modelling (Rastetter et al., 2004). Yet, the long-term prospect of continued permafrost thaw in the Arctic renders it critical to investigate landscape-scale plant responses, because enhanced transport and availability of permafrost-N could lead to important changes in species composition, plant productivity and ultimately carbon balance.

To examine the in situ coupling between topographical N transport and corresponding plant uptake, we used stable isotope labelling ($^{15}$N) to simulate pulse-release of NH$_4^+$ and NO$_3^-$ in the deep active layer near the permafrost thaw front at the top of an arctic hillslope. Plant species-specific N uptake was followed from the up-slope point-of-release to the bottom of the slope through 4 years. We address the complex interactions between space, time and plant species-specific responses through four research questions:

1. Can plants along an arctic hillslope acquire topographically transported permafrost-N at the point-of-release and further downslope?
2. How do the patterns of N transport, redistribution and plant uptake change over multiple years after pulse release?
3. Does plant N uptake along the slope depend on the initial N-form of release (ammonium or nitrate)?
4. What are the plant species-specific N uptake patterns along the slope?

Understanding the dynamics of plant uptake of permafrost-released N along arctic hillslopes will improve our ability to predict long-term and landscape-scale vegetation responses to climate change in the Arctic.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The study was conducted in the low Arctic, Qeqertarsuaq (Disko Island), western Greenland (69°16′N, 53°28′W). Mean annual air temperature is ~3.0°C, with warmest and coldest months July and February (7.9°C and −13.5°C, respectively) (based on data 1991–2018, Arctic Station Monitoring Programme 2020), exhibiting an annual warming trend of 1.6°C per decade (Zhang et al., 2019). Mean annual precipitation amounts to 411 mm, of which 153 mm falls as rain during the summer months May–September (Greenland Ecosystem Monitoring Programme, ClimateBasis Disko, 2020; Arctic Station Monitoring Programme 2020). During the study period, 2014–2018, mean summer air temperature averaged 4.6 ± 0.3°C (May–September). Summer precipitation was highest in 2018 and 2014 (281 and 258 mm, respectively), followed by 2017, 2015 and 2016 (194, 139 and 80 mm, respectively).

The field site is located on a south-facing slope in the river valley Błæsedalen, bounded by a moraine ridge to the north and a lake to the south (Figure S1). The site is underlain by permafrost and stretches 30 m from approximately 119 to 115 m a.s.l. (even slope of ~7.5°), ending a few metres away from the lakeshore. Even though the upper boundary of the site is located approximately mid-way on the greater slope, for simplicity we use the term ‘top of slope’ to refer to the top of the field site.

Vegetation composition varies along the slope from moss and dwarf-shrub-dominated at the top of the slope to wetland vegetation at the bottom of the slope (Figure S1). Dwarf shrubs include the evergreen Empetrum hermaphroditum and the deciduous Betula nana, Salix glauca, Salix herbacea and Vaccinium uliginosum. Sedges, only present near the bottom of the slope, include Carex aquatilis ssp. stans (hereafter, C. aquatilis), Carex rariﬂora and Eriophorum angustifolium. The vascular cryptogam Equisetum arvense is found throughout the site. A dense moss cover includes Aulacomnium palustre, Hygrohypnum sp., Hyllocomium splendens, Paludella squarrosa, Sanionia uncinata and Tomentypnum nitens.

### 2.2 | Experimental design

To study the downslope movement and plant uptake of upslope-released permafrost-N, the site was divided into 13 parallel 30 m transects along the slope, located at least 2 m apart, to capture the natural variation across the slope (Figure S1). Sampling points were established at five distances along each transect: 0 (top of the slope), 2, 10, 26 and 30 m (bottom of the slope). In the final year of study, an additional distance at 5 m from the top was also sampled. To compare plant uptake by N-form, the experimental site was divided into two parts with five replicate transects each of NO$_3^-$ and NH$_4^+$ treatment. Three untreated control transects, one on each side of the experiment and one in the middle to separate the NO$_3^-$ and NH$_4^+$ treatments, were used for root biomass and soil nutrient analyses.

### 2.3 | Stable isotope labelling: Simulated permafrost N-release

In the initial year of study, $^{15}$N stable isotope labelling was used to simulate upslope N-release in the deep active layer soil near the permafrost thaw front. At the top of each transect, at the ‘0 m’ distance (later referred to as ‘point-of-release’), $^{15}$N-enriched NO$_3^-$ or NH$_4^+$ was injected through a narrow, hollow tube inserted to the bottom of the active layer (mean 28 ± 1 cm thaw depth at the time of isotopic labelling). For each transect, 10 ml of dissolved inorganic N was injected in the form of 1874 mg KNO$_3$ or 1000 mg NH$_4$Cl, equivalent to 275 mg $^{15}$N per injection point (99 atom% $^{15}$N; Cambridge Isotope Laboratories). After the injection, each tube was rinsed with 20 ml demineralised water to ensure that all isotopic label had been flushed to the bottom of the tube. The tubes were left in the soil to avoid potential contamination of surface layers at the point of injection. The isotopic labelling was done on 8 August 2014. Two major precipitation events occurred on 9 and 16 August 2014, with 71 and 92 mm of rainfall per day, respectively (Figure 1). Both of these rainfall events occurred after the isotopic labelling and prior to the first sampling round.
We assume an equal spread of the isotopic label within a radius of 50 cm around each injection point in accordance with the discussion presented in Pedersen et al. (2020). Data from control transects show some degree of lateral spread of isotopic label (Figure S2a). However, isotopic enrichment in the middle control transect, which could potentially receive N input from two sides, was no more elevated than in the edge transects (Figure S2b). This confirms that the N-form treatments were spaced sufficiently far apart to render potential cross-contamination unimportant. Further downslope, we cannot exclude the possibility that lateral spread increased, but this is a logical consequence of downhill transport in natural ecosystems.

We added $^{15}$N- NH$_4^+$ and $^{15}$N- NO$_3^-$ in trace amounts as a pulse addition, to measure N uptake based on $^{15}$N enrichment relative to background levels. The quantity of N added was sufficient to detect plant N uptake, yet with no assumed fertilisation effects, similar to amounts applied in other $^{15}$N tracer studies (e.g. Clemmensen et al., 2008; Oulehle et al., 2016). The added N amount is therefore not necessarily representative of actual N-release from thawing permafrost, but reveals the mechanistic processes of transport and plant uptake along the slope.

## 2.4 Plant sampling and analysis

To determine plant N uptake along the slope and over time, species-specific vascular plant and moss samples were collected throughout the study period. Prior to isotopic labelling, plant samples were collected from all sampling points across the site for $^{15}$N natural abundance analysis. Leaves were picked directly from live stems (shrubs) or cut at the base (graminoids and shoots of *E. arvense*). Moss samples were collected as small tufts. After isotopic labelling, vascular plant samples were collected from all sampling points after 10 days (18 August 2014), 1 year (9 August 2015), 2 years (12 August 2016) and 4 years (9–11 August 2018). Samples were gathered within a maximum radius of 50 cm from the centre of each sampling point, comprising all dominant species: *Equisetum arvense*, *Salix glauca*, *Vaccinium uliginosum*, *Empetrum hermaphroditum*, *Carex aquatilis*, *Carex rariflora* and *Eriophorum angustifolium*. Moss samples were collected in the first and final year of study (2014 and 2018) and included *Aulacomnium palustre*, *Hylocomium splendens*, *Tomentypnum nitens*, *Paludella squarrosa*, *Hygrohypnum sp.* and *Sanionia uncinata*. Since the isotopic label moved naturally along the slope, we cannot determine the exact area to which the $^{15}$N spread. Therefore, we did not collect total biomass samples to quantify N pools, but rather focus on excess $^{15}$N concentrations in leaves as an indicator of species- and location-specific plant uptake.

Following field sampling, plant samples were dried (60°C, 48 h), finely ground and folded into tin capsules (~5 mg) for analysis of $^{15}$N concentration using an Isoprime isotope ratio mass spectrometer (Isoprime Ltd.) connected to a Eurovector CN elemental analyser (Eurovector).
2.5 Soil sampling and analysis

To investigate the distribution of isotopically labelled N within the soil column and along the slope, soil samples were collected after 3 weeks during the initial year (2014) and again after 4 years (2018). Soil cores (diameter 4.5 cm) were taken as close as possible to the centre of each sampling point down to the bottom of the active layer and divided into 10 cm intervals. Soils were moist and mostly organic with slightly increasing mineral content towards the bottom of the active layer. Because the permafrost table varied across the site, the length of individual soil cores ranged from 30 to 50 cm. The soil corer was rinsed between each sample to avoid contamination between sampling points. Soil samples for natural abundance analysis were obtained from all sampling points prior to isotopic labelling.

Bulk soil samples were weighed and dried (60°C, 48 h), and gravimetric soil moisture and bulk density were determined. Dry soil samples were ground, folded into tin capsules (4–16 mg) and analysed for isotopic composition as described above.

Seasonal active layer thaw depth was examined by non-destructively measuring active layer depth with a thin metal rod at each sampling point during the initial and final year (2014 and 2018) (Figure 1). To establish the patterns of soil characteristics across the site, separate soil cores were taken from control (unlabelled) transects. Using the same core holes, permafrost soil was collected at each sampling point during the initial and final year (2014 and 2018) destructively measuring active layer depth with a thin metal rod at 10 cm) were obtained by hammering a stainless steel pipe to the maximum active layer depth (70–80 cm depth) at three transects. Using the same core holes, permafrost soil was collected from control (unlabelled) transects. To establish the patterns of soil characteristics across the site, separate soil cores were taken from control (unlabelled) transects. Using the same core holes, permafrost soil was collected from control (unlabelled) transects.

Active layer soil samples collected from the control transects were sorted by hand immediately after field collection to remove live fine (diameter <1 mm) and coarse roots. Roots were dried (60°C, 48 h) and weighed to determine root biomass by distance and soil depth. Within 24 h of root sorting, the remaining soil from each of these samples and permafrost samples was homogenised, and a subsample (10 g fresh weight) from each soil sample was used for cold water extraction (demineralised water, ratio 1:10 fresh weight soil:water) and filtration (2.7 μm mesh size; Whatman GF/D filters) to determine concentrations of water-extractable NH$_4^+$, NO$_3^-$, dissolved organic carbon (DOC), total dissolved nitrogen (TDN) and dissolved organic nitrogen (DON; calculated as the difference between TDN and the sum of NH$_4^+$ and NO$_3^-$) using flow injection analysis (FIASTAR 5000 Analyser). Cold water extractions were used to simulate the process of soil nutrient dissolution (Clemmensen et al., 2008), thereby representing the plant-available fraction of nutrients likely to move with hydrological transport.

2.6 Calculation of isotopic enrichment

Plant uptake of added NO$_3^-$ or NH$_4^+$ was determined by isotopic enrichment. For both plants and soil, excess $^{15}$N concentration ($^{15}$N enrichment) relative to background levels was calculated based on the difference in atom percent $^{15}$N between samples collected prior to isotopic labelling (natural abundance or pre-labelling) and samples collected after isotopic labelling (post-labelling):

$$\text{atom%}_{\text{excess}} = \text{atom%}_{\text{post-labelling}} - \text{atom%}_{\text{pre-labelling}}$$  \hspace{1cm} (1)

where

$$\text{atom\%} = \frac{100 \times (\delta + 1000)}{\delta + 1000 + \frac{1000}{R_{15}}}$$  \hspace{1cm} (2)

and $\delta$ is the $^{15}$N-value of the sample (‰), $R_{15}$ is the $^{15}$N-$^{14}$N ratio of the international reference material atmospheric N$_2$ (0.003676). Excess $^{15}$N concentrations are expressed as the excess concentration of $^{15}$N per g N in plant leaves, moss samples and bulk soil samples.

2.7 Statistical analyses

Differences in excess $^{15}$N concentrations in plant leaves, mosses and soil were analysed using a linear mixed-effects model (R statistical software; R Core Team, 2020, version 4.0.2; package lme4: Bates et al., 2015). Overall effects of time, distance along slope and N-form were analysed with a three-way analysis-of-variance (ANOVA) with fixed factors (discrete, categorical variables): Year, Distance and N-form (lmerTest: Kuznetsova et al., 2017). The factor Year comprised time points after isotopic labelling: 10 days (year 0), 1 year, 2 years and 4 years. N-form encompassed $^{15}$N-NH$_4^+$ and $^{15}$N-NO$_3^-$, and Distance included 0, 2, 10, 26, 30 m from the top of the slope (5 m only examined in the last year of study and therefore excluded from overall analyses to avoid statistical issues of missing factor combinations). Data were analysed separately per species (plant data) and per depth (soil data). Sampling point nested in Transect was used as random factor to account for natural spatial variation across the site and repeated sampling from the same locations across years. Models were validated using visual estimation of residual and quantile–quantile plots (rcompanion: Mangiafico, 2020), and data were transformed using the Box–Cox transformation principle (MASS: Venables & Ripley, 2002). Model reduction was based on the principle of backwards elimination of insignificant terms (Quinn & Keough, 2002), using a cut-off at $p > 0.1$.

To further explore significant main and interaction effects, two-way ANOVAs were conducted for each year, per species and per soil depth with fixed factors Distance and N-form, and random factor Transect. To identify specific differences between distances, N-form or years, post-hoc tests were run on the reduced models with Tukey’s Honestly Significant Difference p-value adjustment for pairwise comparisons between years, year by distance, distance, N-form by distance and distance by N-form (EMMEANS: Lenth, 2020). To investigate plant and moss species-specific differences, three-way ANOVAs were run per time point with factors Species, Distance, N-form. Significant species effects were further investigated with post-hoc pairwise comparisons between species, species by distance and species by N-form. To verify that low $^{15}$N enrichment levels at downslope distances (26,
30 m) represented true enrichment rather than random variation, δ^{15}N-values for samples collected prior to and after isotopic labelling were compared in a linear model and two-way ANOVA with factors Enrichment (pre- vs. post-labelling) and Species. An α-level of 0.05 was used as cut-off for statistical significance, but tendencies (p < 0.1) are also reported.

3 | RESULTS

3.1 | Ecosystem characteristics

Across the site, thaw depth averaged 43 cm, ranging from 32 to 63 cm in mid-August (averaged by distance during the study period) (Figure 1). At the time of isotopic labelling, the active layer thaw depth averaged 28 ± 1 cm at the upper boundary of the site (hereafter termed ‘top of slope’), where deep-soil N-release was simulated (Figure 1a). The permafrost table formed a depression at the 2 m distance (approximately 5 cm deeper than adjacent distances), and thaw depth was greatest at the bottom of the slope (7 cm deeper at the 30 m distance relative to 0 m) (Figure 1).

The soil was organic (mean 22.9 ± 0.7% C, 0.98 ± 0.03% N across all distances and soil depths) and wet (mean gravimetric soil water content 254.2 ± 9.6%) (Figure 2; Figure S3). Soil water content, fine and total root biomass, water-extractable DON and DOC, soil N, C and C/N ratio all decreased with depth (Figure 2; Figure S3), demonstrating a progression from highly organic surface soil to increased mineral content with depth. Root biomass was highest in the top of the soil column (0-20 cm soil depth), fine root biomass 150.4 ± 16.0 g m⁻²), but roots were detected all the way to the bottom of the active layer during peak growing season (Figure 2ef). Ammonium (NH₄⁺) and nitrate (NO₃⁻) concentrations showed no distinct patterns along the slope (Figure 2cd). A slight increase in NH₄⁺ in the deep active layer at the bottom of the slope (30 m distance) indicated the potential release of NH₄⁺ from thawing permafrost or accumulation of leached NH₄⁺ at the frost barrier (Figure 2c). Upper permafrost soil contained 1.5 times as much NH₄⁺ as average active layer concentrations, while permafrost NO₃⁻ concentrations were nearly seven times higher than mean active layer concentrations (Figure 2cd). Because we used water-extractable inorganic N as a proxy for plant-available N (Clemmensen et al., 2008; McLaren & Buckeridge, 2019; Yano et al., 2010), the concentrations presented in our study may appear low compared to results displayed in other studies using stronger extraction agents (Beerman et al., 2017; Clemmensen et al., 2008; Elberling et al., 2010; Keuper et al., 2012; Salmon et al., 2018), which are known to increase the concentration of soluble N (Wheatley et al., 1989).

3.2 | Plant N uptake over time

At the top of the slope, plants and mosses took up isotopically labelled N within 10 days following simulated N-release in the deep active layer (N uptake is expressed as ^15N enrichment in leaves relative to background levels [excess ^15N concentration per g N]) (Figures 3a and 4a). Additionally, a low amount of ^15N had already been transported and taken up by plants downslope (Figures 3a and 4a; Figure S4a). Excess ^15N concentrations changed over the course of the study period depending on distance along slope (three-way ANOVA, Distance × Year p ≤ 0.001 for nearly all plant species) (Table 1). During the first year, excess ^15N concentrations in plant leaves increased by 2-3 orders of magnitude at the top of the slope, equivalent to on average 300 times higher enrichment levels after 1 year (0 and 2 m distances; p < 0.001 for comparison 10 days vs. 1 year for S. glauca and E. arvense) (Figure 3b). During subsequent years, excess ^15N concentrations decreased somewhat in some cases, but this did not give rise to significant differences between years (comparisons between 1, 2 and 4 years not significant for S. glauca, E. arvense, V. uliginosum), and enrichment levels remained within the same order of magnitude, even after 4 years (Figure 3b-d). In contrast to the initial increase near the point-of-release (0 and 2 m distances), excess ^15N concentrations in downslope plants did not change significantly throughout all years (comparisons between years not significantly different for distances 10, 26 and 30 m for any species) (Figure 3; Figure S4). Mosses also exhibited some N uptake during the initial year of the study, but significantly increased excess ^15N concentrations upslope after 4 years (p < 0.03, comparisons 10 days vs. 4 years at distances 0 and 2 m, for A. palustre, H. splendens, T. niten) (Figure 4).

3.3 | Plant N uptake along the slope

Vascular plant and moss N uptake differed by distance along the slope (two-way ANOVA by species, Distance p < 0.04 after 10 days and p ≤ 0.001 after 1, 2 and 4 years for species present at all distances) (Figures 3 and 4; Table S1). Especially after the first year and during subsequent years, excess ^15N concentrations were highest at the top of the slope (p ≤ 0.01 compared to 2 m distance, and p < 0.001 for comparisons with distances further downslope) (Figures 3b-d and 4b). Excess ^15N concentrations remained relatively high at the 2 m distance downslope (p < 0.01 for most comparisons with distances further downslope), but decreased markedly and remained low further downslope (distances 5, 10, 26, 30 m not significantly different from each other) (Figures 3 and 4). Plant ^15N enrichment levels at the bottom of the slope (26 and 30 m) were detectable throughout all years and significantly higher than background levels (p < 0.05 for Enrichment or Enrichment × Species per year) (Figures 3 and 4; Figure S4; Table S2).

3.4 | Plant N uptake from different N-forms

Shortly after simulated N-release (10 days), vascular plant and moss N uptake did not differ according to the original N-form, NO₃⁻ or NH₄⁺ (Figures 3a and 4a; Table S1). However, after the first year, a distinct N-form pattern evolved at the top of the slope, where nearly all plant and moss species exhibited significantly higher N
**FIGURE 2** Soil characteristics by soil depth along the slope: (a) gravimetric soil water content, (b) bulk density, (c) water-extractable ammonium (NH$_4^+$) per dry weight soil, (d) water-extractable nitrate (NO$_3^-$) per dry weight soil, (e) fine root biomass and (f) total root biomass. Distance 0 m represents the top of the slope, distance 30 m corresponds to the bottom of the slope. Mean ± standard error (SE), n = 10 for soil water content and bulk density, n = 3 for other parameters, per distance and soil depth (lower replication for deepest soil depth, 40–50 cm). The break on the y-axis and dashed line indicate the thaw depth at the time of sampling (rounded to the nearest 10 cm depth interval). Permafrost soil samples (PF) were collected below the maximum active layer depth (70–80 cm depth), from distances 0, 10 and 30 m. ‘NA’ indicates no sample. Soil samples for dissolved nutrients and root biomass were collected 2 weeks earlier than soil samples for water content and bulk density, hence the slightly shallower active layer.
Figure 3  Plant N uptake (excess $^{15}$N concentration in plant leaves) along the slope after (a) 10 days, (b) 1 year, (c) 2 years, and (d) 4 years, by species (Salix glauca, Equisetum arvense, Vaccinium uliginosum, Empetrum hermaphroditum) and N-form ($\text{NH}_4^+$, $\text{NO}_3^-$). Distance 0 m represents the top of the slope, distance 30 m corresponds to the bottom of the slope. N-form treatments refer to isotopic labelling ($^{15}$N) at the top of the slope during the initial year to simulate permafrost N-release. Mean $\pm$ SE, $n = 5$ per bar. Note that the y-axis is shown as logarithmic scale, range 50,000. Statistical results from linear mixed-effects model two-way ANOVAs are noted on each plot (Distance, N-form, Distance $\times$ N-form). Upper case letters indicate statistical difference ($p < 0.05$) between distances across treatments. Due to low replication, pairwise comparisons exclude distances where one or both of the treatments had missing samples (‘NA’). Despite overall Distance effects in plot (a), specific differences between distances could not be detected with the pairwise comparison post-hoc test. Symbols above bars indicate statistical difference between N-forms per distance. Significance levels: ***$p < 0.001$, **$0.001 \leq p < 0.01$, *$0.01 \leq p < 0.05$, †$0.05 \leq p < 1$; ‘NA’ indicates no sample (species not present); ‘0’ means no enrichment.
uptake from originally NO$_3^-$-derived N compared to NH$_4^+$-sourced N ($p<0.05$ for NO$_3^-$ vs. NH$_4^+$ comparisons at the 0 m distance for nearly all plant and moss species in years 1, 2 and 4) (Figures 3b–d and 4b). Further downslope, N-form differences were less apparent.

3.5 | Plant species-specific N uptake

All vascular plants and mosses followed similar patterns of N uptake according to time, distance along slope and N-form (Figures 3 and 4). However, plant species differed markedly in magnitude of $^{15}$N uptake. *Equisetum arvense* was most efficient at taking advantage of N released in the deep active layer soil, both shortly after release and in the long term ($p<0.001$ for comparisons between *E. arvense* and other plant species) (Figure 3). After the first year, excess $^{15}$N concentrations in *E. arvense* shoots were 3–5 times higher than in leaves of *Salix glauca* and up to 55 times higher than in *Vaccinium uliginosum* and *Empetrum hermaphroditum* leaves (Figure 3b–d). A strong hierarchical order of N uptake developed over time with *E. arvense* > *S. glauca* > *V. uliginosum* = *E. hermaphroditum* (after 1, 2 and 4 years; Figure 3b–d). Nevertheless, species differences were specific to distance along the slope (three-way ANOVA per time point, $p<0.001$ for Species × Distance interaction) (Table S3), driven exclusively by N uptake near the point-of-release (0 and 2 m distances) ($p<0.02$ for *E. arvense* compared to other vascular plant species after 10 days and $p<0.001$ after 1, 2 and 4 years; $p<0.005$ for *S. glauca* compared to *V. uliginosum* and *E. hermaphroditum* after 2 and 4 years). In contrast, species did not differ significantly downslope (10, 26 and 30 m) (Figure 3; Figure S4). Moss N uptake was on the same order of magnitude for all species and followed patterns similar to the vascular plants (Figure 4; Figure S4).

3.6 | Soil $^{15}$N enrichment

Soil excess $^{15}$N concentrations differed significantly as an interaction between year, distance along slope and N-form (three-way
<table>
<thead>
<tr>
<th>Plant species</th>
<th>Distance N-form</th>
<th>Year</th>
<th>Distance × N-form</th>
<th>Distance × Year</th>
<th>N-form × Year</th>
<th>Distance × N-form × Year</th>
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<td><em>Salix glauca</em></td>
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<td>(4.32.4)</td>
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<td>(3.105.4)</td>
<td>(4.32.4)</td>
<td>(11.105.3)</td>
<td>(3.105.4)</td>
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<td>&lt;0.001</td>
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<td>&lt;0.001</td>
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<td><em>Equisetum arvense</em></td>
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<td>(4.39.1)</td>
<td>(1.12.5)</td>
<td>(3.92.5)</td>
<td>(4.38.8)</td>
<td>(11.91.0)</td>
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<td>10.91</td>
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<td>0.86</td>
<td>3.12</td>
<td>6.54</td>
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<td>0.412</td>
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<td><em>Paludella squarrosa</em></td>
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<td>0.042</td>
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<th>Distance × Year</th>
<th>N-form × Year</th>
<th>Distance × N-form × Year</th>
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<td>(1.37.7)</td>
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<td>&lt;0.001</td>
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<td>0.004</td>
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<td>9.98</td>
<td>9.98</td>
<td>9.98</td>
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<td>(1.34.7)</td>
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<td>0.003</td>
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ANOVA, \( p \leq 0.05 \) for soil depths 0–30 cm) (Table 1). Soil excess \( ^{15}\text{N} \) concentrations along the slope corresponded to the observed plant uptake patterns, with highest excess \( ^{15}\text{N} \) concentrations at the top of the slope, followed by the 2 m distance, and finally 5, 10, 26 and 30 m downslope at similar levels (\( p < 0.001 \) for Distance [Table 1: Table S4] and \( p < 0.05 \) for pairwise comparisons between distance 0 m and other distances downslope) (Figure 5). Downslope (26 and 30 m) soil excess \( ^{15}\text{N} \) concentrations were low, yet detectable (\( p < 0.001 \) for Enrichment during the first year) and significant for both N-form treatments, although visually more so for NO\(_3^-\) (Figure 5a; Figure S2c; Table S5). Nevertheless, after 4 years, downslope soil excess \( ^{15}\text{N} \) concentrations had decreased significantly (\( p < 0.05 \) comparisons between years for distances 10, 26 and 30 m), indicating that some \( ^{15}\text{N} \) had left the soil system (Figure 5). Additional differences between N-forms occurred primarily at the top of the slope (two-way ANOVA Distance \( \times \) N-form \( p \leq 0.06 \) for all soil depths after 4 years) (Table S4). During the initial year, \( ^{15}\text{N} \)-NO\(_3^-\) concentration was highest at the deepest soil depth (30–40 cm depth), that is, closest to the point of simulated N-release (Figure 5a). However, after 4 years, the pattern was reversed with significantly increased NO\(_3^-\) derived \( ^{15}\text{N} \) in upper soil layers (0 m distance, \( p < 0.03 \) for 0–10 and 20–30 cm depth), indicating vertical redistribution of \( ^{15}\text{N} \) (Figure 5b).

### 4 | DISCUSSION

To determine the coupling between permafrost N-release, topographical transport and plant uptake, we used stable isotope labelling to track the plant species-specific uptake of simulated upslope-released permafrost-N along an arctic hillslope through 4 years (Figure 6). We show that plants effectively acquired N in the deep active layer at the upslope point-of-release, and that this N was strongly retained in the plant–soil system over multiple years. At the same time, we demonstrate that simulated permafrost-released N was transported along the slope and taken up by plants up to 30 m downslope. Both N-form and plant species-specific characteristics shaped the patterns of plant uptake along the slope. The potential for plants to take advantage of permafrost-released N, not only at the point-of-release but also at a considerable distance downslope, may have important implications for long-term vegetation change across the Arctic.
4.1 | Plants acquire both locally released and topographically transported N

Within 10 days following simulated permafrost N-release at the top of the slope, vascular plants and mosses acquired isotopically labelled N at all points along the slope (Figures 3 and 4). One year later, plant $^{15}$N enrichment was significantly higher at the top of the slope compared to downslope, indicating strong N uptake near the point-of-release. Because $^{15}$N was injected in discreet points, the isotopic label would logically have been most concentrated within the first few metres of the injection point. A slight depression in the permafrost table around the 2 m distance (Figure 1) may also have contributed to retention of downslope-moving N (Wright et al., 2009), in combination with the ability of plants to forage widely via root and mycelial networks (Blume-Werry et al., 2019; Hewitt et al., 2020). However, as a consequence of the sloping terrain and the precipitation events following the isotopic labelling, we expected upslope-released N to be washed downslope before considerable local uptake. Contrary to our expectation, the magnitude of the measured $^{15}$N enrichments at the point-of-release was comparable to observations in other studies on plant uptake of permafrost-N, which took place in non-sloping terrain (Blume-Werry et al., 2019; Hewitt et al., 2018; Pedersen et al., 2020). Our results therefore demonstrate that even along hillslopes, arctic plants effectively capitalise on locally released permafrost-N.

Downslope plant and soil excess $^{15}$N concentrations were small, yet significant up to 30 m from the point-of-release (Figures 3-5). The limited downslope $^{15}$N enrichments are likely due to initial N uptake and retention near the point-of-release combined with increasing lateral spread down the slope (Yano et al., 2010). While we cannot estimate the exact area to which the isotopic label spread, this spread of N is a natural consequence of the topography of arctic hillslopes and thus illustrates the potential travel distance of permafrost-released N along the slope. Limited downslope plant $^{15}$N uptake could also be attributed to the fact that some N transported along the permafrost table may have been beyond the reach of shallow-rooted plants, or because flattening of the slope and increased soil water content reduced the flow rate and restricted plant uptake (Harms & Jones Jr., 2012; Mekonnen et al., 2021; Yano et al., 2010). Nevertheless, despite the spatial dilution and potentially constraining factors at the bottom of the slope, plants succeeded in capturing topographically transported permafrost-N.

4.2 | Plants strongly retain permafrost-released N over multiple years

The pulse-released and transported $^{15}$N was quickly captured by plants and subsequently locked in the plant-soil system. At the top of the slope, plant $^{15}$N enrichment increased significantly up to 3 orders of magnitude within the first year, after which excess $^{15}$N concentrations in plant leaves remained near-stable throughout subsequent years (Figure 3). N-limited arctic plants can take up inorganic N within a few days following pulse release (Andresen et al., 2008; Clemmensen et al., 2008; Olehle et al., 2016; Pedersen et al., 2020). However, since we only investigated leaf $^{15}$N enrichment, the low...
initial N uptake (Figure 3a) may not reflect total uptake. This may partly be explained by a temporal asynchrony between leaf and root production, especially in shrubs, with leaf production occurring early in the growing season, whereas root production takes place later and continues for longer (Blume-Werry et al., 2016; Sloan et al., 2016). Therefore, some N was likely stored below-ground upon release, in roots, rhizomes, root-associated fungi (Blume-Werry et al., 2019; Clemmensen et al., 2008; Hewitt et al., 2018; Keuper et al., 2017) and microbial biomass (Grogan & Jonasson, 2003; Larsen et al., 2012; Nordin et al., 2004; Sorensen, Clemmensen, et al., 2008), and only transferred to above-ground plant parts during leaf production the following growing season as a result of microbial death and root-leaf transfer, leading to a strong $^{15}$N enrichment signal in plant leaves after 1 year (Figure 3b). However, the fact that plant $^{15}$N enrichment levels remained within the same order of magnitude after the first year (Figure 3b–d) demonstrates that arctic plants effectively retain and recycle newly available N within the local plant-root-soil system (Rastetter et al., 2004; Yano et al., 2010).

The magnitude of downslope plant and soil excess $^{15}$N concentrations remained low throughout the study period (Figures 3–5). Downslope plant excess $^{15}$N concentrations did not differ between years, which suggests that the pulse-released N was primarily transported during the first summer, with little to no transport during subsequent years. The rapid initial transport may have been facilitated by the two major precipitation events (Harms & Jones Jr, 2012; McNamara et al., 2008; Rastetter et al., 2004), which occurred within a week after the isotopic labelling (Figure 1). The lack of similar precipitation events during subsequent years (Arctic Station Monitoring Programme 2020) in combination with strong N retention in plants at the top of the slope likely constrained interannual N transport and uptake along the slope.

4.3 | N-form determines plant N availability

Both NO$_3^-$ and NH$_4^+$ were present in the permafrost soil (Figure 2), confirming that thawing permafrost could release plant-available N. However, of the two N-forms, NO$_3^-$-derived N was more easily redistributed vertically in the soil column. This was clearly illustrated by a shift from deep-soil $^{15}$N enrichment during the initial year to increased upper soil $^{15}$N enrichment after 4 years in the NO$_3^-$ treatment (Figure 5). Correspondingly, plant excess $^{15}$N concentrations from the NO$_3^-$-treatment were much higher than from the NH$_4^+$ treatment at the point-of-release (Figure 3). While some plant species may prefer specific N-forms (Clemmensen et al., 2008; McKane et al., 2002; Sorensen, Clemmensen, et al., 2008), N uptake patterns can also depend on the most abundant N-form (McKane et al., 2002; Nordin et al., 2004). Because NO$_3^-$-N was more easily redistributed in the soil profile compared to NH$_4^+$, the NO$_3^-$-derived N perhaps became more accessible to plants. Hence, enhanced plant $^{15}$N enrichment in the NO$_3^-$-treatment may simply reflect easier access to N, rather than specific N-form preference.

Despite a tendency towards slightly elevated $^{15}$N-NO$_3^-$ concentrations compared to $^{15}$N-NH$_4^+$ concentrations at downslope distances (Figure 5; Figure S2c), we may not be able to clearly distinguish between N-forms at the bottom of the slope due to lateral spread. It is likely that NO$_3^-$-derived $^{15}$N was more easily transported downhill during the precipitation events than $^{15}$N-NH$_4^+$ with low solubility. However, as a consequence of lateral spread across the slope (Figure S2), we cannot exclude the possibility that some cross-contamination between the N-forms occurred at downslope distances, and N-form transformations likely took place over time. Therefore, downslope plant $^{15}$N enrichment primarily illustrates uptake of topographically transported N, rather than uptake of specific N-forms.

4.4 | Plant species-specific characteristics define N uptake and redistribution

Plant species-specific N uptake patterns were particularly distinct at the top of the slope, at the point of N-release (Figure 3). The vascular cryptogam *Equisetum arvense* was the strongest competitor for simulated permafrost-released N, both in terms of timing and magnitude of N uptake. First, *E. arvense* rapidly transferred N to above-ground plant parts immediately following release. This response is similar to observations for graminoids (Hewitt et al., 2018; Oulehle et al., 2016; Pedersen et al., 2020; Sloan et al., 2016; Sorensen, Clemmensen, et al., 2008), where early root production and a high N demand may promote fast uptake of readily-available N (Andersen et al., 2020). In contrast, shrubs invest in longer term N storage in below-ground structures, above-ground stems, and in some cases, evergreen leaves (Andresen et al., 2008; Hewitt et al., 2018; Oulehle et al., 2016). Later root production in shrubs (Sloan et al., 2016) could also result in a slower N transfer to above-ground plant biomass, potentially explaining the high initial $^{15}$N enrichment in *E. arvense* compared to the shrubs. Second, *E. arvense* exhibited higher N uptake than other species. *Equisetum* spp. have deep and complex rhizome structures and extensive root hairs (Husby, 2013; Marsh et al., 2000), which may allow them to access nutrients at deeper soil depths where shallow-rooted species are less likely to forage. In combination with the ability to survive anoxic conditions and disturbance (Husby, 2013), these below-ground traits likely make *Equisetum* spp. well adapted to the seasonally and inter-annually changing soil environment of permafrost ecosystems. Thus, while other studies have highlighted the plasticity of graminoids in terms of vertical rooting depth and N uptake in relation to permafrost thaw (Blume-Werry et al., 2019; Hewitt et al., 2018; Wang et al., 2017; Wang et al., 2018), we here show similar characteristics for the species *E. arvense*.

Within the shrub species, *Salix glauca* acquired more N than *Vaccinium uliginosum* and *Empetrum hermaphroditum*, perhaps explained by ectomycorrhizae, which contribute to extending the foraging depth (Hewitt et al., 2020; Weigl et al., 2012). *Salix* species have also been shown to reach deeper water and N sources than other...
species (Jespersen et al., 2018; Pedersen et al., 2020), potentially providing S. glauca with a competitive advantage for permafrost-N compared to the ericoid shrubs V. uliginosum and E. hermaphroditum.

Despite not being able to separate roots by species, the results of above-ground $^{15}$N enrichment during the first year of sampling indicate that in this ecosystem, the deep roots (Figure 2) may belong to especially E. arvense. Not only are Equisetum species known to have deep root systems (Husby, 2013; Marsh et al., 2000), but they also potentially function as ‘nutrient pumps’ (Marsh et al., 2000). Thereby, deep-soil nutrients can be redistributed vertically via the rhizome and root networks, temporarily stored in below-ground or above-ground biomass, and eventually released to surface soil layers via root exudation or litter fall, by which deep-soil N may become available to shallow-rooted species (Husby, 2013; Marsh et al., 2000).

In contrast to differing uptake patterns at the top of the slope, plant acquisition of downslope-transported N did not differ between species at the bottom of the slope (Figure 3; Figure S4). Despite previous findings of differences between graminoid and shrub N uptake (Blume-Werry et al., 2019; Hewitt et al., 2018; Keuper et al., 2017; Wang et al., 2017, 2018), we attribute the lack of such patterns in our study to the fact that downslope-available $^{15}$N following topographical transport may have been present in such small quantities that species differences were indistinguishable. Furthermore, as a result of vertical water movement towards the surface of the soil profile at the bottom of the slope, a more even distribution of $^{15}$N within the soil column may have diminished the competitive advantages of deep-rooting species.

Finally, we show that even mosses can take advantage of permafrost-released N, both in the short term and over multiple years (Figure 4). Initial moss N uptake rates were low and likely explained by hydrological redistribution and downslope transport associated with precipitation. Particularly at the bottom of the slope, deep-soil N could become available to mosses as a result of vertical water movement towards the surface of the soil column associated with palsa formation and spring water (Seppälä, 2011). In the long term, simulated permafrost-release N may have become available to mosses via surface root litter deposition, root exudates and above-ground leaf litter inputs assisted by the nutrient-pump function of deep-rooting plant species (Blume-Werry et al., 2019; DeMarco et al., 2014; Keuper et al., 2017; Marsh et al., 2000). Thus, in contrast to previous studies which have primarily investigated moss responses to increased N availability derived from surface N application (Chapin III, 1995; Hobbie et al., 2005; Sorensen, Michelsen, & Jonasson, 2008), we here demonstrate that mosses also have the potential to gain access to deep-soil permafrost-released N.

4.5 Implications of topographical N transport for arctic vegetation change

A warming arctic climate gives rise to a suite of biogeochemical and environmental changes along hillslopes, including active layer deepening, altered hydrology, thermokarst formation, erosion, as well as increased N availability stemming from both permafrost thaw and accelerated active layer decomposition (e.g. Harms & Jones Jr, 2012; Olefeldt et al., 2016; Salmon et al., 2018). As such, the release and transport of permafrost-N comprise one component of the total N redistribution along arctic hillslopes. We here demonstrate that N released from thawing permafrost can be effectively taken up and retained within the local plant-soil system, despite downhill transport in sloping terrain. Specifically, our results point towards plant community shifts in favour of deep-rooted species such as Equisetum and shrubs like Salix. Combined with subsequent vertical redistribution of N to shallow-rooted species and mosses, these plant responses could modify species composition and potentially contribute to continued arctic greening (Myers-Smith et al., 2020). Thus, considering the tight N cycling observed near the point-of-release, locally released permafrost-N will likely continue to play an important role in driving arctic plant community change.

At the same time, we show that topographically transported permafrost-released N can be actively taken up by downslope-located recipient plant communities. A back-of-the-envelope-calculation based on the data presented in this study (supplementary discussion) suggests that the N released from thawing permafrost could provide a hitherto rarely considered N contribution to stimulated plant productivity, especially over decade-to-century time-scales. However, a full understanding of the quantitative implications of permafrost-released and downslope-transported N for plant growth and the corresponding ecosystem C budget requires detailed information on actual quantities of N-release, permafrost thaw rates, downslope transport rates and lateral spread, coupled with quantitative estimates of local plant N retention, plant species-specific root distribution, above-ground and below-ground plant biomass changes and associated C uptake and turnover rates. This highlights the need for extensive nutrient addition experiments and deep-soil fertilisation studies combined with development of hydrological models, which simulate the complex array of biogeochemical changes associated with permafrost thaw. Ultimately, this will disclose the ecological consequences of topographical N transport for arctic vegetation change.

5 CONCLUSIONS

In topographically diverse arctic ecosystems, the transport of permafrost-released N can play an important role in N cycling and plant uptake. Here, we show how the intricate link between strong local N retention and downslope transport governs plant N uptake, and thereby potentially plant community change, along arctic hillslopes. Using this ecosystem as a representative model system for other arctic hillslopes, we conclude the following:

1. Arctic hillslope plants effectively capture locally released permafrost-N and successfully retain this N over multiple years, indicating strong biological retention of initially acquired N.
2. Upslope-released permafrost-N can be transported and taken up by plants at a considerable distance downslope, thereby potentially affecting the growing conditions of plant communities located far from the point-of-release.

3. NO$_3^-$ is more likely to be redistributed vertically in the soil column than NH$_4^+$. Consequently, NO$_3^-$-N derived from permafrost thaw or deep-soil nitrification may be more easily accessed by plants compared to other N-forms.

4. Plant species with deep roots and fast N uptake capacity (in this ecosystem exemplified by Equisetum arvense and Salix glauca) may have competitive advantages for acquiring permafrost- and topographically transported N. Yet, even mosses can gain access to permafrost-N via vertical and spatial redistribution. Such species differences may contribute to shaping long-term plant community change.

In conclusion, arctic hillslopes may serve as conduits for permafrost-N transport, facilitating plant uptake both locally at the point-of-release and at a considerable distance downslope. As permafrost continues to thaw, the combination of physical slope properties, N-form and plant species-specific characteristics will contribute to determining long-term and landscape-scale changes in plant productivity, species composition and ultimately climate feedbacks across the Arctic.

AUTHORS’ CONTRIBUTIONS
A.M. and B.E. designed the field experiment; A.M., E.P.P. and B.E. collected the field data; A.M. and E.P.P. processed and analysed the field samples; E.P.P. analysed the data and wrote the paper with contributions from all authors.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

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