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# Warming Weakens Soil Nitrogen Stabilization Pathways Driving Proportional Carbon Losses in Subarctic Ecosystems

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## ABSTRACT

Climate warming poses a significant threat to the nitrogen (N) and carbon (C) retention capacities of subarctic ecosystems, with cascading effects on soil nutrient cycling and long-term ecosystem functioning. Here, we investigated the effects sustained soil warming on the temporal retention and stabilization of N in key ecosystem pools in a subarctic grassland performing a <sup>15</sup>N-tracing experiment in different seasons. Our results reveal that warming reduced N retention across key soil pools, with the largest proportional losses occurring in the non-extractable soil fraction, a critical long-term reservoir of organic matter. These losses were driven by the depletion of organic compounds involved in *ex vivo* N stabilization and the weakening of *in vivo* stabilization mechanisms. Warming also decreased microbial and fine root biomass, limiting their ability to temporarily immobilize N during the snowmelt period, when soil N retention is most critical. In contrast, warming increased aboveground plant biomass and N uptake during the growing season, indicating a shift in resource allocation towards aboveground tissues. However, the increase in plant N uptake, both due to its magnitude (0.14% of N gained °C<sup>-1</sup>) and seasonality, was insufficient to offset the loss of N retention in the microbial biomass and fine roots (1.99% of N lost °C<sup>-1</sup>) and non-extractable soil pools (1.7%–2.6% of N lost °C<sup>-1</sup>). As a consequence, we observed coupled and proportional C losses across all soil pools. These findings suggest that warming disrupts key pathways of soil N stabilization, leading to the “opening” of the N cycle and proportional, potentially irreversible, C losses from cold ecosystems.

## 1 | Introduction

Global warming accelerates soil organic matter (SOM) decomposition, resulting in significant CO<sub>2</sub> emissions, which in turn

contribute to climate change feedbacks (Jenkinson et al. 1991; Davidson and Janssens 2006). Temperatures have risen, especially in high-latitude ecosystems, where a substantial portion of the Earth's soil carbon (C) is stored (Tarnocai et al. 2009; Allen

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et al. 2018). This makes high-latitude cold soils potentially significant contributors to rising atmospheric CO<sub>2</sub> levels (McGuire et al. 2009). However, the extent of this contribution remains uncertain due to the complexity of plant–soil microbial interactions and nutrient cycling (Friedlingstein et al. 2006; Bradford et al. 2016).

The coupling between the C and nitrogen (N) cycles is particularly strong in high-latitude ecosystems, where slow organic matter decomposition limits the release of available N for plants (Schimel and Bennett 2004; Todd-Brown et al. 2013). Rising temperatures are expected to accelerate SOM decomposition, alleviating plant N limitations in northern ecosystems (Dormann and Woodin 2002; Wu et al. 2011; Natali et al. 2012). This increased N availability, coupled with longer growing seasons, could enhance plant productivity and C inputs to the soil (Piao et al. 2007), potentially offsetting soil C losses due to warming (Melillo et al. 2002; IPCC 2013; Sistla et al. 2013). However, responses of microbial N mineralization and plant N uptake to warming may differ (Beier et al. 2008), leading to asynchronies or imbalances between the fluxes of N release and uptake (Salmon et al. 2018; Lacroix et al. 2022). The resilience of soil C stocks to warming thus depends on soil nutrient retention and on the capacity of plant productivity to benefit from alleviated nutrient limitations.

Microbial biomass plays a crucial role in retaining soil N in low-productivity ecosystems like high latitudes (Haugwitz et al. 2011; Xu et al. 2013; Marañón-Jiménez et al. 2019). This N pool has high turnover rates compared to other soil nutrient fractions, making it a dynamic component of soil nutrient fluxes (Bardgett et al. 2003; Haugwitz et al. 2011). Seasonal oscillations of microbial biomass are a consequence of this fast microbial turnover (Wardle 1998; Turner and Henry 2010). In cold soils, microbial biomass typically peaks at the end of winter, followed by a release of soil nutrients (Kuhnert et al. 2012; Edwards and Jefferies 2013; Schneckner et al. 2023). Therefore, microbial biomass can serve as a short-term soil N reservoir during periods of low plant productivity and N uptake, such as the cold winters with short photoperiods at high latitudes, whereas microbial turnover and subsequent release of N into the plant–soil system can represent the largest annual flux of available N for plants during the growing season (Lipson et al. 2000; Bardgett et al. 2003). The soil microbial biomass N pool is then crucial to maintain a soil N reservoir during relatively long winter periods and regulate soil N availability across seasons (Jonasson et al. 1996; Groffman et al. 2011; Kaiser et al. 2011).

Climate warming may disrupt the coupling between microbial N mineralization and plant N uptake, potentially leading to N losses in cold ecosystems (Dawes et al. 2017; Marañón-Jiménez et al. 2019). Warming can deplete the labile soil C pool and exacerbate microbial C limitation for growth if the increased microbial activity and respiration are not offset by higher vegetation productivity and C inputs (Sullivan et al. 2020). Winter warming in particular, can impact negatively the soil microbial N reservoir (Edwards and Jefferies 2013), affecting the timing and magnitude of the posterior N release to the soil. In addition, pulses of available N during thawing events, when plant N uptake is low, can lead to denitrification and N leaching from high-latitude ecosystems (Turner and Henry 2010; Salmon et al. 2018). Therefore,

repeated cycles of low microbial N immobilization during warm winters may deplete N from high-latitude soils, limiting plant N availability, productivity, and the ability of vegetation to offset soil C losses caused by warming (Salmon et al. 2018; Harms et al. 2019; Marañón-Jiménez et al. 2019).

There is limited information on potential asynchronies or imbalances in N biogeochemical processes within the soil–plant continuum mediated by warming, despite its crucial role in the resilience of soil C stocks at high latitudes. Understanding these interactions is essential for predicting the long-term stability of soil C in response to climate change. In addition, climate projections estimate a rise in global mean temperatures of 1.4°C–4.4°C, with disproportionately strong warming at northern latitudes (IPCC 2023). While most field experiments simulate moderate warming, there remains a critical knowledge gap regarding the impacts of extreme warming, which may become increasingly relevant under future climate trajectories (IPCC 2023). Here, we investigate the effects of a broad gradient of soil warming intensities, ranging from ambient to +12°C, which includes both projected and extreme warming levels (Sigurdsson et al. 2016). Studying this wide range of warming intensities enables us to detect non-linearities, critical thresholds, and identify robust ecological responses applicable to various climate scenarios. Geothermal gradients provide a unique opportunity to address these gaps, as they offer a natural, continuous, and long-term warming treatment across a wide range of temperatures without introducing experimental artifacts or perturbations. For these reasons, we conducted an isotope tracing experiment in subarctic grasslands at different seasons, using a mixture of <sup>15</sup>N-labeled amino acids applied along decade-old natural soil geothermal gradients. Two weeks after each seasonal tracing campaign, we measured the remaining N and <sup>15</sup>N pools in roots, aboveground vegetation, soil, and microbial biomass.

We hypothesized that warming would cause an imbalance in N biogeochemical processes, where rising temperatures reduce microbial biomass, thus diminishing the soil capacity to retain N, particularly during winter periods. This would contribute to ecosystem N losses and lower N availability for plant productivity. We also expected a N biogeochemical asynchrony, where winter soil N losses are not compensated by increased plant productivity and N uptake during the warmer growing seasons. Consequently, this would result in overall N losses in the subarctic ecosystem under a warmer climate. Lower soil N availability would imply a reduced vegetation productivity in cold ecosystems, weakening the capacity of these ecosystems to counteract warming-induced soil C losses and causing stoichiometrically equivalent soil C losses.

## 2 | Materials and Methods

### 2.1 | Study Site

Samples were collected from an unmanaged grassland located near the village of Hveragerði in southwest Iceland (64°00′01″ N, 21°11′09″ W; 83–168 m a.s.l.). The study site is part of the ForHot research infrastructure ([www.forhot.is](http://www.forhot.is)) and is described in detail by Sigurdsson et al. (2016). Between 2003 and 2015, the mean annual temperature, precipitation, and wind speed were 5.2°C,

1457 mm, and  $6.6 \text{ m s}^{-1}$ , respectively, according to records from the Eyrarbakki synoptic station, located 9 km south of the site (Icelandic Meteorological Office). The warmest month is July, with a mean temperature of  $12.2^\circ\text{C}$ , while the coldest month is December, averaging  $-0.1^\circ\text{C}$ . The growing season typically spans from late May to late August. Although snow cover is generally intermittent due to the region's mild oceanic climate, soils usually freeze for at least several weeks during mid-winter (Sigurdsson et al. 2016).

Vegetation in the study sites includes dominant species adapted to withstand cold conditions and regrow rapidly when favorable conditions return, giving them a competitive advantage (Chapin III et al. 1986; Starr and Oberbauer 2003; Larsen et al. 2012). Among these species is *Agrostis capillaris*, a perennial grass with short-lived aboveground parts that annually regrow from underground stems or rhizomes. These structures store energy and nutrients, supporting new growth each spring. *Ranunculus acris* is another perennial herb that can maintain a rosette of leaves close to the ground throughout the winter. Additionally, *Equisetum pratense* is a perennial horsetail that maintains green aboveground shoots during winter. There are no N-fixing plant species in the study sites (Meynzer 2017). The soil is classified as Silandic Andosol (IUSS Working Group WRB 2022) with a fine silt loam texture, exhibiting strong binding strength, high water-holding capacity, and soil pH values ranging from 5.43 to 6.15. The estimated annual atmospheric deposition rate in the study sites is  $1.3\text{--}1.4 \text{ kg N ha}^{-1} \text{ year}^{-1}$  (Gislason et al. 1996; Leblans et al. 2014).

In 2008, a magnitude 6.3 earthquake disrupted the local geothermal system, causing hot groundwater to heat the underlying bedrock and rise through newly formed faults in the soil crust. This led to the development of geothermal bedrock channels, with soil temperatures highest near the faults and decreasing with distance, thereby creating natural gradients of soil warming across previously unaffected areas (Halldórsson and Sigbjörnsson 2009). This gradients range from ambient conditions to plots experiencing substantial geothermal heating ( $> 20^\circ\text{C}$  and beyond), offering a unique opportunity to study terrestrial ecosystem responses across a broad spectrum of long-term soil warming intensities. Importantly, the warming remains relatively stable over time and mirrors the seasonal cycle of soil temperature observed in ambient plots. Furthermore, soil chemical analyses confirmed the absence of geothermal contamination (e.g., no elevated exchangeable sulfur) at the study sites (Sigurdsson et al. 2016).

## 2.2 | Experimental Design

Plots measuring  $0.5 \times 0.5 \text{ m}$  were established in homogeneous areas with similar exposure, plant communities, and soil types, spanning soil temperature gradients from ambient to  $+12^\circ\text{C}$  above ambient ( $n = 20$  plots). The selected plots were distributed across two clusters of approximately  $1000 \text{ m}^2$  each, centered around two main geothermal hot spots located about 700 m apart. To ensure balanced representation across the entire warming range, plots were initially selected based on instantaneous differences between soil temperature at potential warmed locations and paired ambient reference plots. This approach

allowed us to achieve an even distribution of soil temperatures along the gradient. We limited our selection to plots with warming up to  $+12^\circ\text{C}$ , as higher temperatures showed clear signs of vegetation die-off, indicating collapse of the plant community, and were therefore considered beyond the ecologically relevant range for assessing climate warming effects. Once the plots were established, soil temperature at a 10-cm depth was continuously monitored in each plot using TidbiT v2 HOBO Data Loggers (Onset Computer Corporation, Bourne, USA), and these data were used to calculate the warming intensity experienced at each plot.

A PVC collar of a 13-cm diameter and 10-cm length was inserted in the soil of each plot, leaving 1 cm of headspace. These collars served to demarcate the soil area for isotope tracing, and they were open cylinders at the upper and lower ends to allow natural water flow and prevent lateral contamination. In July 2018, soil cores up to 10 cm of mineral soil (corer  $\phi = 5.12 \text{ cm}$ ) were taken within each subplot, and soil bulk density was determined according to the approach described in detail in Verbrigghe et al. (2022).

## 2.3 | Isotope Tracing and Field Sampling

Isotope tracing was conducted at four dates under contrasting seasonal conditions: in summer (August 2017), autumn (November 2017), during the snowmelt period in the colder plots (April 2018), and in spring (June 2018). During each tracing campaign, 15 mL of a 5 mM  $^{15}\text{N}$ -algal amino acid mixture (referred to as  $^{15}\text{N}$ -Aa) with 98% atom enrichment (Cambridge Isotope Laboratories Inc., UK) was injected into the soil within each PVC collar using a syringe with a 7-cm needle. An organic source of  $^{15}\text{N}$  was chosen as an N tracer since organic N represents about 99.9% of the total N and 69.9% of the total dissolved N in these soils (Marañón-Jiménez et al. 2019). The  $^{15}\text{N}$ -labeled algal amino acid mixture used in this study contained a broad spectrum of 17 amino acids that ranged widely in chemical properties, including molecular weight, C:N ratio, average net charge, hydrophobicity, and polarity. Notably, eight of the most abundant and commonly detected amino acids in high-latitude soils—aspatic acid, glutamic acid, serine, glycine, threonine, alanine, histidine, and arginine (Weintraub and Schimel 2005; Kielland 1995; Andresen et al. 2022)—accounted for approximately 56.6% of the total molar composition of the solution. These compounds are not only ubiquitous in the free amino acid pool of cold soils, but have also been widely shown to be preferentially taken up by soil microbes and plants across a variety of boreal, subarctic, and alpine ecosystems (Ravn et al. 2017; Månsson et al. 2014; Nordin et al. 2004; Wilkinson et al. 2014). The inclusion of these key amino acids ensures that the labeling solution reflects the composition of biologically relevant organic N sources commonly available in these ecosystems.

To ensure uniform distribution over the upper 7 cm of soil (the needle length), 1 mL of the  $^{15}\text{N}$ -Aa solution was injected at 15 evenly spaced points within the collars using a grid placed over the soil surface. We also used a manual syringe injection method adapted for vertical delivery. A stopper was fixed at the top of the syringe plunger to control the injection volume, and the barrel of the syringe was gradually retracted upward

during injection (7–0-cm depth). This controlled motion ensured a homogeneous vertical distribution of the solution within the targeted soil layer. The amount of N injected in the  $^{15}\text{N}$ -Aa solution represented an average of 15.1% of total dissolved N and 46.3% of the total soil free amino acids, but only a 1.48% of the daily amino acid production through gross protein depolymerization.

Previous studies in the same study plots showed that natural abundance of the  $^{15}\text{N}$  isotope in bulk soil was not significantly affected by soil warming ( $\delta^{15}\text{N} = -0.25 \pm 0.17\text{‰}$ ,  $p = 0.475$ ). For this reason, deionized water was injected similarly into five additional collars located at ambient temperatures to account for the natural abundance of  $^{15}\text{N}$ . The 15 mL of  $^{15}\text{N}$ -Aa solution only caused an increase of 5.5% on the soil water content inside the collars.

Two weeks after the  $^{15}\text{N}$  tracing, all soil and vegetation growing within each collar was sampled destructively. For that, the soil surrounding one side of the collar was first excavated with a shovel to facilitate the removal of the entire PVC collar content, and then the entire PVC collar containing soil and vegetation was carefully extracted using a trowel to prevent soil loss from the collar bottom. These PVC collars, each containing soil and vegetation, were placed in individual plastic bags and transported to the laboratory.

## 2.4 | Sample Processing

Aboveground vegetation within the collars was cut at ground level, separated into green and litter and senescent plant material (green and senescent aboveground vegetation, hereafter), and rinsed with deionized water. The soil core, including roots and stones, was then removed from the PVC collar. All fresh soil within each core was sieved through a 2-mm mesh, weighed, and stored at 4°C for subsequent analyses. Roots were meticulously separated from the soil, cleaned with deionized water, and sorted into fine roots (<2 mm) and coarse roots (>2 mm) and rhizomes (fine roots and coarse roots and rhizomes). All plant material from each core, including sorted aboveground plant material and roots, was oven-dried at 60°C for 48 h, weighed, and ground using a ball mill. Similarly, a 5-g soil subsample from each collar was dried in an oven at 60°C for 48 h, then weighed and ground (bulk soil).

All tools and materials used for sample processing and sorting were cleaned and washed with acetone between samples to prevent cross-isotopic contamination. Samples injected with deionized water were processed using a separate set of tools and materials to avoid contamination by labeled samples.

## 2.5 | Sample Analyses

Dried, ground, and homogenized soil and plant materials from each sorted plant pool (green and senescent aboveground vegetation, fine roots, coarse roots and rhizomes, and bulk soil) were analyzed for total organic C, total N, and  $^{15}\text{N}$  using an elemental analyzer (Carlo Erba 1110, CE Instruments, Wigan, UK) coupled to an isotope-ratio mass spectrometer (Finnigan

MAT DeltaPlus; Fisher Scientific, Vienna, Austria) via a ConFlo III interface (Thermo Fisher, Waltham, EEUU). Aliquots of 2 g of homogenized fresh soil subsamples were extracted using 0.5 M  $\text{K}_2\text{SO}_4$  and analyzed for dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) (Dissolved soil fraction) with a TOC/TN analyzer (TOC-VCPH/CPN/TNM-1, Shimadzu, Austria). Microbial C and microbial N (Soil microbial biomass) were calculated from the difference between DOC and TDN in non-fumigated and fumigated soil samples using the chloroform fumigation-extraction method (Jenkinson and Powlson 1976). The  $^{15}\text{N}$  isotopic composition of the dissolved soil fraction and microbial biomass was also determined. For this, we oxidized aliquots of the respective fumigated and non-fumigated 0.5 M  $\text{K}_2\text{SO}_4$  extract solutions with alkaline persulfate solution ( $\text{K}_2\text{SO}_8$  with  $\text{H}_3\text{BO}_3$ ) to convert organic N compounds and  $\text{NH}_4$  to  $\text{NO}_3$  (Cabrera and Beare 1993; Doyle et al. 2004). Subsequently,  $\text{NO}_3$  was converted to  $\text{NO}_2$  with vanadium (III) chloride ( $\text{VCl}_3$ ) under acidic conditions, and  $\text{NO}_2$  was further reduced to  $\text{N}_2\text{O}$  by sodium azide ( $\text{NaN}_3$ ) (Lachouani et al. 2010). Measurements of  $\text{N}_2\text{O}$  concentrations and isotopic compositions were done by PT-IRMS, using a Gasbench II headspace analyzer (Thermo Fisher, Bremen, Germany) with a cryo-focusing unit, coupled to a Finnigan Delta V Advantage IRMS (Thermo Fisher, Bremen, Germany) as outlined in Lachouani et al. (2010). The  $^{15}\text{N}$  in atom percent (at%) in the microbial biomass ( $^{15}\text{N}_{\text{micro}}$ ) was calculated as:

$$^{15}\text{N}_{\text{micro}} = \left( ^{15}\text{N}_{\text{F}} * \text{TDN}_{\text{F}} - ^{15}\text{N}_{\text{NF}} * \text{TDN}_{\text{NF}} \right) / \text{microbial N} \quad (1)$$

where  $^{15}\text{N}_{\text{F}}$  and  $^{15}\text{N}_{\text{NF}}$  are the  $^{15}\text{N}$  content in atom percent in the extracts of the fumigated and non-fumigated samples, respectively, and  $\text{TN}_{\text{F}}$  and  $\text{TN}_{\text{NF}}$  are the total dissolved nitrogen in fumigated and non-fumigated samples, respectively. The concentrations in the microbial fraction presented here were not corrected for extraction efficiency.

The  $^{15}\text{N}$  isotopic enrichment (at%) of labeled samples ( $^{15}\text{N}_{\text{labeled}}$ ) was corrected by the  $^{15}\text{N}$  isotopic enrichment of non-labeled samples ( $^{15}\text{N}_{\text{non-labeled}}$ ) to calculate the atom percent excess of each sample (APE) as:

$$\text{APE} (\%) = ^{15}\text{N}_{\text{labeled}} - ^{15}\text{N}_{\text{non-labeled}} \quad (2)$$

All fractions are presented relative to soil dry mass.

## 2.6 | Data Analyses

The amount of added  $^{15}\text{N}$  remaining in each pool 2 weeks after the tracer addition was calculated using the following equations:

$$^{15}\text{N remaining} (\%) = \frac{\text{APE} * \text{TN} * \text{Pa}^{15}\text{N}}{100 * \text{Pa}^{14}\text{N}} * 100 \quad (3)$$

where APE is the atom percent excess of each sample, TN is the total N stock in the correspondent pool,  $\text{Pa}^{15}\text{N}$  and  $\text{Pa}^{14}\text{N}$  are the atomic weights of  $^{15}\text{N}$  and  $^{14}\text{N}$ , respectively, and  $^{15}\text{N}_{\text{add}}$  is a constant, representing the  $^{15}\text{N}$  injected in each collar per square meter (84.757 mg/m<sup>2</sup>). Then, the percentage of added  $^{15}\text{N}$  remaining in the non-extractable soil fraction was calculated as:

$$^{15}\text{N remaining}_{\text{non-extractable}} (\%) = ^{15}\text{N remaining}_{\text{bulk soil}} - ^{15}\text{N remaining}_{\text{microbes}} - ^{15}\text{N remaining}_{\text{dissolved}} \quad (4)$$

where  $^{15}\text{N remaining}_{\text{bulk soil}}$ ,  $^{15}\text{N remaining}_{\text{microbes}}$ ,  $^{15}\text{N remaining}_{\text{dissolved}}$  are the percentages of added  $^{15}\text{N}$  recovered in the bulk soil, soil microbial biomass, and in the dissolved soil fraction, respectively. We also calculated the percentage of added  $^{15}\text{N}$  that was not recovered from the sampled ecosystem pools as:

$$^{15}\text{N}_{\text{lost}} = 100 - ^{15}\text{N remaining}_{\text{bulk soil}} - ^{15}\text{N remaining}_{\text{vegetation}} \quad (5)$$

where  $^{15}\text{N remaining}_{\text{vegetation}}$  is the percentage of added  $^{15}\text{N}$  recovered in all vegetation pools (green and senescent aboveground vegetation, fine roots and coarse roots and rhizomes).

The effects of soil warming, seasons, and their interaction on the C and N stocks, C:N ratios, and the  $^{15}\text{N}$  enrichment of soil and vegetation pools were analyzed using linear models, with soil warming as a continuous independent variable, seasons as a factor and their interaction. When significant, differences among seasons were further tested by post hoc tests with Sidak corrections for multiple testing while accounting for the effects of warming. Differences in C:N ratios between soil microbes and the dissolved soil fraction within seasons were further tested using one-way ANOVAs.

Differences in the effect of soil warming among the C and N stocks of different soil pools (bulk soil, soil microbes, and dissolved soil fraction; bulk soil, fine roots and coarse roots) were analyzed using robust linear models (RLMs) on previously standardized soil variables. Soil warming was included as a continuous independent variable, along with the interaction term between soil warming and the pool variable. Heteroskedasticity-consistent standard errors were used to evaluate the significance of the effects. A significant interaction term would indicate that soil warming has a differential effect on the C and N stocks of the different soil pools.

The effect of seasons was tested on the percentage of  $^{15}\text{N}$  remaining in each pool at the ambient temperature plots using one-way ANOVAs, and differences among seasons were further tested by post hoc tests with Sidak corrections for multiple testing. Then, the effect of soil warming was also tested for each pool and season separately using linear models and generalized linear models from the quasibinomial family, including soil warming as a continuous independent variable.

To ensure the validity of the linear models, the residuals were tested for normality and homoscedasticity. The Shapiro–Wilk test was used to assess whether the residuals followed a normal distribution, and the Breusch–Pagan (linear regression models) or Levene tests (ANOVAs) were used to check for homoscedasticity. When necessary, Box–Cox transformations were applied to dependent variables prior to model fitting to meet the assumptions of parametric models. The optimal transformation parameter ( $\lambda$ ) was estimated for each response variable using the `boxcox()` function from the MASS package in R (Venables and Ripley 2002). Because  $\lambda$  values varied across variables, a summary of the applied transformations is provided in Table S1. All

models were interpreted on the transformed scale. We note that non-linear  $\lambda$  values imply non-linear relationships between predictors and responses. All statistical analyses were conducted using R (version 4.4.1). The results are presented as means  $\pm$  standard errors.

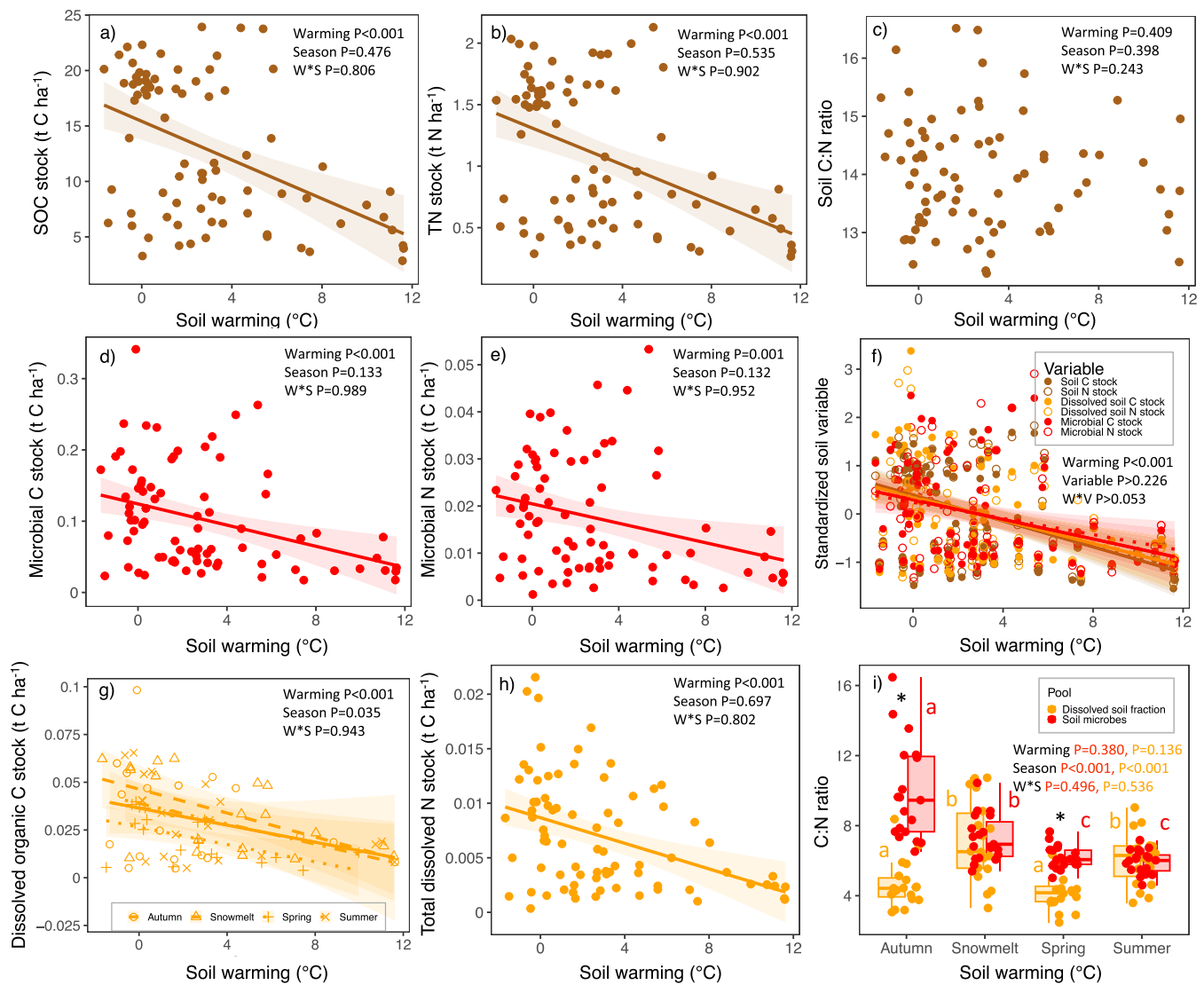
### 3 | Results

#### 3.1 | Warming and Seasonal Effects on C and N Pools

In this subarctic grassland, total N stocks, including all considered ecosystem pools at ambient soil temperatures, were  $174.92 \pm 0.86 \text{ g m}^{-2}$ . The non-extractable soil N fraction was the largest pool ( $161.9 \text{ g m}^{-2}$  and 92.5% of the N pools), followed by fine roots ( $3.7 \text{ g m}^{-2}$  and 2.1%) and senescent aboveground vegetation ( $3.2 \text{ g m}^{-2}$  and 1.8%). Soil microbial biomass ( $2.6 \text{ g m}^{-2}$  and 1.5%), the coarse roots and rhizomes ( $1.3 \text{ g m}^{-2}$  and 0.7%) and the dissolved soil fraction ( $1.17 \text{ g m}^{-2}$  and 0.7%) followed in magnitude, while the smallest N pools were represented by the green aboveground vegetation ( $1.1 \text{ g m}^{-2}$  and 0.6%).

Key soil C and N stocks exhibited consistent declines along the soil temperature gradient across seasons (Figure 1). Soil organic carbon (SOC) and total soil nitrogen (TN) stocks decreased with warming ( $p < 0.001$ , Figure 1a,b) in the same proportion, maintaining a constant soil C:N ratio despite temperature variation (Figure 1c). Similarly, microbial biomass and dissolved C and N stocks also decreased consistently in response to temperature increases ( $p < 0.001$ , Figure 1d,e,g,h), leading to constant microbial biomass and dissolved C:N ratios along the soil temperature gradient (Figure 1i). The rates of decline of C and N stocks in bulk soil, microbial biomass, and dissolved soil fractions were similar, as indicated by the lack of significant interaction between warming and the standardized soil variables (Figure 1f). Nonetheless, C:N ratios of microbial biomass were larger than the C:N ratios of the dissolved soil fraction during autumn and spring (Figure 1i).

Key vegetation C and N stocks also changed with soil warming consistently across seasons (Figure 2). Root C and N stocks, both from fine roots, coarse roots, and rhizomes, declined with soil warming ( $p > 0.02$ , Figure 2a,b,d,e). Nonetheless, the C content in fine roots decreased more than its N content, causing a consistent decrease in fine roots C:N ratios with warming across seasons (Figure 2c), where values were lower in spring and snowmelt. By contrast, C and N stocks in green aboveground vegetation increased proportionally and consistently with soil warming across seasons ( $p < 0.02$ , Figure 2g,h), without changes in C:N ratios along the warming gradient (warming:  $p = 0.573$ , season:  $p = 0.071$ , warming  $\times$  season:  $p = 0.771$ ). Consequently, root:shoot ratios declined with soil warming consistently across seasons (warming:  $p < 0.001$ , season:  $p = 0.579$ , warming  $\times$  season:  $p = 0.270$ ). The rate of decline of bulk soil C stocks was similar to that of fine roots C stocks, as indicated by the lack of significant interaction between warming and the standardized soil variables ( $p = 0.070$ ), but differed from fine roots N stocks



**FIGURE 1** | Effect of soil warming and seasons on (a) soil organic C stocks, (b) total soil N stocks, (c) total soil C:N ratios, (d) microbial C stocks, (e) microbial N stocks, (f) standardized soil, microbial and dissolved C and N stocks, (g) dissolved organic C stocks, (h) total dissolved N stocks, and (i) C:N ratios in dissolved and microbial fractions. *p* values indicate the effect of warming, season and their interaction according to linear models on previously transformed variables. Lines indicate significant ( $p < 0.05$ ) effect of warming. Shaded areas around lines represent the confidence intervals of the regressions. Box plots indicate significant ( $p < 0.05$ ) effect of seasons only. Different letters indicate significant differences among seasons within each pool according to post hoc Sidak corrections for multiple comparisons. Asterisks indicate significant differences between pools within seasons.

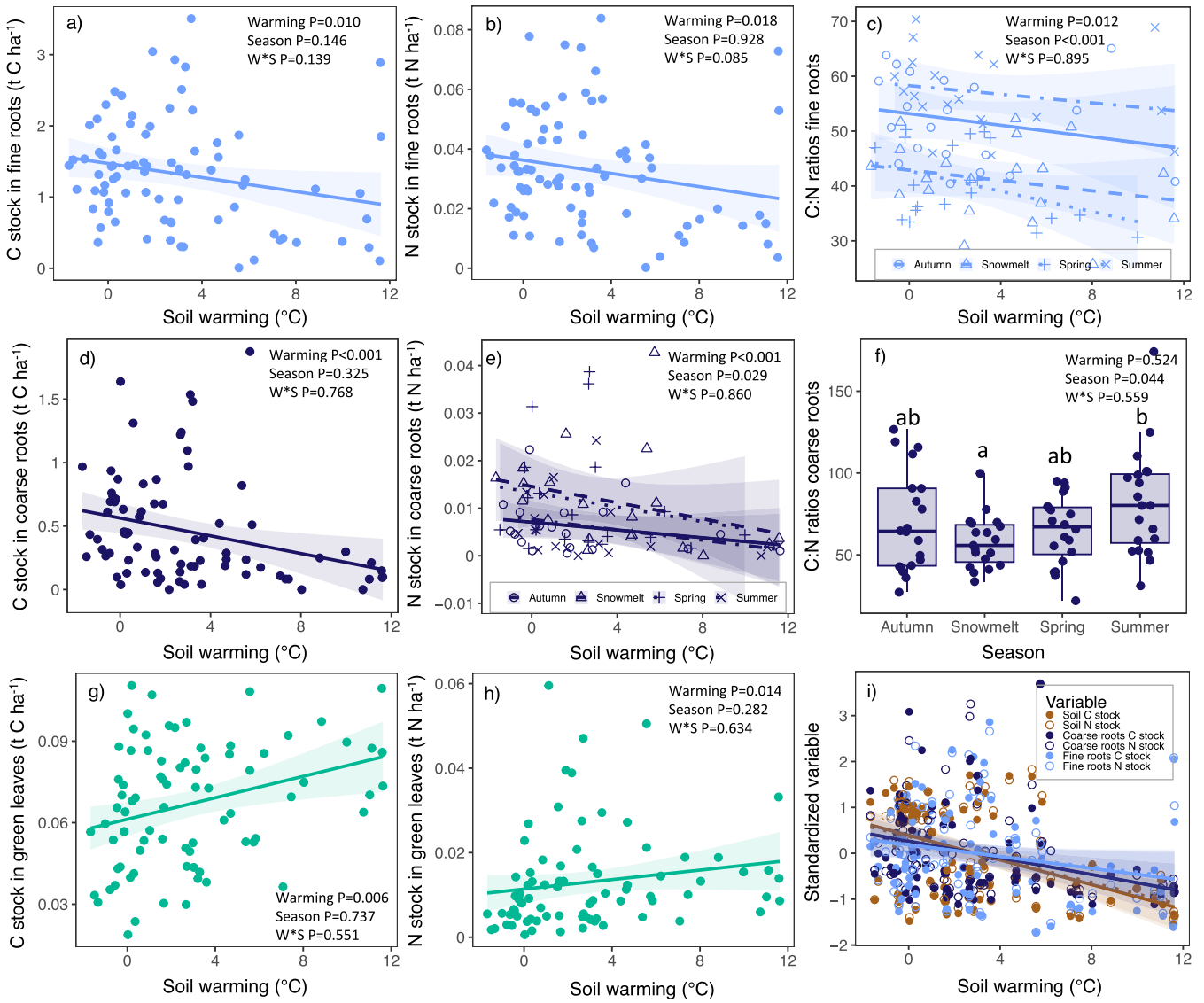
(warming  $\times$  variable:  $p = 0.041$ ) and from the C and N stocks in coarse roots and rhizomes (warming  $\times$  variable:  $p = 0.028$  and  $p < 0.001$ , respectively) (Figure 2i). Carbon and N stocks in senescent aboveground vegetation were not affected by soil warming ( $p > 0.21$ ), but were higher in summer and autumn ( $p < 0.001$ ).

### 3.2 | Warming and Seasonal Effects on $^{15}\text{N}$ Pools Recovered After Tracing

In plots at ambient temperatures, 90.1%–77.4% of the added  $^{15}\text{N}$  in the algal amino acid mixture was recovered from either the vegetation or the upper 9 cm of soil (the depth of the PVC collar insertion), although there were no significant differences among seasons. A 10.1%–22.6% of the added  $^{15}\text{N}$  was

recovered in the soil microbial biomass pool, and 2.1%–10.8% was recovered from fine roots, with the highest recoveries during snowmelt and the lowest in spring ( $p = 0.005$  for soil microbes,  $p = 0.013$  for fine roots, Figure 3). On the contrary, the  $^{15}\text{N}$  recovered from the dissolved soil fraction was highest in spring (ca. 6.4%) and lowest in autumn (ca. 1.6%,  $p = 0.033$ ). An important  $^{15}\text{N}$  portion (45.6%–67.5%) was also recovered from the non-extractable soil fraction, with some effect of seasons ( $p = 0.040$ ) but without significant pairwise differences after Sidak post hoc correction. Senescent aboveground vegetation, coarse roots, and rhizomes, and green aboveground vegetation contained 0.7%–2.4%, 0.3%–2.3%, and 0.1%–1.1% of the added  $^{15}\text{N}$ , respectively.

Soil temperatures affected the  $^{15}\text{N}$  recovered from soil and vegetation pools (Figure 4). The decline in the  $^{15}\text{N}$  recovered in the



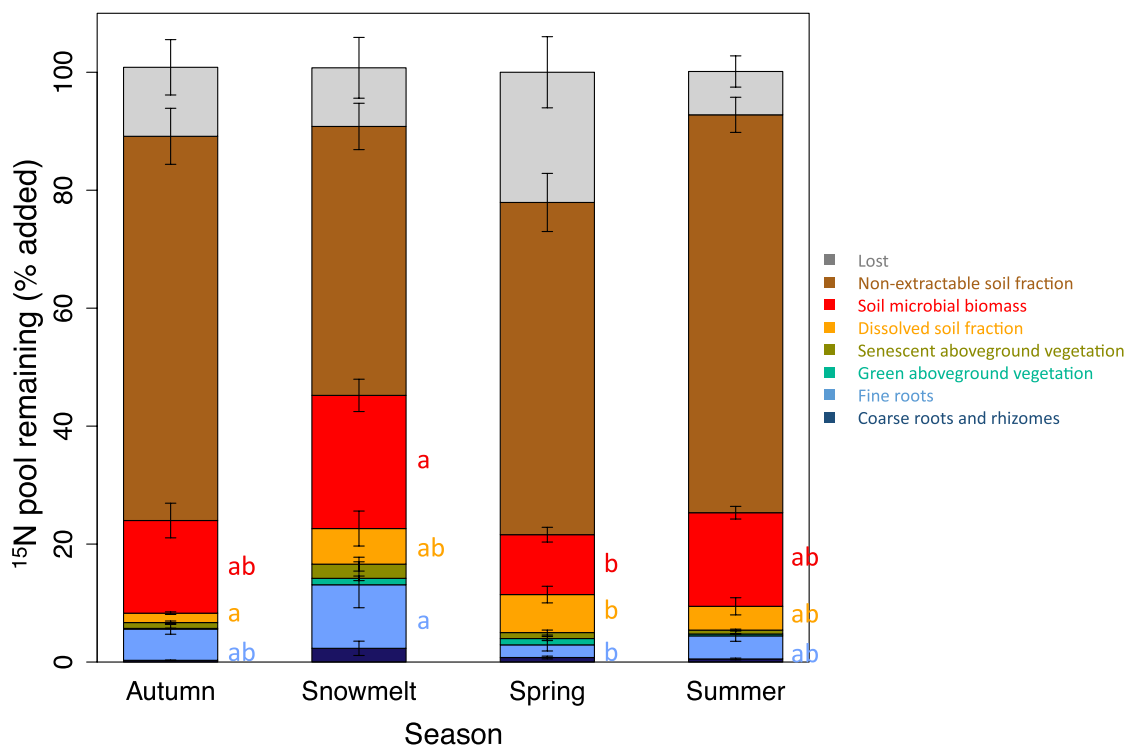
**FIGURE 2** | Effect of soil warming and seasons on (a) C stocks, (b) N stocks, and (c) C:N ratios in fine roots, (d) C stocks, (e) N stocks, and (f) C:N ratios in coarse roots and rhizomes, (g) C stocks and (h) N stocks in green aboveground vegetation, and (i) standardized soil and root C and N stocks. *p* values indicate the effect of warming, season and their interaction according to linear models on previously transformed variables. Lines indicate significant ( $p < 0.05$ ) effect of warming. Shaded areas around lines represent the confidence intervals of the regressions. Box plots indicate significant ( $p < 0.05$ ) effect of season only. Different letters indicate significant differences among seasons according to post hoc Sidak corrections for multiple comparisons.

non-extractable soil pool, despite being significant only for autumn, summer, and the snowmelt period, had the highest influence on the global <sup>15</sup>N retention, due to his large magnitude compared to the other ecosystem pools considered. As a result, N losses detected in this pool accounted for 1.7%–2.6% of the total N loss per degree °C of warming. Nonetheless, the decrease in <sup>15</sup>N pool recovered in the soil microbial biomass and fine roots during the snowmelt period ( $p = 0.013$  and  $p = 0.002$ , respectively) together accounted for  $2.0\% \text{ °C}^{-1}$  of the N loss during this period. By contrast, soil warming increased the <sup>15</sup>N pool retained by green aboveground vegetation in spring ( $0.17\% \text{ °C}^{-1}$ ,  $p = 0.016$ ) and summer ( $0.12\% \text{ °C}^{-1}$ ,  $p = 0.001$ ), as well as the <sup>15</sup>N recovered in senescent aboveground vegetation during summer ( $0.15\% \text{ °C}^{-1}$ ,  $p = 0.002$ ), which contributed to compensate the N loss in the dissolved soil fraction

during these seasons (spring:  $0.42\% \text{ °C}^{-1}$ ,  $p = 0.022$ ; summer:  $0.22\% \text{ °C}^{-1}$ ,  $p = 0.003$ ).

### 3.3 | Warming and Seasonal Effects on the <sup>15</sup>N Enrichment of Ecosystem Pools After Tracing

Soil microbial biomass was the ecosystem reservoir with the highest <sup>15</sup>N enrichment 2 weeks after the tracer addition, followed by the fine roots, coarse roots, and green leaves. Bulk soil and the senescent aboveground vegetation were the ecosystem pools with the lowest <sup>15</sup>N enrichment (Figure 5). While the <sup>15</sup>N enrichment of the bulk soil was not affected by soil warming or seasons (Figure 6a), the <sup>15</sup>N enrichment of the soil microbial biomass, dissolved soil fraction, and fine roots pools was affected



**FIGURE 3** | Percentage of the <sup>15</sup>N pool recovered in the different ecosystem pools of ambient temperature plots 2 weeks after tracing with <sup>15</sup>N amino acids. Bars represent averages of ambient temperature plots per ecosystem pool and season ( $n = 5$ ). Error bars represent the standard errors. Letters indicate significant differences of each pool among seasons according to one-way ANOVAs ( $p < 0.05$ ), where different letters indicate significant differences among seasons according to post hoc Sidak corrections for multiple comparisons.

only by seasons (Figure 6b–d), where soil microbes and fine roots were more enriched in <sup>15</sup>N during the snowmelt period and the dissolved soil fraction during the spring and snowmelt period. The <sup>15</sup>N enrichment of green and senescent aboveground vegetation increased with soil warming and showed the lowest values in autumn (Figure 6e,f).

## 4 | Discussion

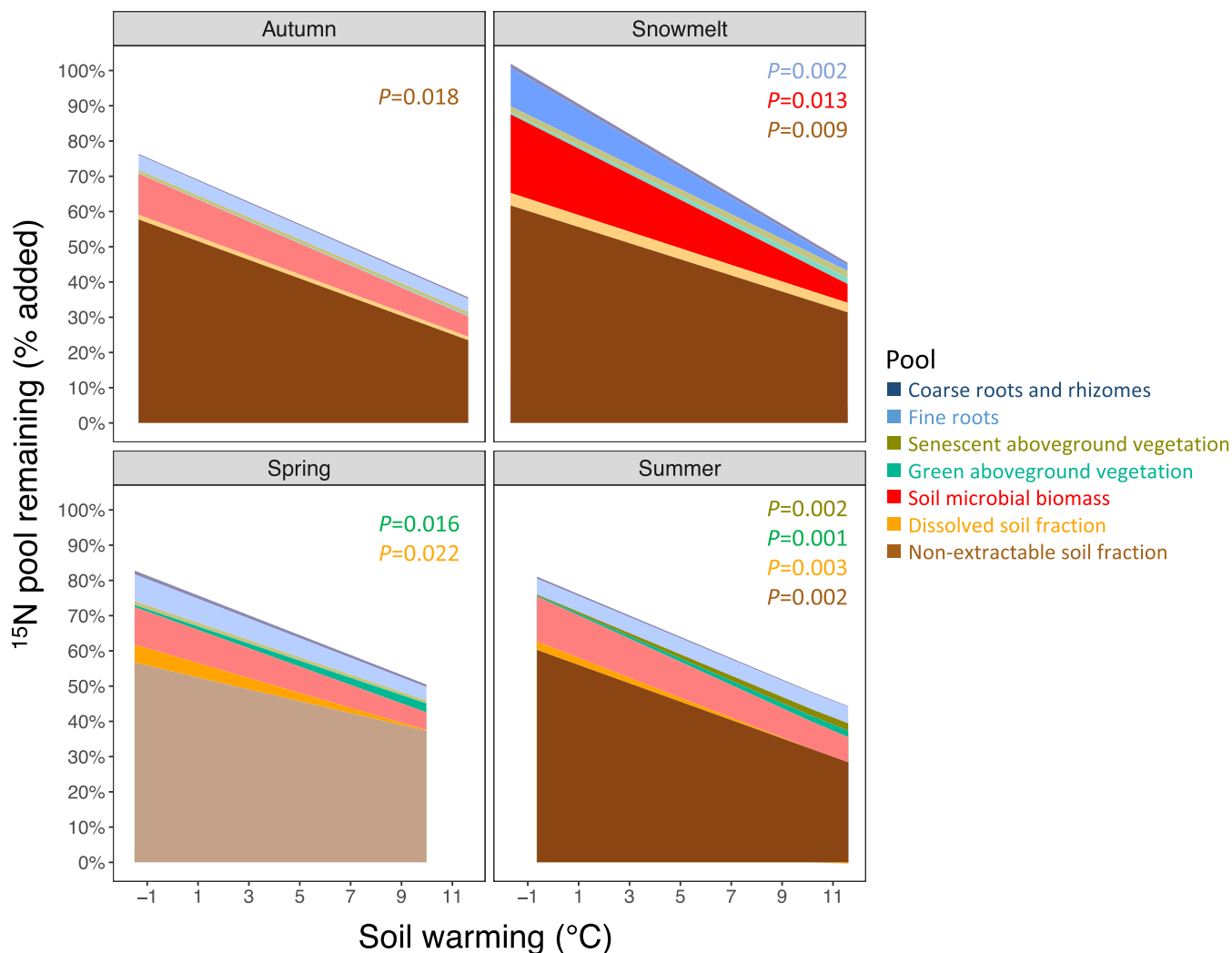
We hypothesized that soil warming disrupts the balance between microbial N mineralization and plant N uptake, causing N losses from the plant–soil system. Our findings reveal that warming compromises the stabilization of N in the non-extractable SOM fraction, a key reservoir of long-term soil fertility. Warming also reduces the capacity of microbial biomass and fine roots to temporarily store N during cold periods, exacerbating N losses when plant uptake is limited. Warming-induced N losses from ecosystems have critical implications for the C biogeochemical cycle, as reduced N availability constrains plant productivity and weakens its capacity to offset soil C losses. By uncovering these mechanisms, our study highlights how increasing temperatures can drive irreversible C losses in cold ecosystems.

### 4.1 | Warming Effects on the N Stabilization in the Non-Extractable Soil Fraction

The non-extractable soil fraction had the greatest influence on total <sup>15</sup>N retention in this subarctic grassland, due to its substantial size relative to other ecosystem pools (Figure 4). Several

mechanisms can contribute to the 1.7%–2.6% lower N stabilization within this pool per °C of warming. Some amino acids used for <sup>15</sup>N tracing and naturally present in soil, such as glutamic acid or lysine, contribute to ex vivo organic matter stabilization through their dissociable functional groups (Schmidt et al. 2011; Lehmann and Kleber 2015) that form stable bonds with clay minerals and organic matter. Additionally, <sup>15</sup>N-enriched microbial necromass interacts with soil minerals, contributing to in vivo stabilization (Cotrufo and Lavelle 2022; Manzoni and Cotrufo 2024). The fast assimilation of amino acids by microbial biomass and later bonding of microbially transformed products to the soil matrix can constitute the most important amino acid stabilization pathway even just a few hours after the addition to the soil (Rothstein 2010; Dippold and Kuzyakov 2013). Importantly, the <sup>15</sup>N-labeled amino acid mixture used for tracing included several of the most abundant and bioavailable amino acids in high-latitude soils—such as alanine, glycine, glutamate, and aspartate—with a wide range of chemical properties, ensuring that the observed amino acid stabilization patterns reflect ecologically relevant pathways (Weintraub and Schimel 2005; Andresen et al. 2022; Kielland 1995). These stabilization processes not only sequester C but also N within the soil matrix, reducing their accessibility to soil microbes and potential losses through mineralization.

While reduced background organic matter under warming could theoretically enhance mineral sorption capacity by lowering competition for binding sites (Charles et al. 2008; Kaiser and Guggenberger 2003), the net effect was a decline in stabilization capacity. This is likely due to the concurrent depletion of microbial biomass, necromass, and sorption-promoting organic



**FIGURE 4** | Effect of soil warming on the  $^{15}\text{N}$  recovered in the different ecosystem pools across seasons. Bright or intense colors indicate statistically significant effects of warming on  $^{15}\text{N}$  retention according to lineal models for each ecosystem pool and season ( $n = 20$ ), as shown by the accompanying  $p$  values ( $p < 0.05$ ). Pale tones indicate non-significant responses.

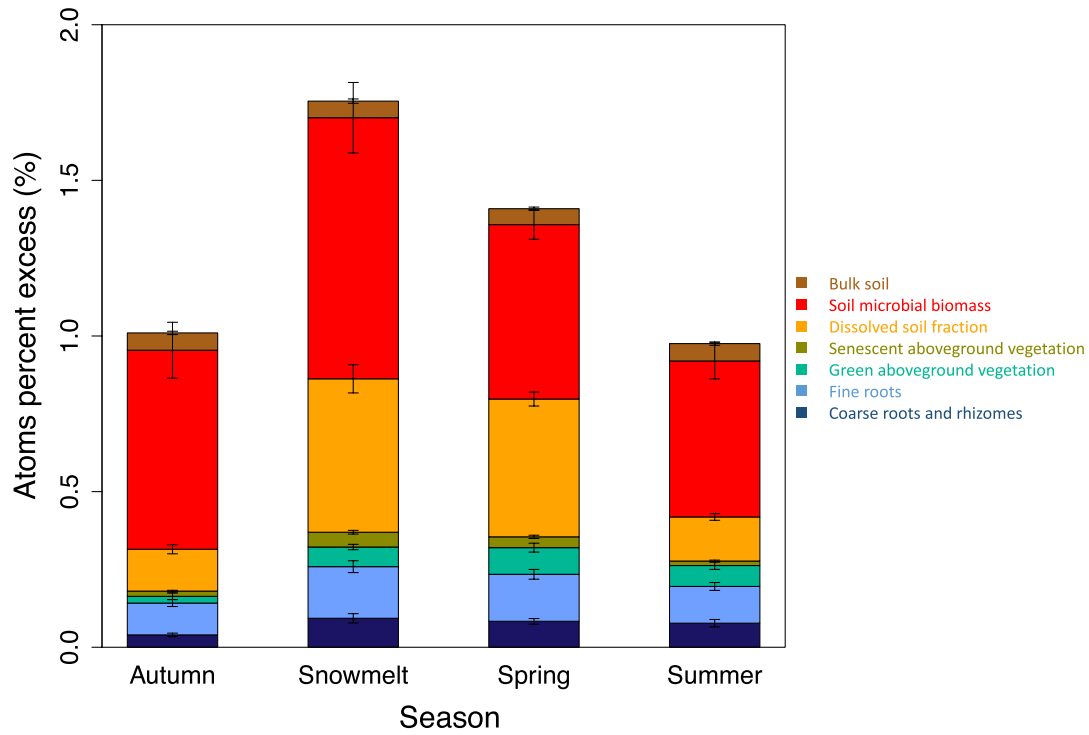
ligands, which play a crucial role in both in vivo and ex vivo N retention (Poeplau et al. 2017; Dwivedi et al. 2019; Liao et al. 2025). Elevated temperatures reduce microbial biomass and necromass production (Figure 1d,e), limiting the supply of residues essential for in vivo stabilization (Allison and Treseder 2008; Marañón-Jiménez et al. 2018; Walker et al. 2018). At the same time, warming causes the depletion of soil organic compounds (Figure 1a,b) involved in ex vivo N stabilization (Rothstein 2010; Dwivedi et al. 2019). This dual effect diminishes the soil capacity to stabilize N, increasing the risk of N losses from the ecosystem.

#### 4.2 | Warming Effects on the N Retention Capacity of Fine Roots and Soil Microbial Biomass

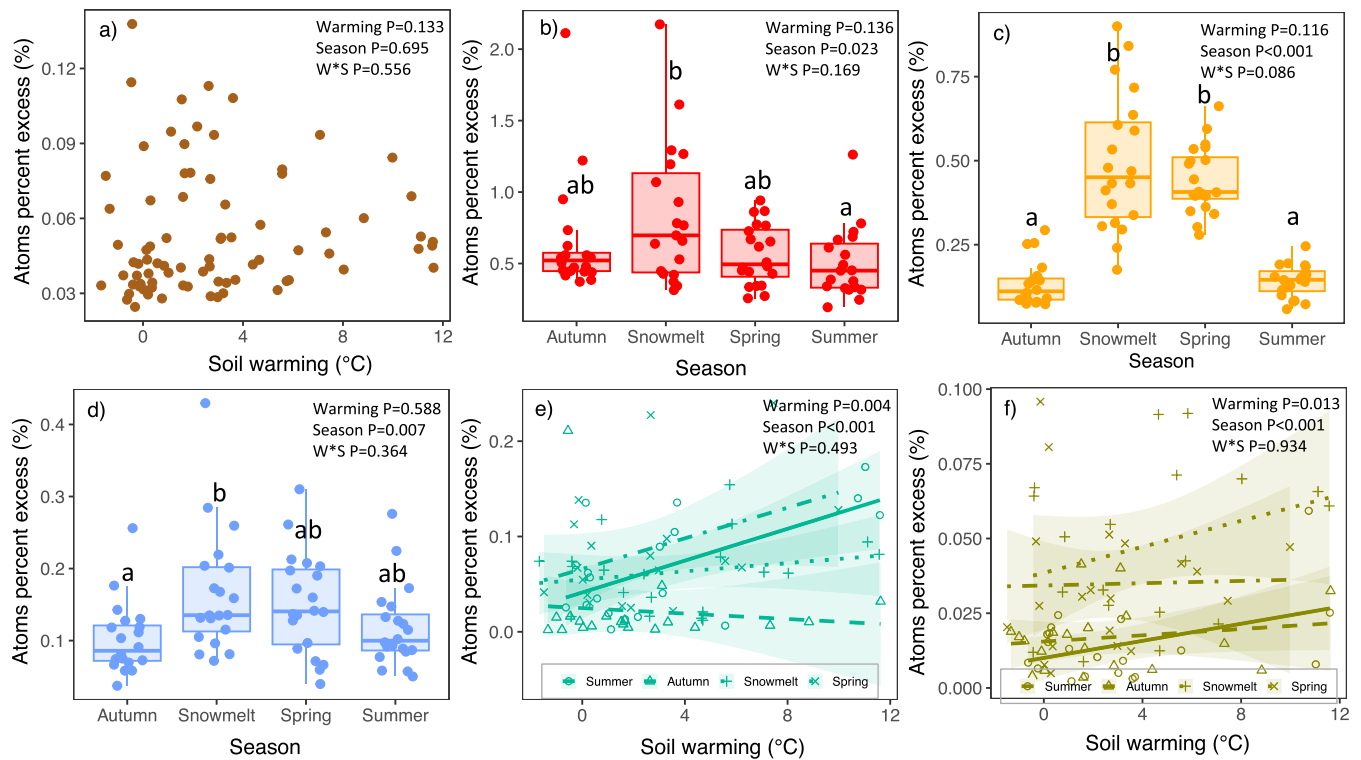
Fine roots and microbial biomass, although accounting for only 2.1% and 1.5% of the N pools in this subarctic grassland, respectively, stored up to 10.8% and 22.6% of the labeled  $^{15}\text{N}$  during the snowmelt period (Figure 3). This highlights their critical role as dynamic N reservoirs, rapidly immobilizing N in response to seasonal availability (Clemmensen et al. 2008; Larsen et al. 2012; Xu et al. 2013). Microbial biomass, in particular,

has high turnover rates and fast N immobilization, making it a key driver of nutrient fluxes in cold soils (Bardgett et al. 2003; Haugwitz et al. 2011). During thawing events, microbial turnover releases substantial amounts of N into the plant–soil system, providing a vital nutrient source for plants during the growing season (Lipson et al. 2000; Sorensen et al. 2008). Although microbial biomass typically reaches its maximum in late winter and declines steeply during soil thaw (Schnecker et al. 2023), we did not detect this seasonal pattern in the total biomass C and N pools (Figure 1d,e). However, the highest  $^{15}\text{N}$  recovery in microbial biomass was observed during the snowmelt period (Figure 3), which was associated with a higher N immobilization capacity in this season (Figures 5 and 6b), consistent with its role in regulating N availability according to plant demands (Isobe et al. 2018).

The same seasonal trend was also observed with the  $^{15}\text{N}$  recovered by fine roots (Figures 3 and 5). Some plant species in subarctic grasslands, conserve over-wintering green aboveground structures and have adaptations to rapidly absorb N released during thawing events to support early spring growth (Chapin III et al. 1986; Starr and Oberbauer 2003; Larsen et al. 2012).



**FIGURE 5** | Comparison of the  $^{15}\text{N}$  enrichment in the different ecosystem pools 2 weeks after tracing with  $^{15}\text{N}$  amino acids. Bars represent averages per ecosystem pool and season ( $n = 20$ ). Error bars represent the standard errors.



**FIGURE 6** | Effect of soil warming and seasons on the  $^{15}\text{N}$  enrichment in (a) bulk soil, (b) microbial biomass, and (c) dissolved soil fraction, (d) fine roots, (e) green aboveground vegetation, and (f) senescent aboveground vegetation.  $p$  values indicate the effect of warming, season and their interaction according to linear models on previously transformed variables. Box plots indicate significant ( $p < 0.05$ ) effect of season only. Lines indicate significant ( $p < 0.05$ ) effect of warming. Shaded areas around lines represent the confidence intervals of the regressions. Different letters indicate significant differences among seasons according to post hoc Sidak corrections for multiple comparisons.

This interplay between microbial biomass and fine roots highlights their complementary roles in regulating N dynamics in cold ecosystems. By immobilizing N during periods of low plant demand and releasing it when demand peaks, microbial biomass buffer seasonal nutrient fluctuations and sustain ecosystem functioning.

However, our results revealed that warming reduces the capacity of microbial biomass and fine roots to temporarily store N during the snowmelt period (Figure 4), just when this function is more important. This reduction was likely due to a decline in the size of these pools (Figures 1e and 2b), as indicated by their unaltered  $^{15}\text{N}$  enrichment under warming (Figure 6b,d), suggesting no changes in their physiological N retention capacity. Consistently, fine root biomass and the correspondent C and N pools declined after 11 years of warming in the same subarctic grassland (Bhattarai et al. 2023), which was associated with shifts in plant community composition toward pioneer species like *Equisetum* spp. Moreover, soil N losses under warming have led to reduced fine root production and thinner roots with higher specific root area (Fang et al. 2023), consistent with lower fine root C:N ratios found here (Figure 2c). Nonetheless, the effects of warming on belowground biomass are complex and can vary across different ecosystems depending on warming magnitude and duration (Wang et al. 2021).

Warming also reduced microbial biomass (Figure 1d,e) due to increased respiratory demands and the subsequent soil C depletion needed for microbial biomass maintenance under chronic warmer temperatures (Marañón-Jiménez et al. 2018; Walker et al. 2018). Strict microbial C:N stoichiometric demands further constrained microbial N retention under chronic warming (Marañón-Jiménez et al. 2019). Consistently, elevated temperatures generally lead to a decrease in microbial N biomass while enhancing N mineralization and nitrification across different ecosystems (Gao and Yan 2019; Dai et al. 2020; Shi et al. 2024; Tian et al. 2023). Interestingly, Peplau et al. (2021) observed that while warming reduced soil C stocks in a subarctic deciduous forest, N was not lost but shifted from particulate organic matter (POM) to mineral-associated organic matter (MAOM), suggesting stabilization of N via microbial necromass incorporation into MAOM. In our study, lower soil C:N ratios ( $14.01 \pm 0.16$  versus  $17.69 \pm 1.74$  in the topsoils investigated by Peplau et al. (2021)) likely exacerbated microbial C limitation, promoting microbial N mineralization rather than immobilization in microbial biomass and contributing to lower N retention capacity under warming (Wild et al. 2015; Marañón-Jiménez et al. 2019). Therefore, temperature-driven shifts in fine roots and soil microbial biomass compromised the temporal N retention function of these reservoirs during the snowmelt period, contributing to the opening of the N cycle.

### 4.3 | Warming-Induced Shifts in Aboveground Plant N Uptake and Allocation

By contrast, warming increased aboveground N uptake during the growing season, as is shown by the positive response of the  $^{15}\text{N}$  pool recovered in living aboveground plant tissues (aboveground green vegetation) during summer and spring (Figure 4). The observed increase in aboveground biomass,

resulting in higher C and N stocks (Figure 2g,h), and the concurrent rise the  $^{15}\text{N}$  concentration in aboveground plant tissues (Figure 6e) suggests that warming influenced not only plant growth, but also N assimilation and allocation. These results are consistent with the increase in maximum annual NDVI values at higher soil temperatures found in the same study sites (Mortier et al. 2024). Increased rates of N mineralization and turnover at warmer temperatures can alleviate plant N limitations in cold ecosystems (Turner and Henry 2010), leading to higher plant N uptake and to shifts toward above-ground plant allocation (Wang et al. 2016). Previous studies demonstrate that plants rely more on free amino acid uptake to support N demands in unfertile soils, as is the case here in warmer soils, and mycorrhizal associations can also influence plant amino acid uptake (Andresen et al. 2022). Indeed, arbuscular mycorrhizal fungal biomass showed a positive response to warming in the same sites (Zhang et al. 2020). Increased plant reliance on associations with arbuscular mycorrhizal fungi would help to explain the observed increases in aboveground vegetation biomass despite reduced soil N stocks and lower root biomass. Shifts on biomass and N allocation of subarctic vegetation towards aboveground parts at warmer conditions could significantly influence C and N cycling by altering the quality, quantity and spatial distribution of litter inputs into the soil.

### 4.4 | Warming-Induced N Imbalances and Asynchronies Between Plant and Soil Microbial N Cycling

Warming can therefore alter the subtle balance between microbial N mineralization and plant uptake (Dawes et al. 2017; Marañón-Jiménez et al. 2019), due to both asynchronies and imbalances between these two N fluxes (Lacroix et al. 2022). Despite aboveground vegetation N uptake increasing slightly with warming during the growing seasons, compensating partially for the N loss in the dissolved N fraction (Figure 4), the magnitude of N released from soil microbial biomass and fine roots in the cold season ( $1.99\%$  of N lost  $^{\circ}\text{C}^{-1}$ ) exceeded by far the small increase in plant N uptake during the growing season ( $0.14\%$  of N gained  $^{\circ}\text{C}^{-1}$ ). The asynchrony between the warming-induced N flux from the microbial biomass and fine root pools during the snowmelt period and the optimum photoperiod for plant growth may have also prevented vegetation from taking much advantage of the extra N released to the soil, limiting the positive response of plant productivity to increasing temperatures (Fang et al. 2023). In addition, soil microbes may have faster response rates and a higher capacity for adaptation to fast temperature increases compared to vegetation or other large organisms with slower turnover rates and generation times, which need longer times to adapt (Classen et al. 2015). These different rates of adaptation could also have contributed to the opening of the N cycle, causing coupled and proportional soil C and N losses (Figure 1).

These results must be interpreted in the context of the specific characteristics of our experimental approach. Geothermal gradients, while primarily heating soils with minimal effect on air temperature (Sigurdsson et al. 2016), offer a unique opportunity to investigate long-term warming effects in situ, including extreme warming levels. Although soil and air temperature

decoupling may affect some aboveground–belowground interactions differently than in climatic warming (Rustad et al. 2001; Hanson et al. 2017; Bai et al. 2023), the focus on soil processes remains particularly relevant in cold ecosystems, where soil temperature is a dominant control on microbial activity, nutrient cycling, and C stabilization (Ferrari et al. 2018). Furthermore, as in most warming experiments, the abrupt onset of warming may have constrained the adaptive capacity of slow-responding organisms, potentially altering trophic interactions and plant–soil feedbacks (Classen et al. 2015; De Boeck et al. 2015; Yin et al. 2023). Ongoing experiments simulating gradual warming through periodical mesocosm transplantations in these study sites will further refine our understanding of ecosystem vulnerability to realistic warming trajectories.

Despite these limitations, the absence of physical disturbance and the stable and continuous nature of the geothermal gradients—spanning both projected and extreme warming levels—make this system highly suitable for assessing subarctic ecosystem responses to warming. Our results reveal a consistent decline in N retention across major soil pools, with the largest proportional losses occurring in the non-extractable soil fraction, a key reservoir for long-term stabilization. Warming reduced the short-term immobilization of N in soil microbial biomass and fine roots, particularly during the snowmelt period, weakening both in vivo and ex vivo soil N stabilization pathways. These shifts disrupted the synchrony between plant and microbial N cycling, opening the N cycle and weakening the system's capacity to conserve N. By revealing how warming destabilizes soil N retention, this study highlights a critical but underappreciated driver of soil C loss and ecosystem vulnerability in a rapidly changing climate.

#### Author Contributions

**Sara Marañón-Jiménez:** conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing – original draft, writing – review and editing. **Xi Luo:** formal analysis, investigation, visualization, writing – original draft, writing – review and editing. **Andreas Richter:** conceptualization, data curation, funding acquisition, investigation, methodology, resources, supervision, writing – review and editing. **Philipp Gündler:** data curation, investigation, methodology, resources. **Lucia Fuchslueger:** data curation, formal analysis, investigation, methodology, supervision, validation, writing – review and editing. **Niel Verbrigghe:** data curation, formal analysis, investigation, methodology, writing – review and editing. **Christopher Poeplau:** data curation, formal analysis, investigation, writing – review and editing. **Bjarni D. Sigurdsson:** data curation, funding acquisition, investigation, project administration, resources, supervision, writing – review and editing. **Ivan Janssens:** conceptualization, funding acquisition, investigation, resources, supervision, writing – review and editing. **Josep Peñuelas:** conceptualization, funding acquisition, investigation, project administration, resources, supervision, validation, writing – review and editing.

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#### 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 Zenodo at [10.5281/zenodo.15625609](https://doi.org/10.5281/zenodo.15625609).

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### Supporting Information

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