

## RESEARCH ARTICLE OPEN ACCESS

# Arctic Tundra Plant Dieback Can Alter Surface N<sub>2</sub>O Fluxes and Interact With Summer Warming to Increase Soil Nitrogen Retention

Wenyi Xu<sup>1,2</sup>  | Bo Elberling<sup>2</sup>  | Dan Li<sup>3</sup> | Per Lennart Ambus<sup>2</sup>

<sup>1</sup>Department of Soil and Environment, Swedish University of Agricultural Sciences, Uppsala, Sweden | <sup>2</sup>Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark | <sup>3</sup>College of Urban Construction, Nanjing Tech University, Nanjing, China

**Correspondence:** Wenyi Xu ([wenyi.xu@slu.se](mailto:wenyi.xu@slu.se))

**Received:** 10 May 2024 | **Revised:** 29 September 2024 | **Accepted:** 30 September 2024

**Funding:** This work was supported by Danmarks Grundforskningsfond (CENPERM100).

**Keywords:** arctic tundra | gross nitrogen transformation | methane | nitrogen-15 tracing | nitrous oxide | summer warming | vegetation cutting

## ABSTRACT

In recent years, the arctic tundra has been subject to more frequent stochastic biotic or extreme weather events (causing plant dieback) and warmer summer air temperatures. However, the combined effects of these perturbations on the tundra ecosystem remain uninvestigated. We experimentally simulated plant dieback by cutting vegetation and increased summer air temperatures (ca. +2°C) by using open-top chambers (OTCs) in an arctic heath tundra, West Greenland. We quantified surface greenhouse gas fluxes, measured soil gross N transformation rates, and investigated all ecosystem compartments (plants, soils, microbial biomass) to utilize or retain nitrogen (N) upon application of stable N-15 isotope tracer. Measurements from three growing seasons showed an immediate increase in surface CH<sub>4</sub> and N<sub>2</sub>O uptake after the plant dieback. With time, surface N<sub>2</sub>O fluxes alternated between emission and uptake, and rates in both directions were occasionally affected, which was primarily driven by soil temperatures and soil moisture conditions. Four years after plant dieback, deciduous shrubs recovered their biomass but retained significantly lower amounts of <sup>15</sup>N, suggesting the reduced capacity of deciduous shrubs to utilize and retain N. Among four plant functional groups, summer warming only increased the biomass of deciduous shrubs and their <sup>15</sup>N retention, while following plant dieback deciduous shrubs showed no response to warming. This suggests that deciduous shrubs may not always benefit from climate warming over other functional groups when considering plant dieback events. Soil gross N mineralization (~ -50%) and nitrification rates (~ -70%) significantly decreased under both ambient and warmed conditions, while only under warmed conditions immobilization of NO<sub>3</sub><sup>-</sup> significantly increased (~ +1900%). This explains that plant dieback enhanced N retention in microbial biomass and thus bulk soils under warmed conditions. This study underscores the need to consider plant dieback events alongside summer warming to better predict future ecosystem-climate feedback.

## 1 | Introduction

The Arctic has warmed more than three times faster than the global average over the past half-century (Rantanen et al. 2022). Consequently, the growing seasons become warmer and longer, leading to an overall increase in vegetation productivity,

known as “arctic greening” (Elmendorf et al. 2012; Myers-Smith et al. 2020). However, in recent years, there has also a decline in productivity in some arctic regions, a phenomenon known as “arctic browning”, which is mainly driven by stochastic biotic and weather events (Bhatt et al. 2013; Miles and Esau 2016; Zhang et al. 2017). Climate change-driven

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2024 The Author(s). *Global Change Biology* published by John Wiley & Sons Ltd.

expansions in the outbreak range of defoliating insects have led to long-term reductions in plant productivity and vegetation shifts at both local and regional scales (Bjerke et al. 2014). Extreme winter warming events (when temperatures above freezing) can cause substantial amounts of snow to melt, and expose plants and soils to freezing conditions once sub-zero temperatures return, resulting in severe freezing and drought damage to plants (De Jong et al. 2012; Preece and Phoenix 2014; Bokhorst et al. 2015; Williams, Henry, and Sinclair 2015; Park et al. 2016).

Plant dieback can immediately reduce vegetation cover and plant nutrient uptake, which likely alters soil microclimate conditions and increases soil nutrient availability (Foley et al. 2022). Moreover, short-term plant dieback may have long-term consequences on vegetation biomass, plant functional types, and the quantity and quality of organic matter inputs, therefore influencing decomposition rates and nutrient mineralization (Mosbacher et al. 2018; Barthelemy et al. 2023; Saunders et al. 2023). These altogether are likely to influence nitrous oxide ( $N_2O$ ), methane ( $CH_4$ ), and carbon dioxide ( $CO_2$ ) fluxes (Butterbach-Bahl et al. 2013; St Pierre et al. 2019; Xu et al. 2023). Previous studies have made a growing season assessment of  $CO_2$  fluxes following plant dieback driven by extreme climatic events (Parmentier et al. 2018; Treharne et al. 2019). Their work in sub-arctic dwarf shrub heathland indicated considerable reductions in ecosystem  $CO_2$  uptake rates (Parmentier et al. 2018; Treharne et al. 2019). However, there is a lack of knowledge on how arctic plant dieback affects  $N_2O$  and  $CH_4$  fluxes. High soil N availability can enhance  $N_2O$  emissions through nitrification and denitrification processes, while it may also affect  $CH_4$  fluxes by altering the balance between methanogenic ( $CH_4$ -producing) and methanotrophic ( $CH_4$ -consuming) bacteria. Therefore, studying soil nutrient contents and  $N_2O$  and  $CH_4$  fluxes together is crucial to understanding how plant dieback and the resulting soil N dynamics influence greenhouse gas emissions and, consequently, their impact on global warming. Experimental summer warming has been reported to increase soil nutrient availability and surface  $N_2O$  emissions and  $CH_4$  uptake in the both short- and long-term in arctic tundra ecosystems (Voigt et al. 2017; Ravn, Elberling, and Michelsen 2020; Kolstad, Michelsen, and Ambus 2021; Xu et al. 2023). Currently, plant dieback and warmer summer air temperatures are both occurring in the Arctic and affect ecosystem properties that control the soil-atmosphere exchange of  $N_2O$  and  $CH_4$  (Gornall et al. 2009; Kelsey et al. 2016; Voigt et al. 2017). However, the extent to which summer warming and plant dieback interact to drive surface  $N_2O$  and  $CH_4$  fluxes, and the differential effects in the short and long term, remain unknown.

Ecosystem N retention, the capacity of the plant–soil–microbe compartments to retain N, is a key function of arctic tundra ecosystems where atmospheric N deposition, and microbial decomposition and mineralization activities in general are lower than most other terrestrial ecosystems (Robinson 2002; Zielke et al. 2002; de Vries and Bardgett 2016; Wang et al. 2018). Due to N limitation in most tundra ecosystems (Schimel and Bennett 2004), plants and soil microbes strongly compete for N, and the retention and losses of N are largely controlled by the interactions between plants and microbes. Immediately

after plant dieback, an increasing amount of N could be immobilized by soil microbes or be lost as gases and by leaching, due to low N uptake by plants (Nordin, Schmidt, and Shaver 2004; Sorensen, Michelsen, and Jonasson 2008; Barthelemy et al. 2017). On the longer time scale, due to reduced quantities of fresh organic matter input, soil microbial N transformation processes and thus soil N retention and N losses could be changed. Moreover, plants have longer turnover rates and longer tissue longevity than soil microbes, and with the recovery and regrowth of vascular plants, plants could acquire N that is previously incorporated into microbial biomass and subsequently released (Nordin, Schmidt, and Shaver 2004; Clemmensen et al. 2008). Plant functional groups, with different traits and life strategies, vary in their ability for N uptake and long-term retention (Hewitt et al. 2019; Pedersen, Elberling, and Michelsen 2020) and in their susceptibility to major disturbances and subsequent recovery capacities (e.g., plant dieback) (McIntyre et al. 1999). For instance, evergreen shrubs (e.g., *Empetrum nigrum* and *Vaccinium myrtillus*) are more vulnerable than deciduous shrubs and graminoids to extreme winter warming or moth grazing events in sub-arctic heath tundra (Bokhorst et al. 2015, 2018). While these studies have examined how the biomass or size of different plants responds to such events, the impact of plant dieback on N uptake capacity among plant functional groups remains unknown (Bokhorst et al. 2011, 2015, 2018).

Temperature plays a crucial role in governing plant productivity and soil biogeochemical processes in arctic ecosystems (Karhu et al. 2014). Climate warming has been reported to stimulate vegetation regrowth, potentially facilitating plants of certain functional groups or species to re-attain competitive advantage for N acquisition and increase N retention in aboveground biomass. For instance, deciduous shrubs, characterized by their expansive canopy coverage and taller stature, exhibit a stronger response to warming compared to graminoids and evergreen shrubs (DeMarco et al. 2014). Such events are thus likely to alter short- or long-term N retention patterns among functional groups. However, studies on long-term ecosystem N retention in the Arctic are rare, and knowledge on how summer warming and plant dieback interact to alter the fate of N in the plant–soil–microbe compartments in the long term is lacking.

In this study, we established long-term treatment experiments to simulate combined plant dieback (cutting vegetation) and warmer summer air temperatures (deployment of open-top chambers (OTCs)) in an arctic heath tundra, West Greenland. Nitrogen-15-labeled ammonium and nitrate were applied on the ground surface to trace the fate of N after the plant dieback. We studied immediate (3–23 days) and short- (1 year) to long-term (2–5 years) responses of soil nutrient contents, and  $N_2O$  and  $CH_4$  fluxes to plant dieback and summer warming. Our research aims were to (I) quantify immediate and short- to long-term changes in soil nutrient contents and  $N_2O$  and  $CH_4$  flux rates following plant dieback; (II) to quantify all ecosystem compartments (plants, soils, and microbial biomass) to utilize or retain N following plant dieback; and (III) to quantify effects of plant dieback on these biogeochemical processes under summer warming. The underlining hypothesis is that (I) due to elevated soil nutrient contents arising from reduced plant uptake immediately and over a short-term basis following plant dieback, surface

$N_2O$  emissions increase while  $CH_4$  uptake rates decrease, and these effects are amplified under warmed conditions; (II) over a long-term basis, surface  $N_2O$  and  $CH_4$  fluxes are expected to show little or no response to plant dieback because of plant recovery and a corresponding decline in soil nutrients over time; (III) compared with the other functional groups, summer warming will benefit the regrowth of deciduous shrubs and their N uptake and retention more due to their stronger response to temperatures; and (IV) plant dieback and summer warming will interact and result in increased soil N retention due to reduced fresh organic matter input and enhanced microbial N immobilization over time.

## 2 | Materials and Methods

### 2.1 | Site Description

The study site is located in the transitional zone between the high and low Arctic (Figure S1) at Blåsedalen Valley (69°16'N, 53°27'W) on the southern tip of Disko Island, West Greenland. The mean annual air temperature is  $-3.0^\circ\text{C}$ , with mean monthly temperature ranging from  $8^\circ\text{C}$  in July to  $-14^\circ\text{C}$  in March, and the mean annual precipitation is 418 mm of which 34% is snowfall (from 1991 to 2017). The active layer has been reported to be 1.5 m deep, with a thin (ca. 5 cm) organic horizon present atop the mineral soil (Blok, Elberling, and Michelsen 2016). The annual mean soil temperature at 5 cm depth is  $-1.9^\circ\text{C}$  and frozen soil conditions prevail from October to late May (D'Imperio et al. 2018). The vegetation is typical for a dry heath tundra, dominated by deciduous dwarf shrubs including dwarf birch (*Betula nana*), grey willow (*Salix glauca*) and bog bilberry (*Vaccinium uliginosum*), and evergreen black Arctic bell-heather (*Cassiope tetragona*), with a mixture of graminoids, lichens and mosses covering the ground. The aboveground biomass averages  $907.2 \pm 219.4 \text{ g dw m}^{-2}$  (control plots).

### 2.2 | Experimental Setup and Design

On July 28th 2017, a combined summer warming and vegetation dieback experiment was established on a gentle northeast-facing slope ( $5.7^\circ$  inclination). The experiment includes four treatments (plot size  $1.2 \times 1.2 \text{ m}$ ), that is, control (CTO), cutting down vegetation to  $< 5 \text{ cm}$  aboveground (VCO), warming only (CTX), and vegetation cut in combination with warming (VCX), randomly distributed in five replicate blocks (block size  $4.8 \times 4.8 \text{ m}$ ). The warming was achieved by mounting year-round hexagonal open-top chambers (OTCs), which were made of transparent polycarbonate, 35 cm tall and had a base diameter of 150 cm and top diameter of 85 cm (Marion 1996).

### 2.3 | Nitrogen-15 Labeling

On July 30th 2017, all plots were amended with equal amounts of ammonium sulfate ( $(^{15}\text{NH}_4)_2\text{SO}_4\text{-N}$ ) and potassium nitrate ( $\text{K}^{15}\text{NO}_3\text{-N}$ ), both enriched at 13.5 atom%  $^{15}\text{N}$ , by using a backpack sprayer. The total application was equivalent to a non-fertilizing amount of  $0.2 \text{ g N m}^{-2}$  (providing 27 mg  $^{15}\text{N}$  excess  $\text{m}^{-2}$ ) dissolved in 1 L per plot.

### 2.4 | Greenhouse Gas Measurement

Surface  $N_2O$  was measured using a static chamber technique (Denmead 2008). Stainless steel collars ( $20 \times 20 \times 10 \text{ cm}$ ) were pre-installed 5 cm into the soil in each plot. White PVC chambers ( $21 \times 21 \times 19.5 \text{ cm}$ ) were mounted in a groove atop the collars, and water was carefully added to establish a gas-tight seal between the chamber enclosure and the outside atmosphere. A watering can with a long spout was used to avoid adding water to the soils. The chambers were left in place for 160 min and five headspace gas samples were taken manually with a 12-mL syringe at 40 min intervals. When collecting the gas sample, the headspace was first mixed by vigorously pumping the 12-mL syringe twice, and the samples were then transferred to 12-mL pre-evacuated Exetainers (Labco Scientific, High Wycombe, UK). Analysis was carried out by gas chromatography (Agilent 7890 GC, Agilent Technologies UK Ltd., Stockport, UK) with an electron capture detector (ECD). The  $CH_4$  flux measurements were conducted by connecting the chambers to a portable Gas Analyzer Picarro G4301 (Picarro Inc.) The changes in  $CH_4$  and  $CO_2$  concentrations were analyzed and logged at a 5 s sampling frequency for 5 min.

Nitrous oxide flux measurements were obtained at three campaigns in 2017, six campaigns in 2018, and four campaigns in 2019, while  $CH_4$  and  $CO_2$  fluxes were measured two times in 2017 (only  $CH_4$ ) and 2018, and four times in 2019. Along with gas measurements, soil temperature, and soil moisture were manually recorded in triplicates within the experimental plot next to the soil collar. Soil temperature and soil volumetric moisture (%vol) at 5 cm depth were measured with a HI93503 (Hanna Instruments, Woonsocket, RI, USA) and a ML2X Theta Probe coupled to a HH2 Moisture Meter (Delta-T Devices, Cambridge, UK), respectively.

### 2.5 | Soil and Plant Analysis

On July 31st, August 17th 2017, August 14th 2018, July 17th 2019, and August 8th 2022, two or three replicate soil samples were collected in the top 3.5 cm soil at each plot by using a 4.5 cm diameter auger. On August 18th 2021, soil samples were taken from each plot in the 0–5.5 cm topsoil, and then were split into 0–3.5 cm and 3.5–5.5 cm soil depths. The replicate samples were subsequently mixed thoroughly into one composite sample. The samples were stored at  $5^\circ\text{C}$  until further processing within 2 days. Root samples were separated from soil samples by hand (collected on August 18th 2021) at both soil depths, and then rinsed with deionized water, dried, and weighed.

On August 18th, 2021, all above-ground biomass (and litter separately) was collected from an area of  $20 \times 20 \text{ cm}$  within each plot. The area was chosen to be representative of the vegetation at each plot in general but also for that inside the collar. The collected biomass samples were sorted into functional groups and separated into leaves and stems/shoots, and then were dried at  $65^\circ\text{C}$  for 48 h and weighed.

Soil moisture was calculated from oven drying weight loss ( $70^\circ\text{C}$ , 48 h), and subsequently dried samples were finely ground

by ball milling. Soil extractions were made by suspending field moist soil in deionized water (10g soil; 50mL water), shaking for 1h at room temperature terminated by filtration through a 2.7 $\mu$ m membrane filter (Whatman GF/D). Microbial biomass C and N contents as well as  $^{15}\text{N}$  concentrations were measured using the chloroform fumigation-extraction method (Brookes et al. 1985). Briefly, soils (collected on August 18th 2021) were fumigated by vacuum incubation with chloroform ( $\text{CHCl}_3$ ) for 24h before extraction as described by (Brookes et al. 1985). Twenty-five mL of filtered extracts of both fumigated and non-fumigated soil were subsequently freeze-dried and then encapsulated for  $^{15}\text{N}$ -concentration analysis. The (remaining) filtered extracts were kept frozen until analysis for ammonium ( $\text{NH}_4^+\text{-N}$ ) and nitrate ( $\text{NO}_3^-\text{-N}$ ) using flow-injection analysis (Tecator 5000 FIAStar, Höganäs, Sweden). Soil-dissolved organic C (DOC) and total dissolved N (TDN) from the extracts were determined using a TOC-TN analyzer (Shimadzu, Kyoto, Japan). Dissolved organic N (DON) was calculated as the difference between total dissolved N and dissolved inorganic N ( $\text{NO}_3^-\text{-N} + \text{NH}_4^+\text{-N}$ ). Microbial biomass C, N, and isotopic  $^{15}\text{N}$  enrichment were calculated as the difference between fumigated and non-fumigated data. Correction factors of 0.4 and 0.45 for extraction efficiency were applied to estimate soil microbial C and N, respectively (Christiansen et al. 2012; Pedersen, Elberling, and Michelsen 2020). The total C and N contents as well as  $^{15}\text{N}$  enrichment of dried soils, plant materials, and precipitates were measured by elemental analysis (EA; CE1110, Thermo Electron, Milan, Italy) coupled in continuous flow mode to a Finnigan MAT Delta PLUS isotope ratio mass spectrometer (IRMS; Thermo Scientific, Bremen, Germany).

## 2.6 | Gross N Transformation

Soil samples were collected at 0–3.5 cm depth on August 18th, 2021, to quantify gross N transformation rates using a  $^{15}\text{N}$  pool dilution technique (Di, Cameron, and McLaren 2000). Fresh samples (5g moist soil) were weighed into 100-mL plastic cups and amended with 1 mL ammonium nitrate ( $^{15}\text{NH}_4\text{NO}_3$  or  $\text{NH}_4^{15}\text{NO}_3$ ; 10 mg  $\text{N L}^{-1}$ ; 5.2 atom%  $^{15}\text{N}$ ). The soils were incubated at their corresponding field temperatures during summer (7 or 9.5°C) to simulate in-situ ambient temperature and summer warming conditions. There were two analytical replicates for each combination of soil and  $^{15}\text{N}$  labeling solution. Incubations were terminated at 0.5h and 2 days after labeling by suspending soil in 50 mL of 2 M potassium chloride (KCl) solution. All soil extractions were filtered through a 2.7 $\mu$ m membrane filter (Whatman GF/D) after 1h of shaking on a horizontal shaker. For analysis of  $^{15}\text{NH}_4^+\text{-N}$ ,  $\text{NH}_4^+\text{-N}$  was vaporized as  $\text{NH}_3$  from the filtered extracts and caught on acidified traps by using the micro-diffusion method (Sørensen and Jensen 1991). The  $^{15}\text{NO}_3^-\text{-N}$  content was subsequently determined in the  $\text{NH}_4^+$ -free extracts following the conversion of  $\text{NO}_3^-$  to  $\text{NH}_4^+$  (Devarda alloy) and then  $\text{NH}_4^+$ -analysis as described above for  $\text{NH}_4^+\text{-N}$  (Sørensen and Jensen 1991). The acid traps were freeze-dried prior to the determination of  $^{15}\text{N}$  enrichment by EA-IRMS.

An additional set of soil samples (5g moist soil) was placed in serum bottles and amended with 1 mL  $\text{NH}_4^{15}\text{NO}_3$  (10 mg  $\text{N L}^{-1}$ ; 5.2 atom%  $^{15}\text{N}$ ). The bottles were crimped gas-tight with butyl

rubber stoppers and then 12 mL of acetylene ( $\text{C}_2\text{H}_2$ ) was added to the headspace to block the reduction of  $\text{N}_2\text{O}$  into  $\text{N}_2$  and to quantify N losses via denitrification and to estimate immobilization of  $\text{NO}_3^-$ . The bottles were incubated at 7 or 9.5°C for 2 days, and 80 mL headspace gas samples were collected and then injected into a  $\text{N}_2\text{O}$  laser (ABB-LGR GLA451 N2O12 Isotopic  $\text{N}_2\text{O}$  analyzer, ABB Inc., Quebec, Canada) for the analysis of concentrations and  $^{15}\text{N}$ -isotopic enrichment of  $\text{N}_2\text{O}$ .

## 2.7 | Calculations and Statistics

The surface  $\text{N}_2\text{O}$ ,  $\text{CH}_4$ , and  $\text{CO}_2$  fluxes were calculated by fitting a linear regression to changes in  $\text{N}_2\text{O}$  ( $p < 0.05$ ,  $R^2 > 0.8$ ),  $\text{CH}_4$ , and  $\text{CO}_2$  concentrations ( $p < 0.05$ ,  $R^2 > 0.9$ ) over time. The contribution of seasonally average  $\text{N}_2\text{O}$  and  $\text{CH}_4$  fluxes (based on campaigns of each growing season) to the total GHG budget was assessed by converting the average fluxes into  $\text{CO}_2$ -equivalents (298 and 35  $\text{CO}_2$ -eq, respectively).

To calculate the proportion of  $^{15}\text{N}$  tracer recovered in soils, roots, microbial biomass, and leaves and stems/shoots, we used the following formula:

$$\% \text{ recovery} = \frac{\text{sample } ^{15}\text{N APE} * \text{total N pool}}{\text{added } ^{15}\text{N excess}} * 100$$

where the sample  $^{15}\text{N}$  APE is the atom% excess in the soils, roots, microbial biomass, and leaves and stems/shoots after subtracting the  $^{15}\text{N}$  natural abundance. Total N pool is expressed as the sum of soil, litter, root, and leaf and stem/shoot N pools ( $\text{g N m}^{-2}$ ) based on soil bulk density or litter, root, leaf, and stem/shoot biomass. Leaves and stems are combined per functional group for total above-ground biomass samples. Added  $^{15}\text{N}$  excess equals 0.027 g  $^{15}\text{N}$  excess  $\text{m}^{-2}$ .

Before statistical analysis, we inspected the QQ-plots and used the Shapiro–Wilk normality test or Levene's test to check data for normal distribution and homogeneity of variance. When necessary, data were log or square root transformed. We tested the effects of shrub cut and/or warming, and/or their interactions, on surface  $\text{N}_2\text{O}$ ,  $\text{CH}_4$ , and  $\text{CO}_2$  fluxes, soil chemical properties (DON, DOC,  $\text{NO}_3^-\text{-N}$  and  $\text{NH}_4^+\text{-N}$ ), soil moisture, and temperature. The treatment effects were also tested on  $^{15}\text{N}$  recovery in bulk soil, litter, root, functional-form specific plant (leaf and stem/shoot), and microbial biomass samples, and soil gross N transformation rates. Tests were conducted separately (for each campaign) or for combined campaigns within each year by using one- or two-way ANOVA in linear mixed effects models with the lme4 and car package (Bates et al. 2015; Fox and Weisberg 2019). Replicate blocks were specified as random factors accounting for spatial variations within the site. Post hoc pairwise comparisons between levels of all significant factors were then conducted using the emmeans package, with Tukey's Honestly Significant Differences (Tukey HSD)  $p$  value adjustment (Lenth 2020). The significant treatment effects are based on  $*p \leq 0.05$  and  $**p \leq 0.01$ . The data of  $\text{N}_2\text{O}$ ,  $\text{CH}_4$ , and soil nutrients from the CTO and CTX plots have been published (Hermesdorf et al. 2022), but these data were presented here for comparisons with the VCO and VCX plots. The correlations between surface  $\text{N}_2\text{O}$  and  $\text{CH}_4$  fluxes, both soil temperature and soil moisture, and between microbial biomass  $^{15}\text{N}$  recovery, and

litter biomass and immobilization of  $\text{NO}_3^-$ -N, were examined by linear regression analysis. All analysis above was performed using R software v. 3.6.1 (Team 2019).

### 3 | Results

#### 3.1 | Soil Chemical Properties

Vegetation cutting had immediate effects on soil  $\text{NO}_3^-$ -N concentrations ( $p=0.017$ ), showing a 23-fold increase 5 days after the treatment (Table 1). After 1 year (days after vegetation cutting, DAC381), the vegetation-cut plots (VCX) had lower soil DON (47%) and  $\text{NH}_4^+$ -N concentrations (33%) than uncut plots under warmed conditions (CTX;  $p \leq 0.05$ ). This was primarily due to stimulatory warming effects only apparent in uncut plots ( $p < 0.05$  for CTO-CTX comparisons; Table 1). Similarly, the vegetation cutting also significantly reduced soil DOC (53%), DON (67%), and  $\text{NH}_4^+$ -N concentrations (49%) after 2 years (DAC718), but only under warmed conditions ( $p < 0.05$  for CTX-VCX comparisons; Table 1). After 5 years (DAC1836), a decrease (85%) in soil  $\text{NH}_4^+$ -N concentrations due to vegetation cutting was still observed under warmed conditions ( $p = 0.05$  for CTX-VCX comparisons; Table 1).

#### 3.2 | Surface $\text{N}_2\text{O}$ and $\text{CH}_4$ Fluxes

Surface  $\text{N}_2\text{O}$  fluxes across all treatments and years were relatively small and ranged from  $-3$  (uptake) to  $2.5$  (emission)  $\mu\text{gN}_2\text{O-Nm}^{-2}\text{h}^{-1}$  (Figure 1a). There was a significant immediate effect of vegetation cutting on surface  $\text{N}_2\text{O}$  fluxes, with more negative rates in vegetation-cut plots (VCO) as compared to control plots (CTO) on DAC12 ( $p=0.05$ ; Figure 1a). The vegetation cutting also showed significant effects on  $\text{N}_2\text{O}$  fluxes after 1 year, reflected by less  $\text{N}_2\text{O}$  uptake (DAC345;  $p=0.043$ ) or less  $\text{N}_2\text{O}$  emission (DAC370;  $p=0.017$ ) in vegetation-cut plots (VCO) as compared with control plots (CTO; Figure 1a). Moreover, summer warming promoted the emission of  $\text{N}_2\text{O}$  at the plots subjected to vegetation cutting (VCO vs. VCX,  $p=0.030$  and  $p=0.033$  for DAC334 and DAC379, respectively; Figure 1a). However, warming effects on uncut plots were not consistent (CTO vs. CTX), either reversing  $\text{N}_2\text{O}$  fluxes (DAC345 and DAC370;  $p < 0.01$ ) or increasing  $\text{N}_2\text{O}$  emission (DAC715;  $p=0.030$ ; Figure 1a). As a result, the vegetation cutting (VCX) either reversed  $\text{N}_2\text{O}$  fluxes (DAC370;  $p=0.018$ ) or reduced  $\text{N}_2\text{O}$  emission (DAC715;  $p=0.030$ ) as compared with uncut plots (CTX) under summer warming conditions (1269%; Figure 1a). Mean soil temperatures at 5 cm depth were increased by  $0.8^\circ\text{C}$ – $1.5^\circ\text{C}$  by summer warming in growing seasons in 2018 and 2019 (Figure 1b). There were no significant treatment effects on soil moisture content (Figure 1c).

Surface  $\text{CH}_4$  flux rates across all treatments and years were negative and ranged from  $-0.111$  to  $-0.016$   $\text{mg CH}_4\text{-C m}^{-2}\text{h}^{-1}$  (Figure S2). The vegetation cutting immediately increased surface  $\text{CH}_4$  uptake rates significantly by 63.6% (DAF3;  $p < 0.001$ ) but had no significant short- or long-term effects on  $\text{CH}_4$  uptake rates (Figures S2). The warming also showed overall positive effects on  $\text{CH}_4$  uptake in both 2018 and 2019 ( $p < 0.01$ ; Figure S2).

Estimations of  $\text{CO}_2$ -eq showed a negative warming potential of non- $\text{CO}_2$  greenhouse gases for this tundra ecosystem, mainly driven by the contribution of  $\text{CH}_4$  uptake (Table S1). The vegetation cutting had significant and immediate effects on non- $\text{CO}_2$  warming potential, with the  $\text{CO}_2$ -eq values becoming more negative (Table S1).

Surface  $\text{N}_2\text{O}$  fluxes increased with soil temperatures in growing seasons in 2017 ( $R^2=0.08$ ,  $p=0.029$ ) and 2019 ( $R^2=0.09$ ,  $p=0.012$ ; Figure S3), while they decreased with increasing soil moisture content in 2018 ( $R^2=0.06$ ,  $p=0.05$ ) 2019 ( $R^2=0.10$ ,  $p=0.006$ ; Figure S4). Surface  $\text{CH}_4$  uptake decreased with increasing soil moisture content in growing seasons in 2018 ( $R^2=0.26$ ,  $p < 0.001$ ) and 2019 ( $R^2=0.2$ ,  $p < 0.001$ ; Figure S5).

#### 3.3 | Soil N Transformation Processes

Four years after the vegetation cutting, gross N mineralization and nitrification rates were decreased by 49.4% and 73.8%, respectively, under ambient temperatures ( $p=0.001$  and  $p=0.019$  for CTO-VCO comparisons; Table 2), and by 46.8% and 71.2%, respectively, under warmed conditions ( $p=0.022$  and  $p=0.003$  for CTX-VCX comparisons; Table 2). The warming significantly increased gross microbial consumption of  $\text{NH}_4^+$  by 71.3% and 53.5% at uncut ( $p=0.001$  for CTO-CTX comparisons) and vegetation-cut plots ( $p=0.029$  for VCO-VCX comparisons), respectively (Table 2). In addition, vegetation-cut plots (VCX) showed significantly higher gross microbial consumption of  $\text{NO}_3^-$  than uncut plots (CTX) under warmed conditions (1905%;  $p=0.043$ ; Table 2). The negligible production of  $\text{N}_2\text{O}$  and no significant  $^{15}\text{N}$  enrichment of produced  $\text{N}_2\text{O}$  indicate negligible N loss via denitrification.

#### 3.4 | Aboveground $^{15}\text{N}$ Recovery

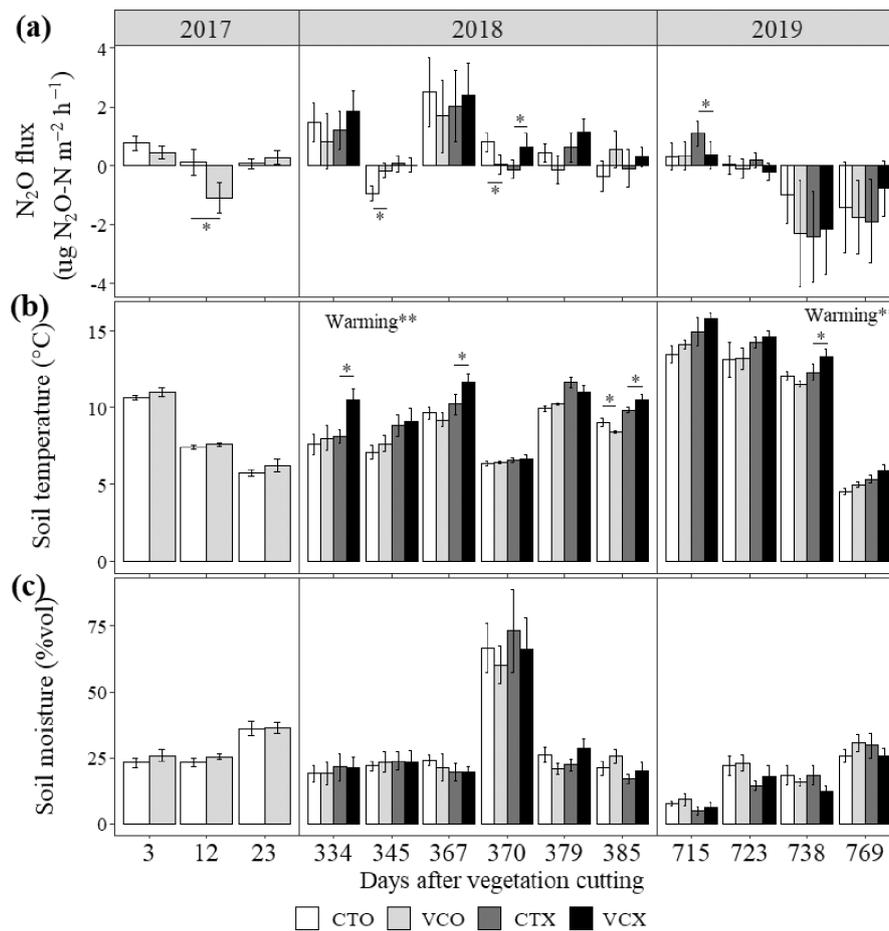
Evergreen shrub biomass was significantly lower at vegetation-cut (VCO) than at control plots (CTO) 4 years after the vegetation cutting (74.5%;  $p=0.015$ ), with its biomass C and N pools decreasing by 73.5% ( $p=0.016$ ) and 72.1% ( $p=0.028$ ), respectively (Figures 2a and S6). In contrast, the aboveground biomass of the other functional groups as well as their biomass C and N pools were not significantly different between vegetation-cut (VCO) and control plots (CTO; Figures 2a and S6). Four years after the application of  $^{15}\text{NH}_4^+$ -N and  $^{15}\text{NO}_3^-$ -N, deciduous shrubs retained significantly lower  $^{15}\text{N}$  in their aboveground biomass at vegetation-cut (VCO) compared with control plots (CTO;  $p=0.03$ ; Figure 2b).

Due to stimulatory warming effects only apparent at uncut plots ( $p < 0.05$  for CTO-CTX comparisons), deciduous shrubs exhibited significantly lower aboveground biomass in vegetation-cut plots (VCX) than warming-only plots (CTX; Figure 2a). As a result, biomass C, N pools and  $^{15}\text{N}$  incorporation of deciduous shrubs decreased by 66.8% ( $p=0.002$ ), 65.7% ( $p=0.02$ ), and 69.7% ( $p=0.001$ ), respectively (CTX vs. VCX; Figures 2 and S6). There were more vegetation-cut plots with graminoid regrowth under warmed conditions as compared with ambient temperature conditions ( $p < 0.05$  for VCO-VCX comparisons; Figure 2a). The moss compartment constituted the majority of the total

**TABLE 1** | Effects of vegetation cutting in combination with summer warming on soil properties at 0–3.5 cm depth in growing seasons 2017–2022 in an arctic heath tundra in Disko Island, Greenland. Numbers show mean ( $\pm$  standard error) of replicate blocks ( $n = 5$ ).

	Year	Days after vegetation cutting	CTO	VCO	CTX	VCX	Treatment effects	
DOC (mg kg <sup>-1</sup> )	2017	5	91.6 $\pm$ 15.5	109.1 $\pm$ 44.9				
		21	102.3 $\pm$ 60.5	61.6 $\pm$ 28.9				
	2018	342	57.2 $\pm$ 9.8	60.4 $\pm$ 15.1	133.0 $\pm$ 10.1	105.3 $\pm$ 27.6	Warming**	
		381	7.4 $\pm$ 1.4	6.8 $\pm$ 1.8	14.4 $\pm$ 1.6	10.3 $\pm$ 2.7	Warming**	
	2019	718	42.9 $\pm$ 8.2	27.2 $\pm$ 8.7	78.6 $\pm$ 23.2	36.6 $\pm$ 9.4	Cutting** Warming*	
		2021	1481	16.7 $\pm$ 4.6	23.6 $\pm$ 5.2	19.3 $\pm$ 5.2	21.0 $\pm$ 5.5	
2022	1836	120.6 $\pm$ 73.8	79.3 $\pm$ 15.1	88.1 $\pm$ 22.7	58.2 $\pm$ 18.4			
DON (mg kg <sup>-1</sup> )	2017	5	8.2 $\pm$ 0.6	9.2 $\pm$ 2.2				
		21	13.4 $\pm$ 6.0	7.5 $\pm$ 2.2				
	2018	342	3.8 $\pm$ 1.0	4.0 $\pm$ 1.4	11.2 $\pm$ 1.5	8.8 $\pm$ 2.9	Warming**	
		381	0.3 $\pm$ 0.1	0.4 $\pm$ 0.1	0.9 $\pm$ 0.2	0.5 $\pm$ 0.1	Warming** Cutting $\times$ warming*	
	2019	718	3.2 $\pm$ 0.8	2.0 $\pm$ 0.7	6.1 $\pm$ 1.4	2.0 $\pm$ 0.5	Cutting** Warming*	
		2021	1481	1.2 $\pm$ 0.4	1.1 $\pm$ 0.2	1.4 $\pm$ 0.5	1.6 $\pm$ 0.5	
	2022	1836	7.1 $\pm$ 4.1	5.6 $\pm$ 1.0	5.2 $\pm$ 1.2	3.0 $\pm$ 0.9		
	NH <sub>4</sub> <sup>+</sup> -N (mg kg <sup>-1</sup> )	2017	5	0.48 $\pm$ 0.13	0.50 $\pm$ 0.14			
			21	0.43 $\pm$ 0.09	0.33 $\pm$ 0.07			
		2018	342	0.27 $\pm$ 0.06	0.35 $\pm$ 0.11	0.59 $\pm$ 0.10	0.50 $\pm$ 0.13	Warming*
381			0.04 $\pm$ 0.01	0.05 $\pm$ 0.00	0.07 $\pm$ 0.01	0.04 $\pm$ 0.01	Cutting $\times$ warming*	
2019		718	0.12 $\pm$ 0.03	0.12 $\pm$ 0.03	0.21 $\pm$ 0.03	0.10 $\pm$ 0.02	Cutting $\times$ warming*	
		2021	1481	0.11 $\pm$ 0.02	0.14 $\pm$ 0.02	0.16 $\pm$ 0.05	0.21 $\pm$ 0.05	
2022	1836	0.74 $\pm$ 0.42	1.38 $\pm$ 0.55	1.60 $\pm$ 0.62	0.24 $\pm$ 0.11	Cutting $\times$ warming*		
NO <sub>3</sub> <sup>-</sup> -N (mg kg <sup>-1</sup> )	2017	5	0.05 $\pm$ 0.02	1.25 $\pm$ 0.94			Cutting*	
		21	0.04 $\pm$ 0.02	0.53 $\pm$ 0.50				
	2018	342	0	0	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01		
		381	0	0	0	0		
	2019	718	0.06 $\pm$ 0.02	0.03 $\pm$ 0.01	0.16 $\pm$ 0.06	0.10 $\pm$ 0.06	Warming*	
		2021	1481	0.03 $\pm$ 0.00	0.06 $\pm$ 0.02	0.04 $\pm$ 0.00	0.05 $\pm$ 0.01	
2022	1836	0	0	0.03 $\pm$ 0.03	0			
MBC (mg kg <sup>-1</sup> )	2021	1481	859 $\pm$ 336	1606 $\pm$ 365	901 $\pm$ 470	1030 $\pm$ 275		
MBN (mg kg <sup>-1</sup> )	2021	1481	39.2 $\pm$ 15.8	63.6 $\pm$ 17.0	36.1 $\pm$ 25.4	46.9 $\pm$ 13.3		

Note: Control and summer warming (CTO and CTX), vegetation cutting and in combination with summer warming (VCO and VCX). Significant vegetation cutting and summer warming effects as well as their interactions are shown as \* $p \leq 0.05$  and \*\* $p \leq 0.01$ . Abbreviations: MBC, microbial biomass C; MBN, microbial biomass N.



**FIGURE 1** | Surface nitrous oxide ( $\text{N}_2\text{O}$ ) fluxes (a), soil temperatures (b) and soil moisture content (c) in growing seasons 2017–2019 in an arctic heath tundra in Disko Island, Greenland.

aboveground biomass, and was the largest fate of  $^{15}\text{N}$  (11%–22%) among the functional plant groups, regardless of the treatments (Figure 2a and Table 3).

### 3.5 | Belowground $^{15}\text{N}$ Recovery

Bulk root biomass as well as its C and N pools, did not significantly vary between vegetation-cut (VCO) and control plots (CTO; Figure S7). There were no direct effects of vegetation cutting on  $^{15}\text{N}$  recoveries in any of the belowground pools (CTO vs. VCO; Figure 3). Meanwhile, the effects of warming and combined effects of warming and vegetation cutting were significant. Under warmed conditions, the vegetation-cut plots (VCX) exhibited higher mean  $^{15}\text{N}$  incorporation in bulk soil (65.7%;  $p = 0.014$ ) and microbial biomass pools (1019%;  $p = 0.004$ ) at 0–3.5 cm soil depth compared with warming only plots (CTX; Figure 3a,d). This was due to the stimulating effects of warming on bulk soil (409%;  $p = 0.003$  for VCO-VCX comparisons) and microbial biomass  $^{15}\text{N}$  incorporation (103%;  $p = 0.008$  for VCO-VCX comparisons) only observed at vegetation-cut plots (Figure 3a,d). Moreover, there was weak evidence for a positive warming effect on root  $^{15}\text{N}$  uptake at both uncut (375%;  $p = 0.075$  for CTO-CTX comparisons at 3.5–5.5 cm soil depth) and vegetation-cut plots (77.8% and 82%;  $p = 0.063$  and  $p = 0.067$  for VCO-VCX comparisons at 0–3.5 cm and 3.5–5.5 cm soil depths, respectively; Figure 3b).

### 3.6 | Correlations Between Microbial Biomass $^{15}\text{N}$ Recovery, and Litter Biomass and Immobilization of $\text{NO}_3^- \text{-N}$

Bulk soil  $^{15}\text{N}$  recovery was positively and significantly correlated with microbial biomass  $^{15}\text{N}$  recovery across treatments and soil depths ( $R^2 = 0.24$ ,  $p = 0.0032$ ; Figure 4a). Microbial biomass  $^{15}\text{N}$  recovery was negatively correlated with litter biomass ( $R^2 = 0.28$ ,  $p = 0.043$ ; Figure 4b), while it was positively correlated with immobilization of  $\text{NO}_3^- \text{-N}$  rates ( $R^2 = 0.54$ ,  $p = 0.045$ ; Figure 4c). Immobilization of  $\text{NO}_3^- \text{-N}$  rates increased with increasing soil temperatures across treatments ( $R^2 = 0.21$ ,  $p = 0.05$ ; Figure 4d).

## 4 | Discussion

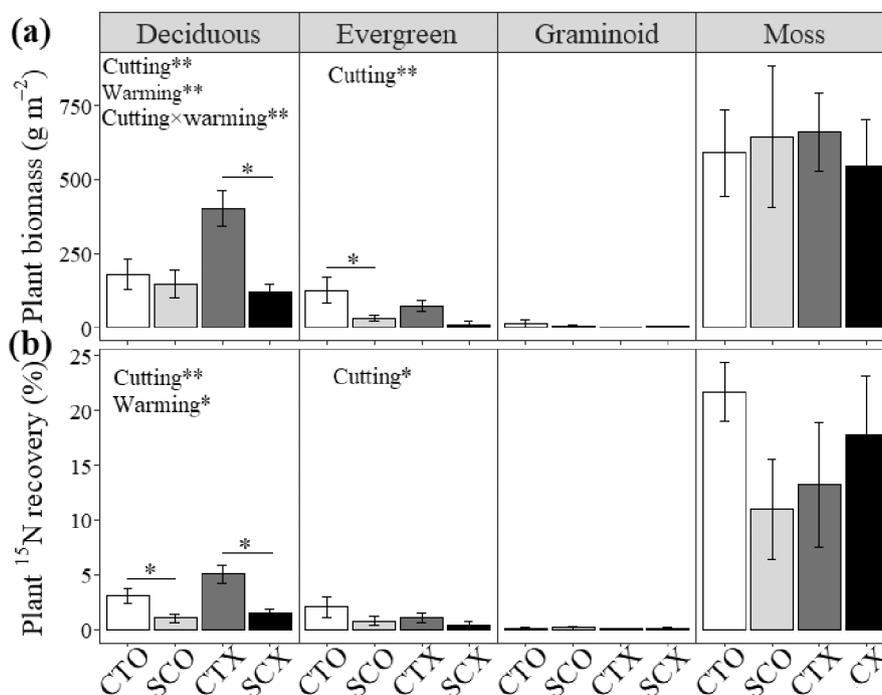
### 4.1 | Plant Dieback and Warming Effects on Soil Nutrients and Surface $\text{N}_2\text{O}$ and $\text{CH}_4$ Fluxes

Immediately after the vegetation cutting (as a simulation of plant dieback), soil  $\text{NO}_3^- \text{-N}$  concentrations significantly increased, likely as a result of reductions in vegetation biomass and plant nutrient uptake. One and 2 years after plant dieback (2018 and 2019), soil DOC and DON concentrations decreased under warm conditions. This reduction in DOC

**TABLE 2** | Effects of vegetation cutting in combination of summer warming on soil gross nitrogen transformation rates. Numbers show mean ( $\pm$  standard error) of replicate blocks.

	CTO	VCO	CTX	VCX	Treatment effects
Gross N mineralization ( $\text{mg N kg}^{-1} \text{ day}^{-1}$ )	$7.5 \pm 1.5$	$3.8 \pm 0.9$	$7.9 \pm 1.2$	$4.2 \pm 0.9$	Cutting**
Gross $\text{NH}_4^+$ -N consumption ( $\text{mg N kg}^{-1} \text{ day}^{-1}$ )	$1.7 \pm 0.4$	$2.0 \pm 0.7$	$5.9 \pm 0.5$	$4.4 \pm 1.4$	Warming**
Gross nitrification ( $\text{mg N kg}^{-1} \text{ day}^{-1}$ )	$7.2 \pm 0.6$	$1.9 \pm 1.0$	$9.4 \pm 3.0$	$2.7 \pm 1.1$	Cutting**
Gross $\text{NO}_3^-$ -N consumption (i.e. immobilization of $\text{NO}_3^-$ -N; $\text{mg N kg}^{-1} \text{ day}^{-1}$ )	$1.0 \pm 0.6$	$0.8 \pm 0.5$	$0.1 \pm 0.1$	$2.8 \pm 1.1$	Cutting $\times$ warming*

Note: Control and summer warming (CTO and CTX), vegetation cutting and in combination with summer warming (VCO and VCX). Significant vegetation cutting and summer warming effects as well as their interactions are shown as \* $p \leq 0.05$  and \*\* $p \leq 0.01$ . Gross  $\text{NO}_3^-$ -N consumption is considered as immobilization of  $\text{NO}_3^-$ -N due to negligible N loss via denitrification.

**FIGURE 2** | Aboveground plant biomass (a) and its  $^{15}\text{N}$  recovery (b) by functional forms (deciduous shrubs, evergreen shrubs, graminoids, mosses) 4 years after vegetation cutting (2021) in an arctic heath tundra in Disko Island, Greenland.

and DON could be due to a lower aboveground litter input (as supported by lower litter biomass in 2021) combined with increased organic matter decomposition (Little et al. 2017; Saunders et al. 2023). Warmer temperatures are known to accelerate organic matter decomposition (Conant et al. 2008; Bracho et al. 2016), amplifying the negative effects of reduced fresh organic matter input on the availability of organic substrates in the soil. In line with the declining trend of soil DON concentrations, gross N mineralization rates and soil  $\text{NH}_4^+$ -N concentrations were also lowered in vegetation-cut plots under warmed conditions. This is expected as the labile fraction of DON is considered the initial substrate for N cycling processes (Cookson and Murphy 2004; Jones et al. 2004; Xu et al. 2021).

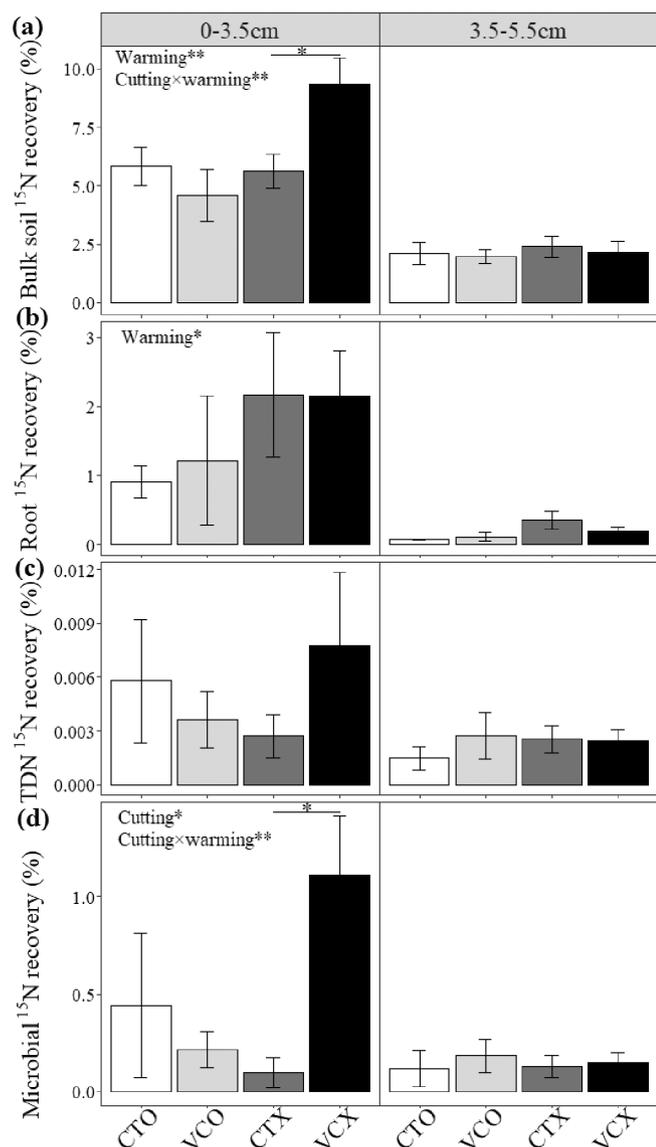
Surface  $\text{N}_2\text{O}$  flux rates were minor and sometimes negative throughout the growing seasons, which are consistent with the range of fluxes reported in nearby areas (Kolstad,

Michelsen, and Ambus 2021; Xu et al. 2023) and other arctic dry tundra ecosystems (Ma et al. 2007; Brummell, Farrell, and Siciliano 2012; Paré and Bedard-Haughn 2012; Chen et al. 2014; Voigt et al. 2017). Overall, the plant dieback only occasionally affected surface  $\text{N}_2\text{O}$  fluxes and in contrasting directions: an immediate increase or short-term decrease in  $\text{N}_2\text{O}$  uptake, and a short-term increase or long-term decrease in  $\text{N}_2\text{O}$  emissions. These results reject hypotheses (I) and (II) that plant dieback increases surface  $\text{N}_2\text{O}$  emissions immediately but has no short- or long-term effects. An explanation for this variable response in  $\text{N}_2\text{O}$  fluxes is not straightforward. Surface  $\text{N}_2\text{O}$  fluxes are the net result of production and consumption within the soil. Soil  $\text{N}_2\text{O}$  production in well-drained dry tundra occurs primarily through the nitrification process (Voigt et al. 2020), while soil  $\text{N}_2\text{O}$  consumption is through the complete reduction of  $\text{N}_2\text{O}$  to  $\text{N}_2$  during denitrification, with both processes being controlled strongly by soil moisture and temperatures (Butterbach-Bahl et al. 2013). In the

**TABLE 3** | Aboveground live and litter biomass, and total ecosystem, aboveground ecosystem, belowground ecosystem and litter  $^{15}\text{N}$  recovery. Numbers show mean ( $\pm$  standard error) of replicate blocks ( $n = 5$ ).

	CTO	VCO	CTX	VCX	Treatment effects
Aboveground live biomass ( $\text{g m}^{-2}$ )	907.2 $\pm$ 219.4	827.8 $\pm$ 227.1	1138.2 $\pm$ 130.1	684.3 $\pm$ 181.8	
Litter biomass ( $\text{g m}^{-2}$ )	512.6 $\pm$ 134.3	341.9 $\pm$ 51.1	519.8 $\pm$ 89.3	302.9 $\pm$ 47.3	Cutting*
Aboveground live biomass $^{15}\text{N}$ recovery (%)	29.9 $\pm$ 2.9	13.0 $\pm$ 4.2	19.4 $\pm$ 4.8	19.8 $\pm$ 5.5	
Litter $^{15}\text{N}$ recovery (%)	19.6 $\pm$ 5.5	11.7 $\pm$ 2.6	20.4 $\pm$ 4.1	16.0 $\pm$ 2.8	
Total ecosystem $^{15}\text{N}$ recovery (%)	55.5 $\pm$ 8.0	33.4 $\pm$ 5.7	49.9 $\pm$ 6.5	48.8 $\pm$ 8.6	Cutting*

Note: Control and summer warming (CTO and CTX), vegetation cutting and in combination with summer warming (VCO and VCX). Significant vegetation cutting effects are shown as \* $p \leq 0.05$ .



**FIGURE 3** | Nitrogen-15 recovery in bulk soil (a) root (b), total dissolved N (TDN) (c) and microbial biomass pools (d) from 0 to 3.5 cm and 3.5–5.5 cm soil depths 4 years after vegetation cutting (2021) in an arctic heath tundra in Disko Island, Greenland.

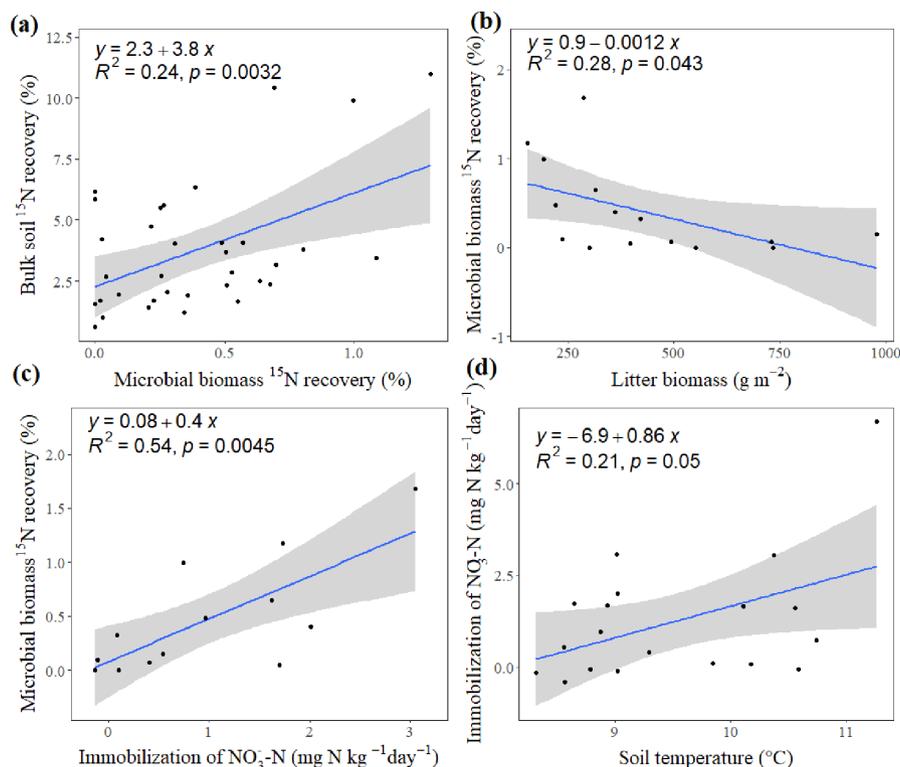
current study,  $\text{N}_2\text{O}$  fluxes correlated positively with soil temperatures and negatively with soil moisture (Figures S3 and S4). However, these conditions seemed decoupled from plant

dieback as there were no effects of vegetation cutting on soil moisture content, and the changes in soil temperatures following the vegetation cutting did not align with the changes in  $\text{N}_2\text{O}$  fluxes. Hence, the dynamic and variable response of  $\text{N}_2\text{O}$  fluxes to plant dieback is seemingly driven by short-duration and complex interactions with soil environment conditions, which could not be fully resolved in the current study. With respect to summer warming, surface  $\text{N}_2\text{O}$  emissions increased occasionally, in line with previous observations in nearby areas (Kolstad, Michelsen, and Ambus 2021; Hermesdorf et al. 2022; Xu et al. 2023) and other places in the Arctic (Voigt et al. 2017, 2020). This could be explained by accelerated soil N mineralization and nitrification processes (Daebeler et al. 2017; Kolstad, Michelsen, and Ambus 2021) and elevated soil inorganic N concentrations due to warmer temperatures.

Surface  $\text{CH}_4$  uptake, as revealed in this study, is typically associated with dry, arctic soils (D'Imperio et al. 2023). It has been documented that  $\text{CH}_4$  uptake rates can be reduced by an increase in soil N availability due to competitive inhibition of  $\text{CH}_4$  monooxygenase or alterations in methanotrophic communities (Lee et al. 2023). Despite an immediate increase in soil  $\text{NO}_3^-$ -N concentrations after plant dieback, surface  $\text{CH}_4$  uptake rates increased, contrasting hypothesis (I) that plant dieback immediately decreases surface  $\text{CH}_4$  uptake. This unexpected response is likely attributed to alleviated N limitation of  $\text{CH}_4$  oxidizing bacteria, since the effects of increasing soil N availability on soil  $\text{CH}_4$  uptake capacity largely depend on soil inherent N conditions (Chang et al. 2021). Over a longer-term basis, observed  $\text{CH}_4$  fluxes were significantly and positively correlated with soil moisture content, suggesting that  $\text{CH}_4$  fluxes in this study area are mainly driven by soil moisture.

#### 4.2 | Plant Dieback and Warming Effects on Plant N Uptake by Functional Groups

Although the biomass of deciduous shrubs had recovered to control levels 4 years after plant dieback, the corresponding aboveground biomass  $^{15}\text{N}$  recovery was significantly lower. This suggests a reduced capacity of deciduous shrubs to take up and retain N following a dieback event. In arctic tundra, deciduous shrubs (e.g., *Betula nana*) have a strong capacity to absorb nutrients through their leaves by creating relatively tall and dense canopy (Bret-Harte et al. 2001; Ejankowski 2010; Blok,



**FIGURE 4** | Correlations between microbial biomass <sup>15</sup>N recovery (square root transformed) and bulk soil <sup>15</sup>N recovery (a), litter biomass and microbial biomass <sup>15</sup>N recovery (b), immobilization of  $\text{NO}_3^-$ -N and microbial biomass <sup>15</sup>N recovery (c), and soil temperature and immobilization of  $\text{NO}_3^-$ -N (d).

Elberling, and Michelsen 2016). However, due to the damage to the canopy associated with the simulated dieback event, the shrubs lost the advantage of acquiring <sup>15</sup>N that was applied immediately after cutting.

Mosses are known to be able to capture a large proportion of nutrients via their effective adsorptive surfaces (Krab et al. 2008) and have the ability to retain most of the absorbed nutrients for several years due to their high nutrient recycling ability (Turetsky et al. 2012; Oulehle et al. 2016). However, the vegetation cutting in the current study did not result in higher <sup>15</sup>N uptake by mosses despite alleviated competition for N and reduced shading arising from reductions in the aboveground cover of vascular plants. We speculate that this could be due to a precipitation event (35 mm) that occurred 21 days after the <sup>15</sup>N application (Xu, Elberling, and Ambus 2022), enabling N previously trapped in the moss layer to enter the soil.

Summer warming alone increased the deciduous shrub biomass, while in combination with plant dieback, it had no effects on deciduous shrub regrowth but promoted the regrowth of graminoids, rejecting hypothesis (III). In tundra ecosystems, tall and woody deciduous shrubs can exhibit enhanced competitiveness and more pronounced responses to warming than other plant functional groups because of their taller canopy heights and often dense canopy structure (Mekonnen et al. 2021). Conversely, due to the alleviation of light limitation and reduced plant litter input arising from the low abundance of tall deciduous shrubs (Jean et al. 2020; Le, Wu, and Gong 2022), the growth of graminoids can be fostered by warming.

Evergreen shrubs were responsive to plant dieback with reduced biomass after 4 years. Hence, evergreen shrubs appear more susceptible to such extreme events and therefore may experience more stress than other functional groups under future climate change and face challenges in maintaining their presence and functionality. This is consistent with the observations by Bokhorst et al. (2015) who found that in a sub-arctic tundra, evergreen shrubs were most disadvantaged and their biomass decreased by 30% following extreme winter warming or moth grazing events.

Overall, our results challenge the previous understanding of summer warming effects on the vegetation community. We suggest that in a future arctic tundra with more stochastic biotic or extreme weather events (causing severe plant damage), summer warming may not always benefit deciduous shrubs over other functional groups.

### 4.3 | Plant Dieback and Warming Effects on Soil N Retention

The plant dieback did not affect longer term <sup>15</sup>N recovery in any of the belowground compartments investigated, that is, bulk soil, roots, microbial biomass and dissolved N. This was unexpected and to some extent in contrast to results from a previous winter warming experiment in the same area (Rasmussen et al. 2024). Here, winter warming, and hence presumed plant dieback, tended to reduce spring-thaw induced N release likely via increasing soil N immobilization (Rasmussen et al. 2024). In the current study, soil microbial

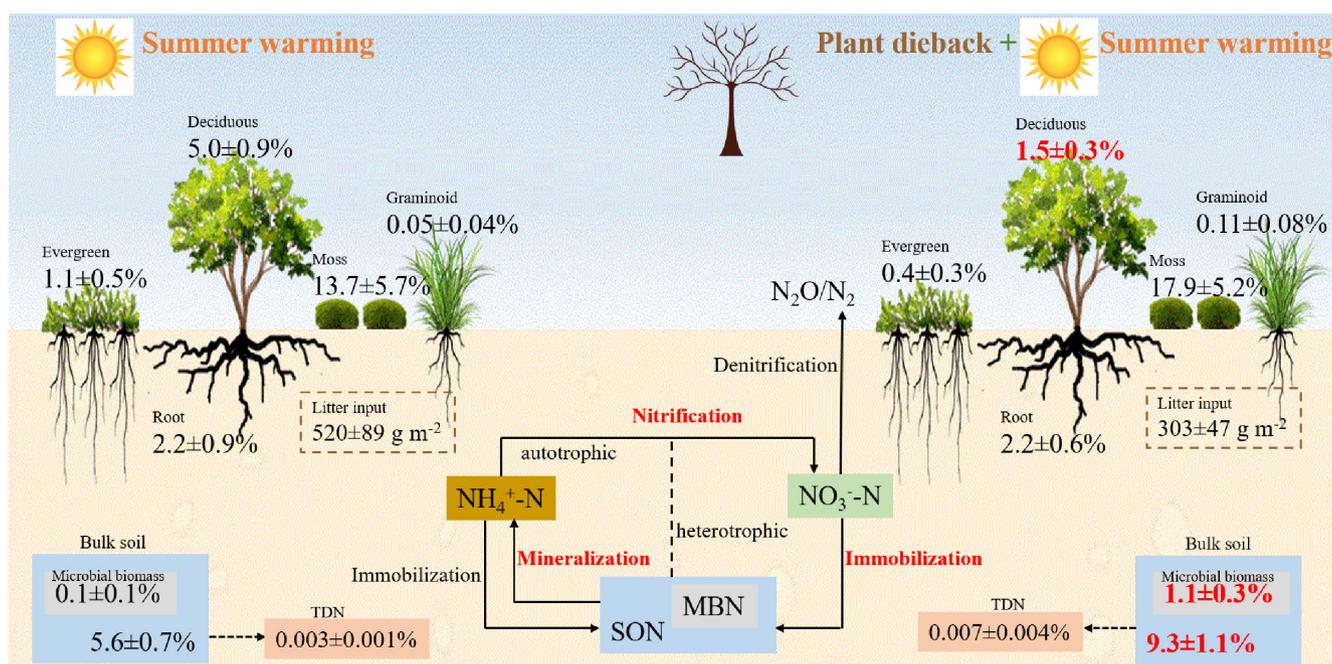
biomass retained a marginal proportion of added  $^{15}\text{N}$  irrespective of vegetation cutting, although this component constitutes a considerable ecosystem N pool. A modest microbial incorporation of various N sources is consistent with observations in other arctic studies, where N was applied over the plant canopy and hence mosses acquired most incoming nutrients (Stark and Väisänen 2014; Barthelemy et al. 2017, 2023). However, the competitive advantage of the mosses needs to be explained with caution, since as noted above some of the added  $^{15}\text{N}$  may have been leached into the soil by rainfall events occurring in the period shortly after the application. Moreover, the peak of microbial N immobilization may take place shortly after the  $^{15}\text{N}$  application, because soil microbes are less efficient competitors for N than plants in the long term, given their faster turnover and shorter tissue longevity (Nordin, Schmidt, and Shaver 2004; Clemmensen et al. 2008).

The vegetation cutting significantly increased bulk soil  $^{15}\text{N}$  recovery, but only under summer warming (Figure 5), suggesting that warming can influence soil N retention capacity following plant dieback. Warmer temperatures were reported to generally accelerate soil N transformation processes in arctic tundra (Biasi et al. 2008; Sistla and Schimel 2013; Xue et al. 2016; Xu et al. 2021). Indeed, we observed that plant dieback increased gross microbial consumption of  $\text{NO}_3^-$ -N (i.e., microbial immobilization of  $\text{NO}_3^-$ -N) only under summer warming, and soil temperatures were positively linked to microbial immobilization of  $\text{NO}_3^-$ -N (Figure 4). The extensive plant damage and reduced amounts of fresh organic matter input in the following years, as indicated by significantly lower vascular plant and litter biomass at vegetation-cut plots (VCO/VCX). This constraint in the supply of labile N to soil microbes likely increased microbial N demands and corresponding microbial N immobilization (Sorensen, Michelsen, and Jonasson 2008). In the current study,

this is further supported by the positive relationship between microbial biomass  $^{15}\text{N}$  recovery, litter biomass, and microbial immobilization of  $\text{NO}_3^-$ -N (Figure 4). Since  $\text{NO}_3^-$  is the most mobile form of mineral N, the increased microbial immobilization of  $\text{NO}_3^-$ -N has the potential to mitigate N losses by leaching and gaseous emissions (Mkhabela et al. 2008; Dong et al. 2022). This, combined with the reductions in gross mineralization and nitrification after plant dieback, indicates a decrease in gross inorganic N production (release) but an increase in gross inorganic N consumption (immobilization). Thus, under summer warming conditions, compared with soils with untouched vegetation, more of the applied  $^{15}\text{N}$  (inorganic N) was incorporated into microbial biomass in soils with vegetation cut down (Figure 5). Moreover, as microbial biomass turns over, it produces chemically reactive microbial residues such as peptides and amides. These residues can react with SOM to form relatively non-soluble N compounds and stabilize in organo-mineral associations (Badía et al. 2014; Marti-Roura et al. 2014; Lavallee, Soong, and Cotrufo 2020). These mechanisms may altogether explain the increased bulk soil N retention after plant dieback with summer warming, supporting our hypothesis (IV). However, there were no effects of plant dieback on bulk soil and microbial biomass  $^{15}\text{N}$  recovery at deeper soil depth (3.5–5.5 cm depth). This can be explained that soil microbes primarily take up N from the uppermost soil layers owing to warmer temperatures and higher availability of labile C (Zhu et al. 2016; Ravn, Elberling, and Michelsen 2017; Salmon et al. 2018).

#### 4.4 | Exploring Temporal Effects of Climate Change in Arctic Tundra

To fully understand the impacts of climate change on arctic tundra ecosystems, it is essential to examine the immediate,



**FIGURE 5** | Schematic illustration showing ecosystem recoveries of inorganic N ( $^{15}\text{N}$ -labelled ammonium and nitrate) and soil nitrogen transformation processes under summer warming conditions (left) and summer warming in combination with plant dieback conditions (right) in an arctic heath tundra, West Greenland.

short-term, and long-term effects of individual and interactive events, such as plant dieback and summer warming. Research should first capture the immediate consequences of these events, including changes in soil nutrient levels, greenhouse gas fluxes, and plant cover, as these direct and initial responses are crucial for predicting to which extent specific ecosystems may respond to disturbances. Following this, studies need to track how these changes evolve in the subsequent years, assessing how plant communities, soil nutrients, and microbial activities adjust or stabilize over time. Short-term findings can reveal transitional phases and help identify critical periods where ecosystems are most vulnerable to additional stresses. Long-term research is equally important to assess how prolonged or repeated events influence ecosystem resilience, nutrient cycling, and vegetation composition, helping to predict potential shifts in ecosystem structure and function. Addressing these different temporal scales will offer a more comprehensive understanding of how climate change affects arctic tundra ecosystems and inform more effective management and conservation strategies.

## 5 | Conclusion

To our best knowledge, this is the first study to quantify immediate and short- to long-term consequences for soil nutrient availability and retention as well as surface  $N_2O$  and  $CH_4$  fluxes following plant dieback in arctic tundra. The research was conducted under ambient temperature conditions, as well as under simulated summer warming to better predict future responses. We observed that plant dieback immediately increased surface  $CH_4$  and  $N_2O$  uptake. Over a short- to long-term basis plant dieback occasionally affected surface  $N_2O$  emissions as well as  $N_2O$  uptake, but not  $CH_4$ , the former supposedly driven by complex interactions with soil moisture and soil temperature conditions. The plant dieback also reduced the capacity of deciduous shrubs to take up and retain N, and the growth of deciduous shrub may not always benefit from warming over other functional groups when taking plant dieback events into consideration. Under ambient temperature conditions, there was no effect of plant dieback on N retention in belowground compartments, while under warmer conditions plant dieback increased bulk soil N retention via elevating immobilization of  $NO_3^-$ -N and microbial biomass N retention. Overall, this study suggests that in future arctic tundra ecosystems, extreme event-driven plant dieback and climate warming may lead to shifts in nutrient uptake and assimilation of plants, and soil nutrient cycling, which could alter ecosystem productivity and functioning. Meanwhile, the results from this research are obtained under constrained experimental conditions and extrapolations would need further investigations. For instance, the findings are based on plant dieback conducted in the growing season, which may not apply to the more variable and extreme conditions during the shoulder season (e.g., snow-melt dynamics, soil-freeze–thaw cycles). The spatial scale of the study also limits the generalizability of the results across the broader Arctic region. Finally, the lack of  $CO_2$  flux measurements prohibits the completeness of the greenhouse gas budget assessment for a warming Arctic. Future studies should investigate how the timing of plant dieback influences all greenhouse gas fluxes and nitrogen cycling, and expand this exploration to broader geographical areas.

## Author Contributions

**Wenyi Xu:** data curation, formal analysis, investigation, methodology, visualization, writing – original draft, writing – review and editing. **Bo Elberling:** funding acquisition, writing – review and editing. **Dan Li:** visualization, writing – review and editing. **Per Lennart Ambus:** conceptualization, funding acquisition, investigation, project administration, resources, supervision, writing – review and editing.

## Acknowledgements

We gratefully acknowledge the financial support from the Danish National Research Foundation (CENPERM DNR100). We are grateful to Arctic Station for collaboration and logistics in performing fieldwork.

## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The data that support the findings of this study are openly available in the Electronic Research Data Archive at University of Copenhagen at <https://doi.org/10.17894/ucph.ba46e42f-cd6f-4cc6-8a93-7bc8e06a9ba6>.

## References

- Badía, D., C. Martí, A. J. Aguirre, et al. 2014. “Wildfire Effects on Nutrients and Organic Carbon of a Rendzic Phaeozem in NE Spain: Changes at Cm-Scale Topsoil.” *Catena* 113: 267–275.
- Barthelemy, H., L. A. Nobel, S. Stark, M. Väisänen, J. Olofsson, and A. Michelsen. 2023. “Short- and Long-Term Plant and Microbial Uptake of  $^{15}N$ -Labelled Urea in a Mesic Tundra Heath, West Greenland.” *Polar Biology* 47: 1–15.
- Barthelemy, H., S. Stark, A. Michelsen, J. Olofsson, and R. Aerts. 2017. “Urine Is an Important Nitrogen Source for Plants Irrespective of Vegetation Composition in an Arctic Tundra: Insights From a  $^{15}N$ -Enriched Urea Tracer Experiment.” *Journal of Ecology* 106: 367–378.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. “Fitting Linear Mixed-Effects Models Using lme4.” *Journal of Statistical Software* 67: 1–48.
- Bhatt, U. S., D. A. Walker, M. K. Reynolds, et al. 2013. “Recent Declines in Warming and Vegetation Greening Trends Over Pan-Arctic Tundra.” *Remote Sensing* 5: 4229–4254.
- Biasi, C., H. Meyer, O. Rusalimova, et al. 2008. “Initial Effects of Experimental Warming on Carbon Exchange Rates, Plant Growth and Microbial Dynamics of a Lichen-Rich Dwarf Shrub Tundra in Siberia.” *Plant and Soil* 307: 191–205.
- Bjerke, J. W., S. R. Karlson, K. A. Høgda, et al. 2014. “Record-Low Primary Productivity and High Plant Damage in the Nordic Arctic Region in 2012 Caused by Multiple Weather Events and Pest Outbreaks.” *Environmental Research Letters* 9: 84006.
- Blok, D., B. Elberling, and A. Michelsen. 2016. “Initial Stages of Tundra Shrub Litter Decomposition May be Accelerated by Deeper Winter Snow but Slowed Down by Spring Warming.” *Ecosystems* 19: 155–169.
- Bokhorst, S., J. W. Bjerke, L. Street, T. V. Callaghan, and G. K. Phoenix. 2011. “Impacts of Multiple Extreme Winter Warming Events on Sub-Arctic Heathland: Phenology, Reproduction, Growth, and  $CO_2$  Flux Responses.” *Global Change Biology* 17: 2817–2830.
- Bokhorst, S., L. Jaakola, K. Karppinen, G. K. Edvinsen, H. K. Mæhre, and J. W. Bjerke. 2018. “Contrasting Survival and Physiological Responses of Sub-Arctic Plant Types to Extreme Winter Warming and Nitrogen.” *Planta* 247: 635–648.

- Bokhorst, S., G. K. Phoenix, M. P. Berg, T. V. Callaghan, C. Kirby-Lambert, and J. W. Bjerke. 2015. "Climatic and Biotic Extreme Events Moderate Long-Term Responses of Above-and Belowground Sub-Arctic Heathland Communities to Climate Change." *Global Change Biology* 21: 4063–4075.
- Bracho, R., S. Natali, E. Pegoraro, et al. 2016. "Temperature Sensitivity of Organic Matter Decomposition of Permafrost-Region Soils During Laboratory Incubations." *Soil Biology and Biochemistry* 97: 1–14.
- Bret-Harte, M. S., G. R. Shaver, J. P. Zoerner, et al. 2001. "Developmental Plasticity Allows *Betula Nana* to Dominate Tundra Subjected to an Altered Environment." *Ecology* 82: 18–32.
- Brookes, P., A. Landman, G. Pruden, and D. Jenkinson. 1985. "Chloroform Fumigation and the Release of Soil Nitrogen: A Rapid Direct Extraction Method to Measure Microbial Biomass Nitrogen in Soil." *Soil Biology and Biochemistry* 17: 837–842.
- Brummell, M. E., R. E. Farrell, and S. D. Siciliano. 2012. "Greenhouse Gas Soil Production and Surface Fluxes at a High Arctic Polar Oasis." *Soil Biology and Biochemistry* 52: 1–12.
- Butterbach-Bahl, K., E. M. Baggs, M. Dannenmann, R. Kiese, and S. Zechmeister-Boltenstern. 2013. "Nitrous Oxide Emissions From Soils: How Well Do We Understand the Processes and Their Controls?" *Philosophical Transactions of the Royal Society, B: Biological Sciences* 368: 20130122.
- Chang, R., X. Liu, T. Wang, N. Li, and H. Bing. 2021. "Stimulated or Inhibited Response of Methane Flux to Nitrogen Addition Depends on Nitrogen Levels." *Journal of Geophysical Research: Biogeosciences* 126: e2021JG006600.
- Chen, Q., R. Zhu, Q. Wang, and H. Xu. 2014. "Methane and Nitrous Oxide Fluxes From Four Tundra Ecotopes in Ny-Ålesund of the High Arctic." *Journal of Environmental Sciences* 26: 1403–1410.
- Christiansen, C. T., S. H. Svendsen, N. M. Schmidt, and A. Michelsen. 2012. "High Arctic Heath Soil Respiration and Biogeochemical Dynamics During Summer and Autumn Freeze-In—Effects of Long-Term Enhanced Water and Nutrient Supply." *Global Change Biology* 18: 3224–3236.
- Clemmensen, K. E., P. L. Sorensen, A. Michelsen, S. Jonasson, and L. Strom. 2008. "Site-Dependent N Uptake From N-Form Mixtures by Arctic Plants, Soil Microbes and Ectomycorrhizal Fungi." *Oecologia* 155: 771–783.
- Conant, R. T., R. A. Drijber, M. L. Haddix, et al. 2008. "Sensitivity of Organic Matter Decomposition to Warming Varies With Its Quality." *Global Change Biology* 14: 868–877.
- Cookson, W., and D. Murphy. 2004. "Quantifying the Contribution of Dissolved Organic Matter to Soil Nitrogen Cycling Using <sup>15</sup>N Isotopic Pool Dilution." *Soil Biology and Biochemistry* 36: 2097–2100.
- Daebeler, A., P. L. Bodelier, M. M. Hefting, T. Rütting, Z. Jia, and H. J. Laanbroek. 2017. "Soil Warming and Fertilization Altered Rates of Nitrogen Transformation Processes and Selected for Adapted Ammonia-Oxidizing Archaea in Sub-Arctic Grassland Soil." *Soil Biology and Biochemistry* 107: 114–124.
- De Jong, R., J. Verbesselt, M. E. Schaepman, and S. De Bruin. 2012. "Trend Changes in Global Greening and Browning: Contribution of Short-Term Trends to Longer-Term Change." *Global Change Biology* 18: 642–655.
- de Vries, F. T., and R. D. Bardgett. 2016. "Plant Community Controls on Short-Term Ecosystem Nitrogen Retention." *New Phytologist* 210: 861–874.
- DeMarco, J., M. C. Mack, M. S. Bret-Harte, M. Burton, and G. R. Shaver. 2014. "Long-Term Experimental Warming and Nutrient Additions Increase Productivity in Tall Deciduous Shrub Tundra." *Ecosphere* 5: art72.
- Denmead, O. T. 2008. "Approaches to Measuring Fluxes of Methane and Nitrous Oxide Between Landscapes and the Atmosphere." *Plant and Soil* 309: 5–24.
- Di, H., K. Cameron, and R. McLaren. 2000. "Isotopic Dilution Methods to Determine the Gross Transformation Rates of Nitrogen, Phosphorus, and Sulfur in Soil: A Review of the Theory, Methodologies, and Limitations." *Soil Research* 38: 213–230.
- D'Imperio, L., M. F. Arndal, C. S. Nielsen, B. Elberling, and I. K. Schmidt. 2018. "Fast Responses of Root Dynamics to Increased Snow Deposition and Summer Air Temperature in an Arctic Wetland." *Frontiers in Plant Science* 9: 1258.
- D'Imperio, L., B.-B. Li, J. M. Tiedje, et al. 2023. "Spatial Controls of Methane Uptake in Upland Soils Across Climatic and Geological Regions in Greenland." *Communications Earth & Environment* 4: 461.
- Dong, Y., J.-L. Yang, X.-R. Zhao, et al. 2022. "Nitrate Leaching and N Accumulation in a Typical Subtropical Red Soil With N Fertilization." *Geoderma* 407: 115559.
- Ejankowski, W. 2010. "Demographic Variation of Dwarf Birch (*Betula Nana*) in Communities Dominated by *Ledum Palustre* and *Vaccinium Uliginosum*." *Biologia* 65: 248–253.
- Elmendorf, S. C., G. H. Henry, R. D. Hollister, et al. 2012. "Plot-Scale Evidence of Tundra Vegetation Change and Links to Recent Summer Warming." *Nature Climate Change* 2: 453–457.
- Foley, K. M., K. H. Beard, T. B. Atwood, and B. G. Waring. 2022. "Herbivory Changes Soil Microbial Communities and Greenhouse Gas Fluxes in a High-Latitude Wetland." *Microbial Ecology* 83: 127–136.
- Fox, J., and S. Weisberg. 2019. *An R Companion to Applied Regression (Third)*. Thousand Oaks CA: Sage.
- Gornall, J. L., S. J. Woodin, I. S. Jonsdottir, and R. Van der Wal. 2009. "Herbivore Impacts to the Moss Layer Determine Tundra Ecosystem Response to Grazing and Warming." *Oecologia* 161: 747–758.
- Hermesdorf, L., B. Elberling, L. D'Imperio, W. Xu, A. Lambaek, and P. L. Ambus. 2022. "Effects of Fire on CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O Exchange in a Well-Drained Arctic Heath Ecosystem." *Global Change Biology* 28: 4882–4899.
- Hewitt, R. E., D. L. Taylor, H. Genet, A. D. McGuire, M. C. Mack, and P. Mariotte. 2019. "Below-Ground Plant Traits Influence Tundra Plant Acquisition of Newly Thawed Permafrost Nitrogen." *Journal of Ecology* 107: 950–962.
- Jean, M., A. M. Melvin, M. C. Mack, and J. F. Johnstone. 2020. "Broadleaf Litter Controls Feather Moss Growth in Black Spruce and Birch Forests of Interior Alaska." *Ecosystems* 23: 18–33.
- Jones, D. L., D. Shannon, D. V. Murphy, and J. Farrar. 2004. "Role of Dissolved Organic Nitrogen (DON) in Soil N Cycling in Grassland Soils." *Soil Biology and Biochemistry* 36: 749–756.
- Karhu, K., M. D. Auffret, J. A. Dungait, et al. 2014. "Temperature Sensitivity of Soil Respiration Rates Enhanced by Microbial Community Response." *Nature* 513: 81–84.
- Kelsey, K. C., A. J. Leffler, K. H. Beard, J. A. Schmutz, R. T. Choi, and J. M. Welker. 2016. "Interactions Among Vegetation, Climate, and Herbivory Control Greenhouse Gas Fluxes in a Subarctic Coastal Wetland." *Journal of Geophysical Research: Biogeosciences* 121: 2960–2975.
- Kolstad, E., A. Michelsen, and P. L. Ambus. 2021. "Nitrous Oxide Surface Fluxes in a Low Arctic Heath: Effects of Experimental Warming Along a Natural Snowmelt Gradient." *Soil Biology and Biochemistry* 160: 108346.
- Krab, E. J., J. H. Cornelissen, S. I. Lang, and R. S. van Logtestijn. 2008. "Amino Acid Uptake Among Wide-Ranging Moss Species May Contribute to Their Strong Position in Higher-Latitude Ecosystems." *Plant and Soil* 304: 199–208.
- Lavallee, J. M., J. L. Soong, and M. F. Cotrufo. 2020. "Conceptualizing Soil Organic Matter Into Particulate and Mineral-Associated Forms to Address Global Change in the 21st Century." *Global Change Biology* 26: 261–273.

- Le, T. B., J. Wu, and Y. Gong. 2022. "Vascular Plants Regulate Responses of Boreal Peatland Sphagnum to Climate Warming and Nitrogen Addition." *Science of the Total Environment* 819: 152077.
- Lee, J., J. Yun, Y. Yang, et al. 2023. "Attenuation of Methane Oxidation by Nitrogen Availability in Arctic Tundra Soils." *Environmental Science & Technology* 57: 2647–2659.
- Lenth, R. 2020. "Emmeans: Estimated Marginal Means, aka Least-Squares Means." Rpackage version 1.4. 7. 2020.
- Little, C. J., H. Cutting, J. Alatalo, and E. J. Cooper. 2017. "Short-Term Herbivory Has Long-Term Consequences in Warmed and Ambient High Arctic Tundra." *Environmental Research Letters* 12: 025001.
- Ma, W. K., A. Schautz, L. A. E. Fishback, A. Bedard-Haughn, R. E. Farrell, and S. D. Siciliano. 2007. "Assessing the Potential of Ammonia Oxidizing Bacteria to Produce Nitrous Oxide in Soils of a High Arctic Lowland Ecosystem on Devon Island, Canada." *Soil Biology & Biochemistry* 39: 2001–2013.
- Marion, G. M. 1996. "Temperature Enhancement Experiments." ITEX Manual. 1722.
- Martí-Roura, M., P. Rovira, P. Casals, and J. Romanyà. 2014. "Post-Fire Mineral N Allocation and Stabilisation in Soil Particle Size Fractions in Mediterranean Grassland and Shrubland." *Soil Biology and Biochemistry* 75: 124–132.
- McIntyre, S., S. Lavorel, J. Landsberg, and T. Forbes. 1999. "Disturbance Response in Vegetation—Towards a Global Perspective on Functional Traits." *Journal of Vegetation Science* 10: 621–630.
- Mekonnen, Z. A., W. J. Riley, L. T. Berner, et al. 2021. "Arctic Tundra Shrubification: A Review of Mechanisms and Impacts on Ecosystem Carbon Balance." *Environmental Research Letters* 16: 053001.
- Miles, V. V., and I. Esau. 2016. "Spatial Heterogeneity of Greening and Browning Between and Within Bioclimatic Zones in Northern West Siberia." *Environmental Research Letters* 11: 115002.
- Mkhabela, M., A. Madani, R. Gordon, et al. 2008. "Gaseous and Leaching Nitrogen Losses From No-Tillage and Conventional Tillage Systems Following Surface Application of Cattle Manure." *Soil and Tillage Research* 98: 187–199.
- Mosbacher, J. B., A. Michelsen, M. Stelvig, H. Hjermstad-Sollerud, and N. M. Schmidt. 2018. "Muskoxen Modify Plant Abundance, Phenology, and Nitrogen Dynamics in a High Arctic Fen." *Ecosystems* 22: 1095–1107.
- Myers-Smith, I. H., J. T. Kerby, G. K. Phoenix, et al. 2020. "Complexity Revealed in the Greening of the Arctic." *Nature Climate Change* 10: 106–117.
- Nordin, A., I. K. Schmidt, and G. R. Shaver. 2004. "Nitrogen Uptake by Arctic Soil Microbes and Plants in Relation to Soil Nitrogen Supply." *Ecology* 85: 955–962.
- Oulehle, F., E. C. Rowe, O. Myška, T. Chuman, and C. D. Evans. 2016. "Plant Functional Type Affects Nitrogen Use Efficiency in High-Arctic Tundra." *Soil Biology and Biochemistry* 94: 19–28.
- Paré, M. C., and A. Bedard-Haughn. 2012. "Landscape-Scale N Mineralization and Greenhouse Gas Emissions in Canadian Cryosols." *Geoderma* 189: 469–479.
- Park, T., S. Ganguly, H. Tømmervik, et al. 2016. "Changes in Growing Season Duration and Productivity of Northern Vegetation Inferred From Long-Term Remote Sensing Data." *Environmental Research Letters* 11: 084001.
- Parmentier, F.-J. W., D. P. Rasse, M. Lund, et al. 2018. "Vulnerability and Resilience of the Carbon Exchange of a Subarctic Peatland to an Extreme Winter Event." *Environmental Research Letters* 13: 065009.
- Pedersen, E. P., B. Elberling, and A. Michelsen. 2020. "Foraging Deeply: Depth-Specific Plant Nitrogen Uptake in Response to Climate-Induced N-Release and Permafrost Thaw in the High Arctic." *Global Change Biology* 26: 6523–6536.
- Preece, C., and G. Phoenix. 2014. "Impact of Early and Late Winter Icing Events on Sub-Arctic Dwarf Shrubs." *Plant Biology* 16: 125–132.
- Rantanen, M., A. Y. Karpechko, A. Lipponen, et al. 2022. "The Arctic Has Warmed Nearly Four Times Faster Than the Globe Since 1979." *Communications Earth & Environment* 3: 168.
- Ravn, N. M. R., B. Elberling, and A. Michelsen. 2017. "The Fate of <sup>13</sup>C/<sup>15</sup>N Labeled Glycine in Permafrost and Surface Soil at Simulated Thaw in Mesocosms From High Arctic and Subarctic Ecosystems." *Plant and Soil* 419: 201–218.
- Ravn, N. R., B. Elberling, and A. Michelsen. 2020. "Arctic Soil Carbon Turnover Controlled by Experimental Snow Addition, Summer Warming and Shrub Removal." *Soil Biology and Biochemistry* 142: 107698.
- Robinson, C. H. 2002. "Controls on Decomposition and Soil Nitrogen Availability at High Latitudes." *Plant and Soil* 242: 65–81.
- Rasmussen, L. H., B. K. Danielsen, B. Elberling, et al. 2024. "Nitrogen Immobilization Could Link Extreme Winter Warming Events to Arctic Browning." *Soil Biology and Biochemistry* 191: 109319.
- Salmon, V. G., C. Schädel, R. Bracho, et al. 2018. "Adding Depth to Our Understanding of Nitrogen Dynamics in Permafrost Soils." *Journal of Geophysical Research: Biogeosciences* 123: 2497–2512.
- Saunders, T., J. Adkins, K. H. Beard, T. B. Atwood, and B. G. Waring. 2023. "Herbivores Influence Biogeochemical Processes by Altering Litter Quality and Quantity in a Subarctic Wetland." *Biogeochemistry* 166: 67–85.
- Schimel, J. P., and J. Bennett. 2004. "Nitrogen Mineralization: Challenges of a Changing Paradigm." *Ecology* 85: 591–602.
- Sistla, S. A., and J. P. Schimel. 2013. "Seasonal Patterns of Microbial Extracellular Enzyme Activities in an Arctic Tundra Soil: Identifying Direct and Indirect Effects of Long-Term Summer Warming." *Soil Biology and Biochemistry* 66: 119–129.
- Sørensen, P., and E. S. Jensen. 1991. "Sequential Diffusion of Ammonium and Nitrate From Soil Extracts to a Polytetrafluoroethylene Trap for <sup>15</sup>N Determination." *Analytica Chimica Acta* 252: 201–203.
- Sorensen, P. L., A. Michelsen, and S. Jonasson. 2008. "Ecosystem Partitioning of <sup>15</sup>N-Glycine After Long-Term Climate and Nutrient Manipulations, Plant Clipping and Addition of Labile Carbon in a Subarctic Heath Tundra." *Soil Biology and Biochemistry* 40: 2344–2350.
- St Pierre, K. A., B. K. Danielsen, L. Hermesdorf, L. D'Imperio, L. L. Iversen, and B. Elberling. 2019. "Drivers of Net Methane Uptake Across Greenlandic Dry Heath Tundra Landscapes." *Soil Biology and Biochemistry* 138: 107605.
- Stark, S., and M. Väisänen. 2014. "Insensitivity of Soil Microbial Activity to Temporal Variation in Soil N in Subarctic Tundra: Evidence From Responses to Large Migratory Grazers." *Ecosystems* 17: 906–917.
- Team R C. 2019. "R: A Language and Environment for Statistical Computing (Version 3.6. 1)[Software Package]." Vienna, Austria: R Foundation for Statistical Computing. Retrieved from ...
- Treharne, R., J. W. Bjerke, H. Tømmervik, L. Stendardi, and G. K. Phoenix. 2019. "Arctic Browning: Impacts of Extreme Climatic Events on Heathland Ecosystem CO<sub>2</sub> Fluxes." *Global Change Biology* 25: 489–503.
- Turetsky, M. R., B. Bond-Lamberty, E. Euskirchen, et al. 2012. "The Resilience and Functional Role of Moss in Boreal and Arctic Ecosystems." *New Phytologist* 196: 49–67.
- Voigt, C., R. E. Lamprecht, M. E. Marushchak, et al. 2017. "Warming of Subarctic Tundra Increases Emissions of all Three Important Greenhouse Gases—Carbon Dioxide, Methane, and Nitrous Oxide." *Global Change Biology* 23: 3121–3138.
- Voigt, C., M. E. Marushchak, B. W. Abbott, et al. 2020. "Nitrous Oxide Emissions From Permafrost-Affected Soils." *Nature Reviews Earth and Environment* 1: 420–434.

Wang, F., G. Shi, O. Nicholas, et al. 2018. "Ecosystem Nitrogen Retention Is Regulated by Plant Community Trait Interactions With Nutrient Status in an Alpine Meadow." *Journal of Ecology* 106: 1570–1581.

Williams, C. M., H. A. Henry, and B. J. Sinclair. 2015. "Cold Truths: How Winter Drives Responses of Terrestrial Organisms to Climate Change." *Biological Reviews* 90: 214–235.

Xu, W., B. Elberling, and P. L. Ambus. 2022. "Fire Increases Soil Nitrogen Retention and Alters Nitrogen Uptake Patterns Among Dominant Shrub Species in an Arctic Dry Heath Tundra." *Science of the Total Environment* 807: 150990.

Xu, W., L. L. Frendrup, A. Michelsen, B. Elberling, and P. L. Ambus. 2023. "Deepened Snow in Combination With Summer Warming Increases Growing Season Nitrous Oxide Emissions in Dry Tundra, but Not in Wet Tundra." *Soil Biology and Biochemistry* 180: 109013.

Xu, W., A. Prieme, E. J. Cooper, et al. 2021. "Deepened Snow Enhances Gross Nitrogen Cycling Among Pan-Arctic Tundra Soils During Both Winter and Summer." *Soil Biology and Biochemistry* 160: 108356.

Xue, K., M. M. Yuan, Z. J. Shi, et al. 2016. "Tundra Soil Carbon Is Vulnerable to Rapid Microbial Decomposition Under Climate Warming." *Nature Climate Change* 6: 595–600.

Zhang, Y., C. Song, L. E. Band, G. Sun, and J. Li. 2017. "Reanalysis of Global Terrestrial Vegetation Trends From MODIS Products: Browning or Greening?" *Remote Sensing of Environment* 191: 145–155.

Zhu, Q., C. M. Iversen, W. J. Riley, I. J. Slette, and H. M. Vander Stel. 2016. "Root Traits Explain Observed Tundra Vegetation Nitrogen Uptake Patterns: Implications for Trait-Based Land Models." *Journal of Geophysical Research: Biogeosciences* 121: 3101–3112.

Zielke, M., A. S. Ekker, R. A. Olsen, S. Spjelkavik, and B. Solheim. 2002. "The Influence of Abiotic Factors on Biological Nitrogen Fixation in Different Types of Vegetation in the High Arctic, Svalbard." *Arctic, Antarctic, and Alpine Research* 34: 293–299.

### Supporting Information

Additional supporting information can be found online in the Supporting Information section.