Arctic Science

OPEN ACCESS | Research Article

Carbon and nitrogen stocks and distributions associated with different vegetation covers and soil profiles in Abisko, northern Sweden

Hugo M.G. Potier[a,b], **Xavier Raynaud**[a], **Yannick Agnan**[c], **Alienor Allain**[b], **Maryse Castrec-Rouelle**[b], **Veronique Vaury**[a], **Luc Abbadie**[a], **and Marie A. Alexis**[b]

[a]Sorbonne Université, Université Paris-Cité, Université Paris-Est Créteil, CNRS, IRD, INRA, Institute of Ecology and Environmental Sciences – Paris, 4 place Jussieu, 75005, Paris, France; [b]Sorbonne Université, CNRS, EPHE, UMR METIS, 4 place Jussieu, 75005, Paris, France; [c]Earth and Life Institute, Université catholique de Louvain, 1348 Louvain-la-Neuve, Belgium

Corresponding author: **Xavier Raynaud** (email: xavier.raynaud@sorbonne-universite.fr)

Arctic Science Downloaded from cdnsciencepub.com by 91.86.0.77 on 12/05/25

Abstract

The composition of vegetation cover in Arctic environments is evolving due to climate change. This study focused on estimating carbon and nitrogen stocks in vegetation and soil for different Arctic habitats (i.e., sub-ecosystem environments) with contrasted plant communities and soil profiles, to better understand the spatial variation of these stocks and the relationships between aboveground vegetation and soil characteristics in these environments. Vegetation composition and soil characteristics were measured in different habitats in a mire and a heathland ecosystem in northern Sweden. Multivariate analyses were used to define dominant vegetation and soil profile types, and carbon and nitrogen stocks were computed and compared across these types. Shrub-dominated and graminoid-dominated vegetation types presented similar carbon stocks but different nitrogen stocks, and shrub-dominated environments presented significantly higher proportions of their stocks distributed in the long-lived (i.e., woody) compartment. Soil stocks varied considerably between ecosystems. However, no clear relationships could be established between current vegetation community composition and soil carbon and nitrogen stocks across environments. The increase in shrub or graminoid abundance may affect carbon and nitrogen cycles most through biomass distribution between plant compartments rather than through the absolute stocks they represent. Ultimately, in Arctic and subarctic ecosystems experiencing climate change, the interactions between plant biomass composition and soil characteristics could have contrasted consequences for ecological functioning and C and N cycles.

Key words: carbon stock, nitrogen stocks, vegetation community, soils, Arctic, long- and short-lived compartment

Introduction

Arctic environments are undergoing significant changes due to rising temperatures, increased precipitation, and permafrost thaw (IPCC 2021). At the large scale, forest cover is expanding northward (Holtmeier and Broll 2007) and is preceded by an increase in the proportion of shrub and dwarf shrub species in plant communities, leading to an ecosystem "greening" that is visible from circumpolar satellite observations (Berner et al. 2020). However, the extent of this overall "shrubification" of Arctic environments is highly controlled by environmental conditions such as topography or the presence of permafrost (Heijmans et al. 2022), which may favour graminoid species (grasses and sedges) at the local scale (Mekonnen et al. 2021*a*) due to increased soil moisture. As vegetation cover and plant functional types (PFTs) are strong primary drivers of soil profile development and nutrient stocks through litter fluxes, additional knowledge is needed to better understand vegetation–soil interactions regarding carbon (C) and nutrient cycles (Mekonnen et al. 2021*b*).

Interactions between vegetation composition and climatic conditions have various consequences on the ecological functioning of Arctic ecosystems (Loranty et al. 2018). For instance, the cover of shrub species has been reported to increase snow cover depth during winter, which increases soil temperature due to the snow insulation effect (Zhang 2005). In tundra heaths and meadows, this increase has been found to promote nitrogen (N) mineralisation and availability in soils (Schimel et al. 2004; Semenchuk et al. 2015). This increased N availability in turn promotes plant and microbial growth, increasing total biomass and carbon sequestration in aboveground biomass and soils (Shaver et al. 1992; Jonasson et al. 1999). In other ecosystems, such as mires, deepened snow cover has also been shown to limit the decrease in soil temperature during winter, promoting permafrost thaw and thermokarst processes (Johansson et al. 2013). Subsequently,

Arctic Science Downloaded from cdnsciencepub.com by 91.86.0.77 on 12/05/25

soil subsidence and increased soil moisture have been found to favour graminoid species and led to waterlogging and anaerobic conditions (Olid et al. 2020), decreasing oxidative degradation of organic matter and increasing methane production (Johansson et al. 2006; Holmes et al. 2022). These findings highlight the importance of considering the complex feedback processes between vegetation dynamics and environmental functions affecting ecosystem trajectories and responses to climate change (Loranty et al. 2018).

From a biogeochemical perspective, in contrast to non-woody species, woody species have two aboveground biomass compartments with distinct dynamics: long-lived (branches) and short-lived (leaves). Thus, beyond a change in the woody:non-woody species ratio, variations in plant community composition also impact the long-lived:short-lived compartment ratio in aboveground biomass, which can affect the dynamics of ecosystem biogeochemical processes.

Wood and leaves, as well as leaves from woody and non-woody species, differ in their C:N ratio and organic composition (Preston et al. 2000; Allain et al. 2022), and are associated with different decomposition rates and residence time in the litter compartment (Preston et al. 2000; Cornelissen et al. 2007; Wilson et al. 2022). Variations of their fluxes to the soil have been shown to affect the composition of soil microbial communities (Eskelinen et al. 2009). Variations in other parameters, such as soil water content, anaerobic conditions, soil profile thickness, and summer and winter temperatures, could also affect biogeochemical processes in those environments and point toward a strong environment-dependant relationship between vegetation and soil C and N stocks (Pold et al. 2021).

The main objective of this study is to investigate the influence of vegetation cover composition on C and N stocks in the vegetation and the soil of different Arctic ecosystems. Vegetation inventories and measurements of soil characteristics were conducted in various Arctic habitats (i.e., sub-ecosystem environments presenting homogeneous plant communities and soil characteristics at the local scale) across a mire and a heathland in Northern Sweden. Carbon and nitrogen were then estimated in the vegetation and the soil of each habitat to (1) evaluate how variations in vegetation cover composition affect the aboveground biomass and stock of this vegetation, and its distribution between plant compartments; (2) investigate the relationship between vegetation cover composition and soil stocks. More specifically, multivariate analyses were performed to identify vegetation cover and soil profile groups across the different inspected habitats and to explore the relationships between vegetation composition, soil characteristics, and vegetation and soil C and N stocks. The hypotheses were made that (a) different vegetation covers are associated with different aboveground biomass and stocks and contrasted distribution of these stocks between plant compartments, and (b) soil and vegetation C and N stocks are correlated through the influence of litter composition and soil moisture effects on soil organic matter degradation. Based on those results, consequences of vegetation changes are discussed regarding C and N biogeochemical cycles in Arctic ecosystems.

Materials and methods

Study area

The study area was located in the Abisko region, northern Sweden, and included various Arctic ecosystems (Fig. 1). Two study sites with contrasted biotic (vegetation cover) and abiotic (altitude, topography, and hydrological dynamics) properties were considered. The first site is a mire ecosystem located in the Storflaket mire complex on the south shore of Lake Torneträsk (68°34′N, 18°97′E; 360 m a.s.l, ~5 ha), in the zone of discontinuous permafrost, with a peat layer underlined by glacial sedimentary deposits and an active layer of 60–80 cm average thickness (Olid et al. 2020). The second site is a heathland ecosystem southwest of the Báddosdievvá hill (68°31′N, 18°86′E; 600 m a.s.l, ~25 ha) with shallow soils on top of metamorphic bedrocks (Agnan et al. 2019). Each site was divided into different habitats based on vegetation composition, microtopography, and the presence of free water to encompass within-site heterogeneity (see Fig. 1 for photographs of ecosystems and habitats).

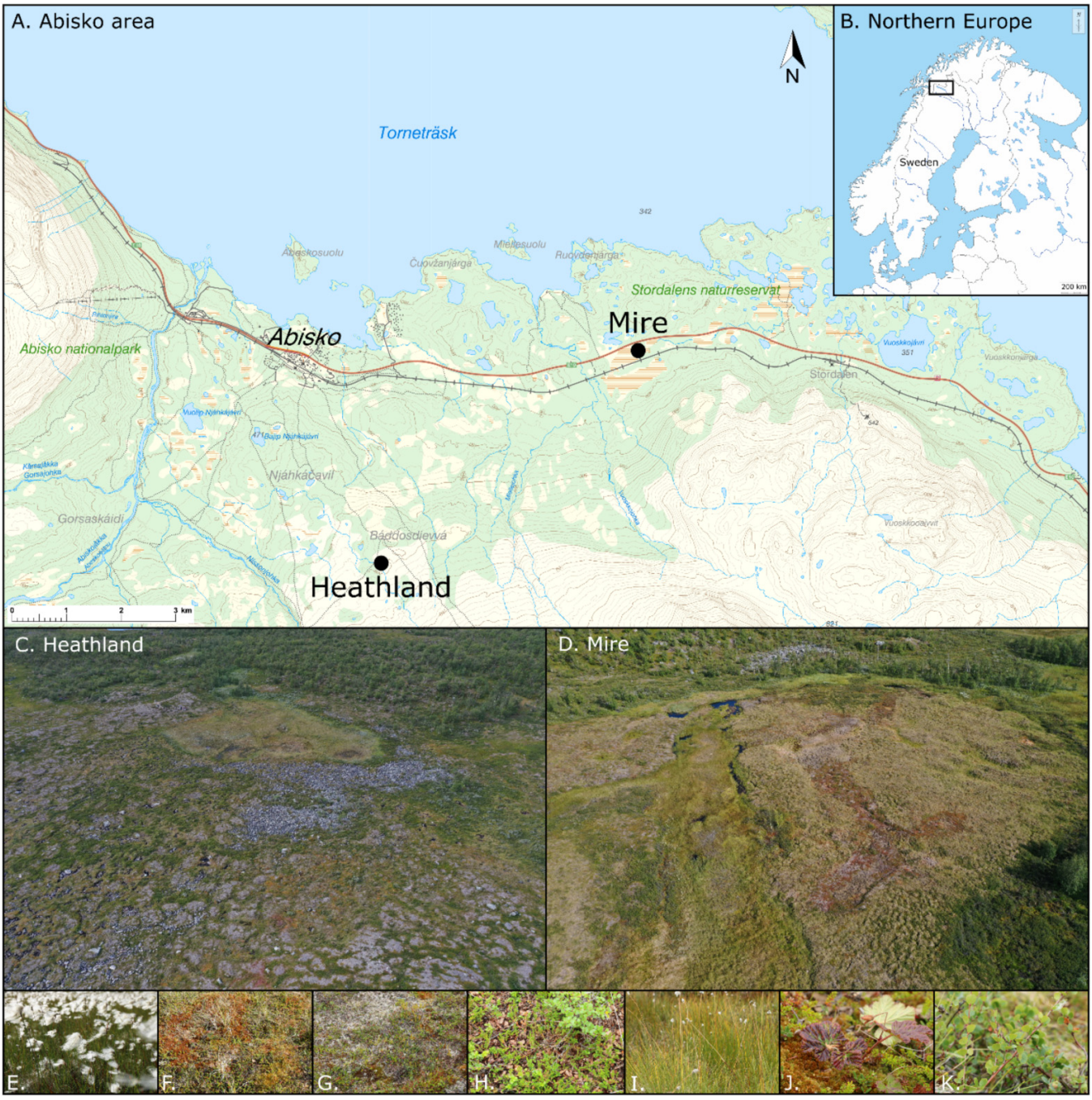
The mire ecosystem was divided into three habitats: (1) a palsa, corresponding to the uplifted part of the mire and dominated by dwarf shrubs, including *Betula nana*, *Empetrum nigrum*, *Vaccinium uliginosum*, as well as patches of the forb *Rubus chamaemorus*; (2) a bog, corresponding to a series of hollows in the palsa, filled with stagnant water (ombrotrophic) and presenting a developed cover of *Sphagnum* sp. and the graminoid *Eriophorum vaginatum*; and (3) a fen corresponding to the lower part of the mire, characterised by the presence of free water and dominated by large aquatic graminoid species such as *Carex rostrata* and *Eriophorum angustifolium*.

Similarly, the heathland ecosystem was divided into four habitats: (1) a wet-heath habitat characterised by some areas of free water and the graminoid species *C. rostrata* and *Eriophorum angustifolium*; (2) a humid-heath habitat dominated by a mixture of small dwarf shrubs, and important surfaces covered by *Sphagnum* sp. and other mosses; (3) a dry-heath habitat with a more developed cover of dwarf shrubs dominated by *B. nana*, *E. nigrum* and *V. uliginosum*; and (4) a birch forest habitat exhibiting a developed ground-level cover of dwarf shrubs similar to the one found in the dry-heath, except that in more open areas *Vaccinium vitis-idaea* was found in place of *V. uliginosum*, and a tree-layer of around 2 m high *Betula pubescens* subsp. *czerepanovii*.

Vegetation characterisation and sampling

Vegetation composition was characterised, and vegetation and soil samples were collected in both ecosystems at the peak of the growing season, at the beginning of August 2021 and 2022. Sampling was conducted in accordance with all applicable laws, guidelines, and regulations. Within each ecosystem, vegetation composition was measured in 1 m × 1 m quadrats, randomly distributed across the different habitats. In the mire, five quadrats were placed in each habitat (palsa, fen, and bog). In the heathland, 20 quadrats were distributed across the wet-heath ($n = 5$), humid-heath ($n = 5$), and dry-heath habitat ($n = 10$) continuum to

Fig. 1. Location of the two study sites (mire and heathland) near Abisko (A), in Northern Sweden (B). Aerial photographs of the mire (C) and the heathland (D) ecosystems and close-up photographs of the ground-level vegetation of their different habitats: wet-heath (E), humid-heath (F), dry-heath (G), and birch forest (H); fen (I), bog (J), and palsa (K) habitats in the mire. Map courtesy of the Geological Survey of Sweden (http://www.sgu.se).



encompass the heterogeneity of the vegetation, and each quadrat was latter attributed to a specific habitat based on its vegetation cover. Ten quadrats were distributed in the birch forest understorey to cover its larger geographical extent. In each quadrat, the surface cover of each ground-level species and non-vegetation surfaces (e.g., free water, rocks, and litter) was estimated visually (Daubenmire 1959). Identifications were performed at the species level for vascular plants and the family or genus level for mosses and lichens. The three to five most abundant species in each habitat were determined and referred to as "dominant species". Across all habitats, these dominant species are *B. nana*, *Empetrum nigrum*, *V. uliginosum*, *V. vitis-idaea*, *C. rostrata*, *E. angustifolium*, *E. vaginatum*, *R. chamaemorus*, *Sphagnum* sp., and "other mosses" (including *Polytricum* sp., *Dicranum* sp., or *Pleurozium* sp., depending on the habitat). Some of these species (e.g., *B. nana*) were found in all habitats, while other were found only in some habitats (e.g., *E. angustifolium* was only present in fen and wet-heath).

Arctic Science Downloaded from cdnsciencepub.com by 91.86.0.77 on 12/05/25

Arctic Science Downloaded from cdnsciencepub.com by 91.86.0.77 on 12/05/25

Aboveground biomass of these dominant species was sampled at all habitats in which they were present to obtain C and N content. For mosses, only the living parts of mats and living stems were included in the aboveground biomass based on visual inspection. In each habitat, one of the quadrats was also clipped entirely to the ground to measure the aboveground biomass of the whole vegetation cover.

Surface cover (visual estimation) and aboveground biomass data (clipping) were also measured in 28 additional quadrats to establish cover-to-biomass allometric relationships for the overall 10 dominant species across all habitats. Species-specific mass ratios were also established for the ligneous dwarf shrub species (*B. nana*, *E. nigrum*, *V. uliginosum*, and *V. vitis-idaea*) to separate the total aboveground biomass into short- (leaves) and long-lived (branches) compartments. More information regarding allometric equations can be found in Supplementary I.

Trees were inventoried in two randomly placed 10 m × 10 m plots in the birch forest next to the heathland. Trees were categorised into small living trees (<1.3 m), tall living trees (>1.3 m), snags (>1.3 m), and stumps (<1.3 m) based on height. Ground-level diameter and diameter at breast height (DBH; i.e., 1.3 m above ground level, only for living trees) were measured. Multiple stems from polycormous individuals were considered distinct individuals for biomass estimations.

Soil sampling and characterisation

Soils were sampled as close to each vegetation quadrat as possible using a stainless-steel auger and a knife (total $n = 39$) at the same time as vegetation sampling and without large precipitation events occurring during this period. When present, litter and living parts of moss mats were carefully removed before sampling and were not included in our analysis. Soil sampling was conducted throughout the total soil depth in the heathland ecosystem (i.e., down to the bedrock, at 10 cm in the dry-heath and 85 cm in the wet-heath), but was limited to the active layer in the mire (45 cm deep in the palsa and 1 m deep in the bog). Soils of the fen and one wet-heath sample point were not sampled because the water table level was higher than ground level. For each soil sampling, two different horizon types were identified based on visual inspection: (1) a "surface" horizon with partially decomposed organic matter and little mineral influence, which included belowground biomass; and (2) a "deep" horizon, located below, with well-decomposed organic matter (for saturated soils) and a more substantial proportion of coarse mineral particles (for drier soils), and little to no belowground biomass. The thickness of each horizon was measured and each horizon, visually homogeneous, was sampled independently for elemental content and moisture content measurements.

Each soil sample was analysed for C and N content, and soil moisture content was measured by the mass difference after drying at 60 °C for over 48 h. Bulk soil density was estimated for surface and deep horizons using a photogrammetry method for some selected habitats in August 2022 (Coulouma et al. 2021). Briefly, this method consists in carefully digging three holes in each horizon and modelling the volume of each hole from a series of 20 pictures taken from different angles before and after the digging. Volume estimations were performed using CloudCompare 2.12.4 (http://www.cloudcompare.org/) after 3D modelling each hole using PhotoScan 1.2.6 (Agisoft LLC, St. Petersburg, Russia), and the extracted soil was weighed after >48 h drying at 105 °C. Masses and volumes were corrected for coarse mineral particles after sieving at 2 mm (considering a standard mineral particle density of 2.6 g cm^{-3}), and bulk soil densities were computed. The photogrammetric method for bulk density measurements is not applicable to saturated soil profiles because it needs the soil to keep its structure and the water table not to be higher than soil level. Thus, those bulk density estimations were limited to the palsa, humid-heath, dry-heath, and forest understorey habitats, and bulk densities of bog and wet-heath habitats were attributed to each horizon based on similarity in soil characteristics with measured horizons (depth, soil moisture, and lithogenic influence), and were used to compute soil stocks. For three sampled points, no deep horizon could be properly identified and were not sampled. The mean soil characteristics and stocks of their habitat's deep horizons were later attributed to those missing horizons for statistical analysis.

Sample preparation and elemental content measurements

Biomass samples were dried at 60 °C for at least 48 h and ground to <250 μm using a grinder (ultra-centrifugal mill ZM200, Retsch, Haan, Germany). Leaves and branches of dwarf shrubs were ground and analysed separately to separate short-lived and long-lived compartments, and the aboveground biomass was ground as a whole for other species. Soil samples were dried at 60 °C for several days and then ground at <250 μm using a soil grinder (planetary ball mill PM200, Retsch, Haan, Germany). Before grinding, deep horizons were sieved at <2 mm to remove coarse mineral particles, while surface horizons were coarsely blended (Blender 8010 EB, Waring Commercial, Stamford, CO, USA) due to their high content in partially decomposed organic material and root biomass. Belowground biomass was not sieved out and is thus included in soil stocks, mainly in the surface horizon.

Carbon and N content of vegetation and soil samples was measured using elemental analysers (Elementar vario PYRO cube, Langenselbold, Germany and FlashHT Thermo Fisher Scientific, Billerica, MA, USA). Analytical standards were used every few samples to validate analytical accuracy and to ensure data comparability between analysers. The overall analytical precision was estimated at 0.3% for C content and 0.06% for N content.

Estimation of carbon and nitrogen stocks

To better compare habitats that displayed different proportions of unvegetated surfaces and to limit sampling bias (no quadrat was placed entirely on bare rocks or free water surfaces), the cover of plant species was rescaled as a proportion of the total vegetation surface of each quadrat (thus by removing the area covered by free water, bare rocks, and

Arctic Science Downloaded from cdnsciencepub.com by 91.86.0.77 on 12/05/25

litter). Aboveground biomass of the quadrat was estimated using the rescaled proportions of all species for which surface-to-biomass allometric relationships were established, i.e., for all dominant species across the habitats. Finally, total aboveground C and N stocks were computed for each quadrat using the estimated biomass and the measured elemental content per dry biomass of each dominant species. Those stocks, therefore, represent *aboveground stocks of dominant species* per *square meter of vegetation* and are given in mass per square meter (g m^{-2}). It is important to note that the aboveground stocks may contain species that were present but not particularly abundant in a quadrat if they were dominant in another habitat (see Supplementary material III Panel A.).

Living tree biomass was computed separately for each compartment (trunk, branches, and leaves) based on ground-level diameter or DBH and using allometric coefficients for *B. pubescens* subsp. *czerepanovii* at Abisko (Starr et al. 1998). Deadwood biomass was estimated using cylinder-like formulas based on heights and estimated diameters to calculate volumes and by applying a density of 0.2746 g cm^{-3} (Swedish National Forest Inventory; Sandström et al. 2007). Tree and deadwood biomass were then converted into C and N stocks per square meter (g m^{-2}) using mean contents of 49.4% and 1.6%, respectively, for both wood and deadwood (Matthews 1993) and 48.53% and 2.0%, respectively, for leaves (data acquired in this study). Details regarding tree biomass estimations can be found in Supplementary II.

Total soil C and N stocks (kg m^{-2}) were calculated for each sample point ($n = 39$) as the sum of surface and horizon stocks, each estimated from their individually measured thickness and elemental content, and a horizon-specific bulk density measurement or estimate for the habitat.

Statistical analysis

All statistical analyses were performed using R 4.0.5 (R Core Team 2021). Principal component analyses (PCAs) were performed on centred and scaled variables using the *ade4* package (Dray and Dufour 2007) to compare vegetation cover (rescaled covers of dominant species) and soil characteristics (except for bulk density data, which could not be measured for each habitat). Non-hierarchical K-means clustering method was used to identify dominant vegetation types and soil profile types across the different habitats from PCAs. Based on the Kaiser criterion (eigenvalue > 1 threshold), only the first three and the first two principal components (PCs) for vegetation cover and soil characteristics, respectively, were considered and retained for clustering. Optimal number of clusters was visually determined using average silhouette and gap statistic methods from the *factoextra* package (Kassambara and Mundt 2022). It was determined to be four and two for dominant vegetation and soil profile types, respectively. A co-inertia analysis was performed between the vegetation and soil PCAs to explore the links between vegetation covers and soil characteristics using the *ade4* package. The significance of the RV coefficient was determined based on a Monte-Carlo test on the sum of eigenvalues of the co-inertia analysis.

Comparisons of elemental stocks between dominant vegetation types and soil profile types were carried out using one-way ANOVAs and comparisons of soil characteristics between soil profile types using student *t* tests. Beta-regressions (*betareg* package, Cribari-Neto and Zeileis 2010) were used to compare stock distributions between long- and short-lived plant compartments across dominant vegetation types. Tukey's honestly significant differences post-hoc test at $p = 0.05$ was applied to determine the significant differences among habitats. Means reported in the text are given ± standard error of the mean.

Results

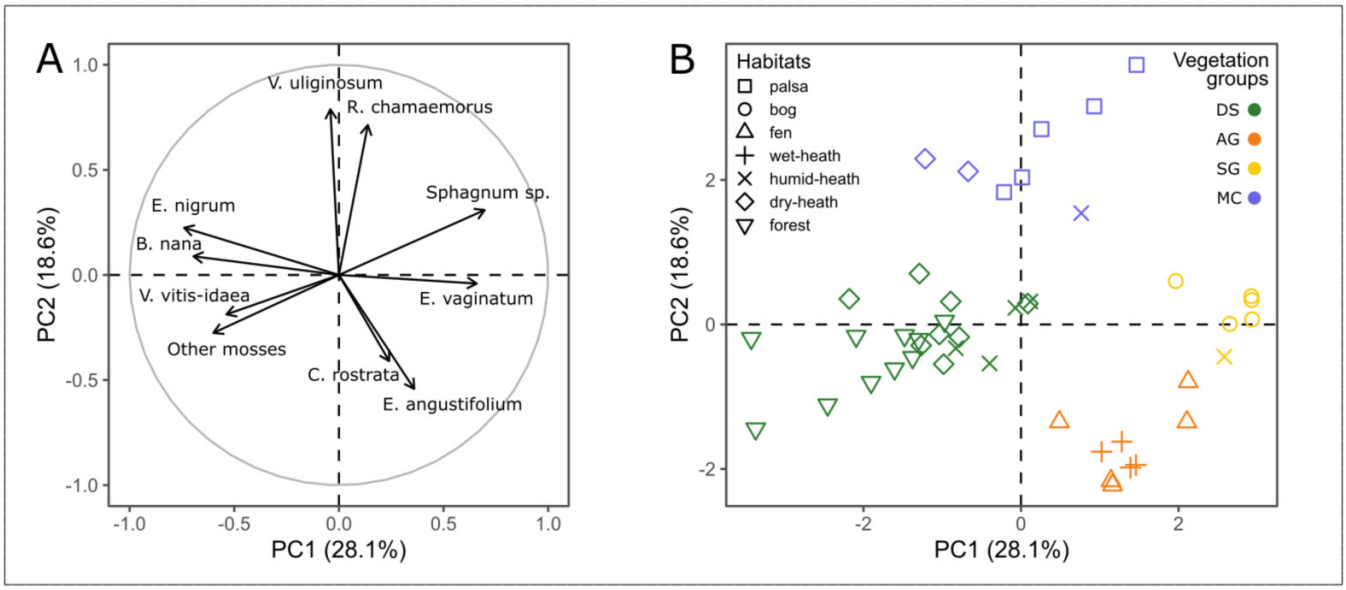
Dominant vegetation types across habitats

A PCA was performed using the scaled vegetation cover to delimit dominant ground-level vegetation groups across the different habitats. The first three PCs explained 60.7% of the data variance. Figure 2 shows the biplot of variables (species covers) and observations (vegetation quadrats) for the first two principal axes. The first PC (28.1% of the data variance) separated *B. nana*, *E. nigrum*, and *V. vitis-idaea* covers from *E. vaginatum* and *Sphagnum* sp. covers, and thus separated humid- and dry-heath from bog habitats (PC1). The second and third PCs (18.6% and 14.0%, respectively) separated *C. rostrata* and *E. angustifolium* from *V. uliginosum* and *R. chamaemorus* (PC2) and from *E. vaginatum* and *Sphagnum* sp. covers (PC3, not shown), and separated fen and wet-heath habitats from the bog and from the palsa habitats (Fig. 2A). K-means clustering on the three PCs identified four different dominant vegetation groups (hereafter referred to as "types"), associated with contrasting dominant species cover across the two ecosystems and the seven habitats (Fig. 2B): a first type characterised by a developed dwarf shrub cover (DS) of *B. nana*, *E. nigrum*, and *V. vitis-idaea*; a second type with important aquatic graminoid covers (AG) of *C. rostrata* and *E. angustifolium*; a third type characterised by sphagnum and small graminoid (*E. vaginatum;* SG); and a fourth type with a mixed cover (MC) of dwarf shrubs, sphagnum, and small graminoids. These types mostly included all quadrats from the same type of habitat, but grouped together habitat types from different ecosystems (e.g., dry-heath and palsa, wet-heath and bog).

Aboveground vegetation stocks and distribution between plant compartments

Aboveground biomass varied from 283.1 + 26.3 g_{DW} m^{-2} in MC to 306.1 ± 35.1 g_{DW} m^{-2} in DS but did not significantly differ across the dominant vegetation types (global average of 297 ± 18.0 g_{DW} m^{-2}; $F = 0.08$, $p > 0.5$). Similarly, carbon stocks associated with those covers varied from 130.5 ± 10.6 g_C m^{-2} in SG to 161.8 ± 19.0 g_C m^{-2} in DS, with a global average of 148.6 ± 9.8 g_C m^{-2}, but no significant differences were detected between the different dominant vegetation types ($F = 0.60$, $p > 0.5$; Fig. 3A). In contrast, nitrogen stocks did vary significantly between dominant vegetation types, from 3.0 ± 0.3 g_N m^{-2} in DS to 4.3 ± 0.2 g_N m^{-2} in AG ($F = 3.20$, $p = 0.033$; Fig. 3C, capital letters), as a result of aquatic graminoid species presenting higher nitrogen

Fig. 2. Principal component analysis of dominant species cover across different mire and heathland habitats in the Abisko area, Sweden: representation of principal component (PC) 1 versus 2 (A) and representation of observations by habitat (symbols) and dominant vegetation groups (colours) determined using the K-means clustering method (B). In (A), variables are rescaled surfaces of each dominant species. In (B), DS = dwarf shrubs; AG = aquatic graminoids; SG = sphagnum and small graminoids; MC = mixed cover.



content than small graminoids, mosses, and dwarf shrub overall biomass (t tests, $p < 0.01$). Moreover, C and N stock distribution between compartments differed significantly between dominant vegetation types ($\chi^2 > 110$, $p < 0.001$ for both C and N): less than 2% of the total carbon and 1% of total nitrogen was stored in long-lived compartments in both AG and SG, compared to 30% and 18% in MC and more than 40% and 25% in DS, for C and N, respectively (Figs. 3A and 3C, lowercase letters).

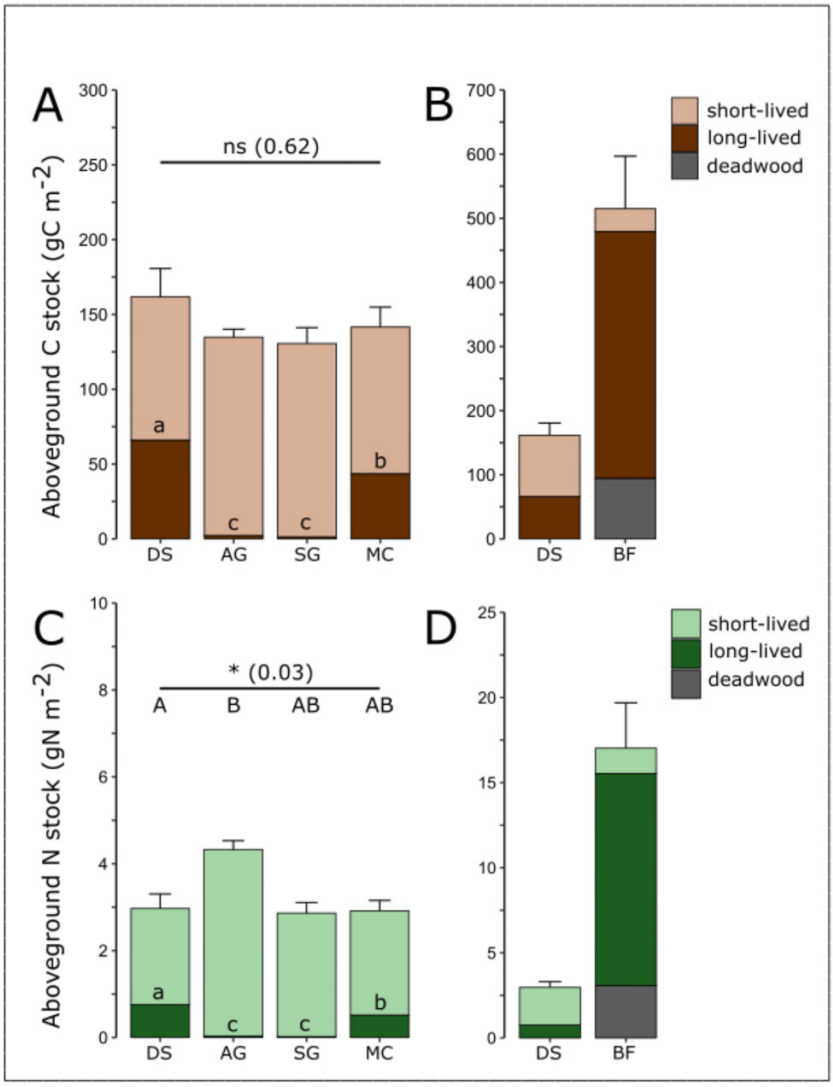
Compared to the DS vegetation type (which includes all understorey quadrats from the birch forest habitat), total C and N stocks in the birch tree layer were twice and five times higher, respectively, with 515.0 ± 27.3 g_C m^{-2} and 17.0 ± 0.89 g_N m^{-2} on average (Figs. 3B and 3D). The stock distribution pattern between plant compartments was also very contrasted: the long-lived compartment (i.e., stem, branches) represented up to 92% and 89% of the total C and N stocks of living trees, respectively. Deadwood biomass represented a stock of 94.6 ± 49.2 g_C m^{-2} and 3.07 ± 1.59 g_N m^{-2} on average, mainly in the form of snags that accounted for about 85% of C and N deadwood stocks.

Soil profile types and classification

A PCA was performed on soil characteristics to identify covariance between horizon characteristics and to determine soil profile groups (therefore referred as "types") across the dataset. The first two PCs explained 67.9% of the total variance and were both kept for visual representation (Fig. 4). The first PC (50.8% of total variance) grouped depth and moisture of both surface and deep horizons and both C and N content of the deep horizon. In contrast, the second PC (17.1%) grouped C and N content of the surface horizon (Fig. 4A). K-means clustering using the first two PCs distinguished two groups of soil profiles (hereafter referred to as "types"). These soil profile types mostly grouped soils from the same ecosystem, thus contrasting mire soil profiles against heathland soil profiles, with the exception of all wet-heath and two humid-heath soil profiles that grouped with mire soils (Fig. 4B). The first type (type 1) exhibited a shallow profile (14.0 ± 1.4 vs. 69.3 ± 8.7 cm; $t = -6.30$, $p < 0.001$) whose depth was mostly limited by the bedrock, with surface and deep horizons drier than the other soil profile type (surface: 2.0 ± 0.3 vs. 7.4 ± 1.1 g g_{DW}^{-1}; $t = -4.95$, $p < 0.001$; deep: 0.5 ± 0.2 vs. 3.0 ± 0.4 g g_{DW}^{-1}; $t = -4.95$, $p < 0.001$). Type 2 soil profiles corresponded to deeper and wetter profiles. Consistent with the heterogeneous nature of the soil profiles across the investigated area, carbon (5.0 ± 1.4 vs 32.5 ± 3.1%; $t = -8.16$, $p < 0.001$) and nitrogen (0.19 ± 0.05 vs 1.69 ± 0.20%; $t = -6.99$, $p < 0.001$) content of the deep horizon also distinguished the two soil profiles, separating mineral (mean C content <5%, type 1) from organic (mean C content >5%, type 2) deep horizons. This difference is consistent with the average bulk density of 0.84 ± 0.09 and 0.22 ± 0.06 g cm^{-3} measured in type 1 and type 2 deep horizons, respectively. In contrast, C and N content in surface horizons of the two soil profile types were not significantly different (40.0 ± 1.1 and 1.54 ± 0.09%; $t = -1.61$ and $t = 0.50$, both $p > 0.1$ for %C and %N, respectively).

Arctic Science Downloaded from cdnsciencepub.com by 91.86.0.77 on 12/05/25

Fig. 3. Carbon (A and B) and nitrogen (C and D) total stocks and their distributions between short-lived and long-lived compartments for the different dominant vegetation types identified using K-means clustering (Fig. 4B) in the Abisko area, Sweden, for ground-level vegetation (A and C) and dwarf shrub vegetation type (representing the birch forest understorey) versus birch tree layer (B and D). Note the different *y*-axis scales between ground-level and tree stocks. The birch forest tree layer includes standing deadwood stock estimations. The "long-lived" compartment corresponds to woody biomass (dwarf shrubs branches and twigs), and the "short-lived" to non-woody biomass (i.e., leaves of dwarf shrubs and overall biomass of graminoid, forb, and moss species). Different capital letters indicate significant differences in total elemental stocks between dominant vegetation types. Different lowercase letters indicate significant differences between dominant vegetation types in long-lived to short-lived stock proportions. Error bars represent standard errors of the mean for total aboveground stocks. DS = dwarf shrubs; AG = aquatic graminoids; SG = sphagnum and small graminoids; MC = mixed cover; BF = birch forest.



Soil total C and N stocks and distribution between horizons

Total soil C and N stocks were both significantly different between soil profile types ($t = 40.88$ and $t = 29.97$, both $p < 0.001$; Fig. 5, capital letters): mean C and N stocks are respectively 5.3 ± 1.0 kgC m^{-2} and 0.22 ± 0.05 kgN m^{-2} for soil profile type 1 and 27.5 ± 4.2 kgC m^{-2} and 1.37 ± 0.26 kgN m^{-2} for soil profile type 2. In contrast, soil mass per square meter did not vary significantly between the two (average of 74.4 ± 0.99 kg m^{-2}, $t = -0.04$, $p > 0.5$). The stock distribution between surface and deep horizons did not vary significantly between soil profile types, with an average of 64% of carbon and 72% of nitrogen distributed in the deep horizon ($\chi^2 = 2.82$, $p > 0.1$ and $\chi^2 = 1.6$, $p = 0.09$). Soil C and N stocks were 1 (type 1) and 2 (type 2) orders of magnitude greater than mean aboveground vegetation stocks.

Links between vegetation and soil stocks

Finally, a PCA was performed on C and N stocks in aboveground vegetation and soils and their distribution between plant compartments (% in the long-lived) and soil horizons (% in the deep horizon). The first three PCs explained 89.9%

Arctic Science Downloaded from cdnsciencepub.com by 91.86.0.77 on 12/05/25

Fig. 4. Principal component analysis of soil characteristics, by horizons, of different mire and heathland habitats in the Abisko area, Sweden: representation of principal component 1 versus 2 (A) and representation of observations by habitat (symbols) and soil profile groups (colours) determined using a K-means clustering method (B). All fen habitat stocks and one wet-heath habitat stock were not estimated because the water table level was higher than ground level and are therefore not included. In (A), "S" refers to the surface horizon and "D" to the deep horizon; "depth", "moisture", '%N', and "%C" variables are, respectively, the horizon depth, water content, nitrogen content, and carbon content.

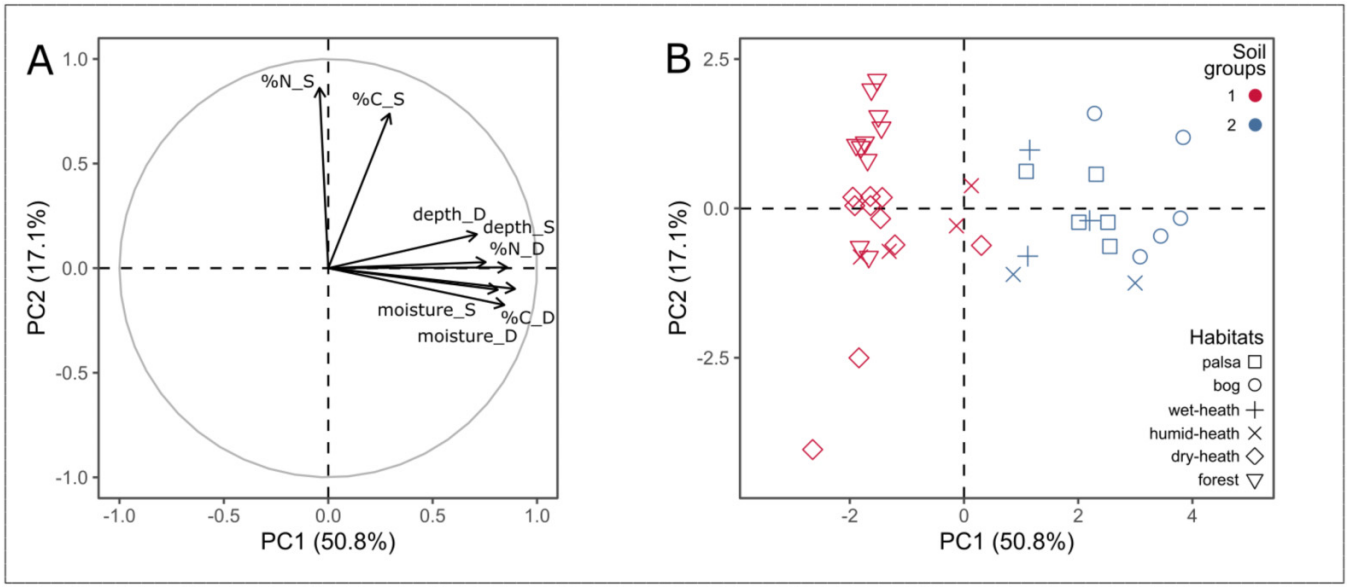
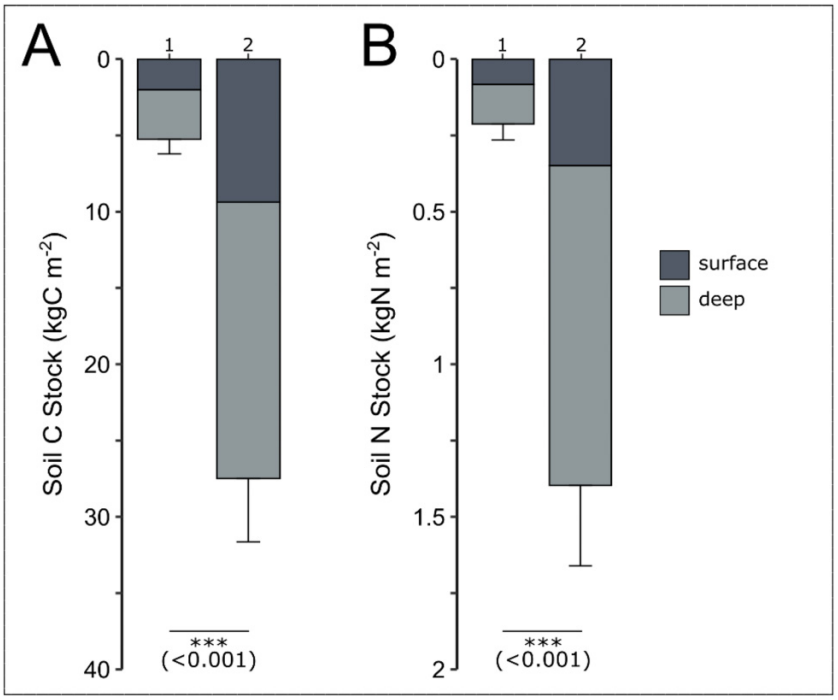


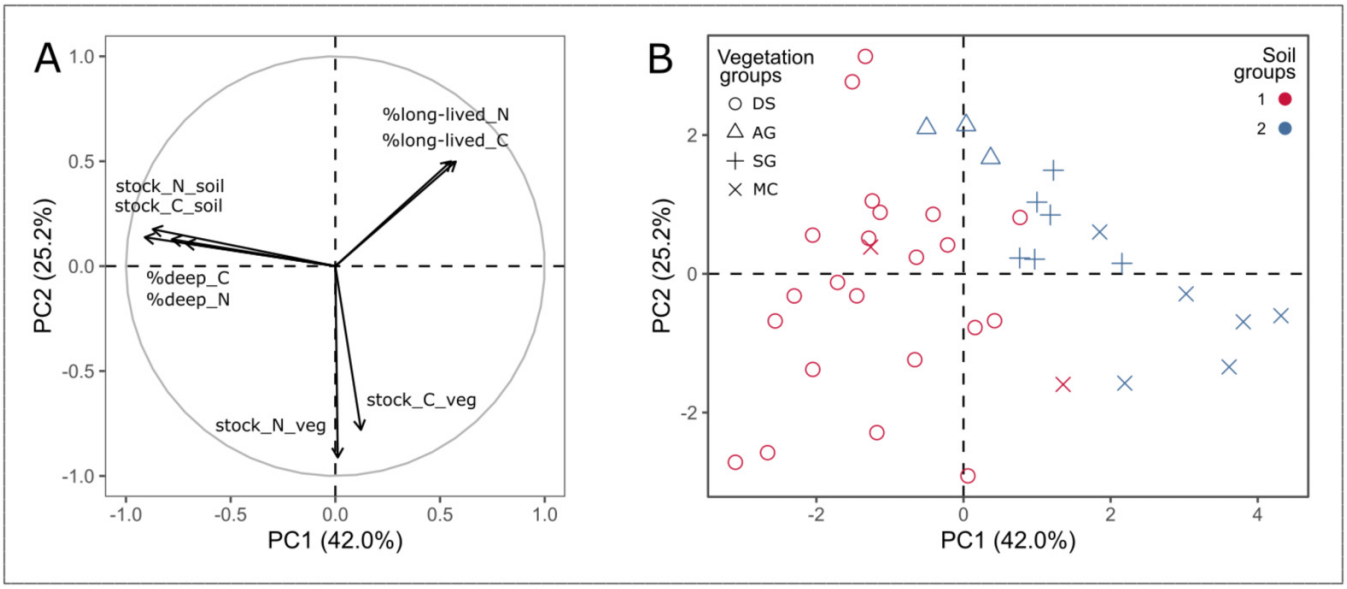
Fig. 5. Carbon (A) and nitrogen (B) stock distributions between surface and deep horizons for the two different soil profile types identified using K-means clustering (Fig. 4B) in the Abisko area, Sweden. Error bars represent standard errors of the mean.



of the total variance. The first PC (42% of the data variance) was strongly driven by total C and N soil stocks and their distribution in the deep horizon (negative scores, Fig. 6A), clearly separating the two soil profile types (Fig. 6B). The second PC (25.2%) grouped both nitrogen and carbon stocks in the vegetation (negative scores, Fig. 6A). However, it did not seem to separate the different dominant vegetation types (Fig. 6B). Vegetation stocks and their distribution between compartment presented contrasted behaviour, from negatively covarying in the PC2 to positively covarying in the PC3

Arctic Science Downloaded from cdnsciencepub.com by 91.86.0.77 on 12/05/25

Fig. 6. Principal component analysis (PCA) of carbon and nitrogen stocks in the aboveground vegetation and the soil profile of different mire and heathland habitats in the Abisko area, Sweden: representation of principal component 1 versus 2 (A) and representation of observations by vegetation groups (symbols) and soil profile types (colours), both determined using clustering methods (B). The PCA did not include all fen habitat stocks and one wet-heath habitat stock due to the lack of soil stock estimations. In (A), "stock_N_soil" and "stock_C_soil" variables are total carbon and nitrogen stocks in soils (both horizons); "stock_N_veg" and "stock_C_veg" variables are total carbon and nitrogen stocks in vegetation (both compartments); "%deep_C" and "%deep_N" variables are, respectively, the proportions of soil total carbon and nitrogen stocks in the deep horizon; "%long-lived_C" and "%long-lived _N" variables are, respectively, the proportions of vegetation total carbon and nitrogen stocks in the long-lived compartment. In (B), DS = dwarf shrubs; AG = aquatic graminoids; SG = sphagnum and small graminoids; MC = mixed cover.



(not shown). Across the three PCs, soil stocks and vegetation stocks were always independent (orthogonality).

Discussion

Variations in vegetation cover composition and associated stocks across habitats

Dominant plant species formed four distinct vegetation types characterised by contrasted PFTs across habitats (Fig. 2), from graminoid and mosses-dominated vegetation covers (AG and SG) to dwarf shrub-dominated ones (DS and MC). This classification separated the three field-identified mire habitats that reflect permafrost degradation (Christensen et al. 2004; Johansson et al. 2013) but grouped together different heathland habitats which, for instance, presented a cover dominated by dwarf shrubs. The classification also grouped together habitats belonging to different ecosystems but presenting similar soil characteristics, such as soil moisture, that differed between dominant vegetation types (4.17 and 2.05 g g_{DW}^{-1} for AG and MC, respectively, $p < 0.001$) and could be related to microtopography (Peterson and Billings 1980). Those results indicate that PFT can be used to define dominant vegetation types at larger scale than habitats (Sulman et al. 2021). However, although the vegetation composition could be linked to local soil characteristics (co-inertia RV coefficient = 0.63 between the two datasets, $p = 0.01$), habitat vegetation composition does not appear to effectively represent large-scale ecosystem properties, such as watershed geomorphology, that have been shown to drive vegetation composition in other environments, such as semi-arid riparian habitats (Engelhardt et al. 2012). This result could be explained by the strong hydric and thermal constraints that primarily drive the composition of vegetation cover and would mask the effect of large-scale properties that have been observed in less constrained environments.

Variations in plant community composition did not lead to significant variations of the aboveground C stocks, and only covers dominated by aquatic graminoids had higher N stocks than dwarf shrub-dominated covers (Fig. 3). These stock estimations are lower than some reported estimations for similar covers presenting greater total biomass (Baillargeon et al. 2022). The higher plant C and N stocks assessed in this work compared to similar covers in Greenland (Arndal et al. 2009) and to older observations in Northern Canada (Camill et al. 2001) could be explained by the seasonal variability (Arndal et al. 2009) and the differences in plant growth parameters, such as warmer growing season that enhance primary productivity (Pold et al. 2021). The absence of significant differences in vegetation C stocks was expected, given the similar aboveground biomass found between vegetation types and the low variations in C content across dominant species and plant compartments (Ma et al. 2018). On the other hand, the higher N stock in the AG cover could reflect the intrinsic higher N

Arctic Science Downloaded from cdnsciencepub.com by 91.86.0.77 on 12/05/25

content of aquatic graminoid species, as well as the higher N soil availability to plants due to nitrogen release from thawing permafrost (Keuper et al. 2012; Fouché et al. 2020).

Variations in stock distribution between plant compartments across vegetation covers

As expected, the distribution of the overall C and N stocks between plant compartments varied considerably between different dominant vegetation types, with increasing C and N stocks found in long-lived (i.e., woody parts) along the increase in the dominance of dwarf shrub (from AG or SG, to MC and DS, Fig. 3). With similar total stocks between these vegetation covers, the higher proportion of long-lived biomass therefore represents lower annual litter fluxes to the soil and variations in the overall chemical composition and stoichiometry of the litter (higher lignin:cellulose and C:N, Preston et al. 2000; Allain et al. 2022), which may be related to slower C and N cycling in dwarf shrub-dominated ecosystems. It should be noted that part of the short-lived compartment in this study includes biomass that are cycled over more than one season. For example, graminoids and evergreen leaves have turnover times of 1.3–1.7 and 2.1–3.3 years, respectively (Shaver and Chapin 1991), and moss biomass has been reported to have slow decomposition dynamics in Arctic ecosystems (Cornelissen et al. 2007; Aerts et al. 2009). However, short-lived biomass is still expected to have a higher cycling rate in the environment compared to the long-lived compartment (i.e., woody biomass). Similar to the higher dominance of dwarf shrubs at ground level, the consideration of the tree layer in the birch forest reinforced the higher distribution of stocks in the long-lived compartment (Fig. 3), which may further slowdown the C and N cycles in this habitat. Tree biomass was greater than in previous studies conducted in this area and seem to result from an increase in DBH and stand density. This result is consistent with previous increases reported for the period 1997–2010 (Hedenås et al. 2011) and follows the global pattern of treeline advancement and subsequent stand densification observed in high-latitude ecosystems (Holtmeier and Broll 2007). Fallen dead trees, not considered in this work, have been shown to represent approximately 75% of the total deadwood biomass in other Arctic forests (Paletto et al. 2021) and would have reinforced this distribution pattern as well.

Soil profiles and their related stocks across habitats

Soil classification separated deep and organic (type 2) from shallow and more mineral soil profiles (type 1), mainly contrasting the two broad ecosystem types examined in this study, dryer heathland and wetter peat-accumulating ecosystems (Fig. 4). We argue that this grouping illustrates current and historical functional differences between soil profiles. The organic-profile type groups historically (palsa) or still active (bog and wet-heath) peat-accumulative soil profiles in which anaerobic conditions caused by soil waterlogging limit organic matter degradation (Olid et al. 2020). In contrast, the mineral-profile type represents soils for which the organic horizon development is limited by unsaturated soil conditions that promote organic matter degradation, and where the mineral horizon accounts for a higher proportion of the sampled profile depth. This functional difference is particularly evident for C and N stocks, which were on average five times higher in the organic profiles (Fig. 5), despite the fact that both profile types have the same soil mass per surface unit, which is in part due to the shallow depths of the mineral soils in this field study. The emergence of this difference is particularly interesting given that the estimation of soil stocks was limited to the active layer in the peat bog and therefore does not include the entire soil profile down to the parent material. These results also suggest that, similarly to vegetation, soil stocks could be approached at a larger scale than habitats using soil characteristics such as soil moisture, which result from both large-scale and small-scale topography, and have been related to organic matter accumulation and soil profile development (Donnelly et al. 1990; Fang et al. 2022). However, the organic-profile type exhibited a high variability in C and N stocks that tended to separate palsa soil profiles with higher stocks from bog and wet-heath soil profiles with lower stocks (see Supplementary III). This variability seems to indicate that the current soil characteristics of these habitats, such as moisture content, do not fully reflect past soil functions that resulted in these C and N stocks.

Relationships between vegetation covers, soil profiles, and their related stocks

Despite the expected correlation between vegetation composition (four different dominant covers) and soil characteristics (two soil profile types) as shown by the co-inertia analysis, the co-occurrence of these features varied within the study area. For example, palsa and dry-heath habitats that both presented shrub-dominated covers (vegetation classification, Fig. 2) belonged to organic- and mineral-profile types, respectively (soil classification, Fig. 4). Similarly, organic-profile types regrouped palsa and wet-heath habitats that represented contrasting vegetation types. In both representations of those habitats, the significant differences in soil moisture between the vegetation and soil groups could be related to its control both over vegetation cover composition (Christensen et al. 2004; Van Der Kolk et al. 2016) and soil organic matter degradation (Olid et al. 2020).

Aboveground vegetation and soil stocks were independent of each other in the dataset (Fig. 6), a result unexpected given the importance of vegetation communities for soil profile development and soil stock through quality and quantity of the litter input (Jobbagy and Jackson 2000). This may have been due to the absence of significant variation in aboveground C stocks between vegetation covers and the lack of soil stock measurements from the fen habitat, which represented more than half of the AG vegetation type, which was the only type with significantly greater aboveground N stocks. However, fen stocks may be primarily driven by soil saturation and anoxic conditions limiting aerobic decomposition, rather than significantly different litter inputs, as suggested by the low dissolved oxygen and high dissolved methane emissions measured (data not shown) and reported for this habitat (Sjögersten et al. 2023). Nevertheless, the

Arctic Science Downloaded from cdnsciencepub.com by 91.86.0.77 on 12/05/25

Arctic Science Downloaded from cdnsciencepub.com by 91.86.0.77 on 12/05/25

independence between vegetation and soil stocks might also highlight a possible decoupling between vegetation composition and soil C and N sequestration. This decoupling could be attributed to the magnitude and timescale of vegetation and soil respective responses to environmental change, with vegetation dynamics responding faster (sub-decadal timescale; Heijmans et al. 2022) than even "fast" pedogenic processes controlling soil stocks (decennial to centennial timescales; Targulian and Krasilnikov 2007). Taken together, these results provide additional evidence for the strong environment-dependant relationship between vegetation and soil stocks (Pold et al. 2021) and point to the primary importance of considering soil profile characteristics when estimating soil stocks at large scales. They also suggest that approaches based on soil surface properties or vegetation cover, which are often used for remote areas where detailed survey maps are lacking, or for circumpolar scale studies, could lose this level of precision and should be considered accordingly when used for local scale estimates (Hugelius et al. 2013).

Implication of vegetation change on C and N biogeochemical cycles

Recent global modelling work has estimated that PFT shifts in vegetation communities would affect the strength of the C sink by an order of magnitude similar to future climate change in these ecosystems (López-Blanco et al. 2022). The results presented here show that, at the local scale, different PFTs are associated with different biomass distributions between plant compartments, but that their relationship with soil characteristics and stocks is unclear. Future climate change and associated changes in vegetation (Berner et al. 2013; Johansson et al. 2013) could therefore have contrasting local impacts on C and N cycling, particularly in the vegetation.

Specifically, this work highlights that the main effect of the observed shrubland expansion (Mekonnen et al. 2021*a*) is likely to be the increase in the long-lived biomass compartment rather than in total stock of C and N within the vegetation. Such a transition from non-woody to woody vegetation cover could significantly slow down C and N cycling in subarctic habitats due to the longer lifespan and lower decomposition rate of wood compared to leaves (Preston et al. 2000; Cornelissen et al. 2007). However, dwarf shrubs dominance in the vegetation cover could enhance soil organic matter decomposition through physical effects on their own microhabitat, such as increased winter soil insulation and reduced summer albedo (Zhang 2005; Kropp et al. 2021), increased evapotranspiration (Loranty et al. 2018), associated shifts from microbial to fungal dominance in soil decomposer communities (Eskelinen et al. 2009), and increased C allocation to nutrient mining through root exudation and mycorrhizal associations (Finzi et al. 2007; Drake et al. 2011). Such increase in organic matter mineralisation could compensate for the slowdown in vegetation C and N cycling caused by Arctic and subarctic shrubification (Weintraub and Schimel 2005). In addition, moss litter, which is also abundant in non-woody vegetation covers, has been shown to be of lower quality and decomposability than dwarf shrub (Dorrepaal et al. 2005; Cornelissen et al. 2007), further illustrating that the relationship between shrubification and slowing of C and N cycling may not be as simple as presented.

This work also highlights that the greater graminoid abundance, resulting from changes in surface hydrology due to permafrost thaw and thermokarstic processes (Christensen et al. 2004; Johansson et al. 2013; Van Der Kolk et al. 2016; Heijmans et al. 2022), can increase both aboveground biomass N stocks and the proportion of the short-lived compartment in this biomass. Opposite to what has been discussed for shrubification, the shorter plant lifespan (Shaver and Chapin 1991) and higher decomposition rate of their organic matter once in the soil (Preston et al. 2000; Cornelissen et al. 2007) could accelerate C and N cycling in these graminoid-dominated ecosystems. However, the concurrent increase in soil moisture and waterlogging, which limit the aerobic decomposition of soil organic matter (Olid et al. 2020), could strongly limits the decomposition of graminoid litter. With elemental cycling in short-lived biomass increasing and soil organic matter decomposition slowing down, nutrient-rich biomass could rapidly accumulate and nutrient bioavailability could rapidly decrease, further limiting plant growth in graminoid-dominated ecosystems. To our knowledge, this pattern has not been observed in these ecosystems, perhaps due to the simultaneous release of nitrogen and nutrients from permafrost thaw (Fouché et al. 2020, 2021). Overall, this also illustrate the complexity between vegetation dynamics and soil processes regarding C and N cycling.

Finally, numerous uncertainties persist regarding the interactions between vegetation shifts and soil properties in Arctic environments (Heijmans et al. 2022). Increasing constraints on elemental cycling, as suggested by this work, could potentially lead to robust feedbacks on plant communities (Mekonnen et al. 2021*a*) and alter key processes such as biological N fixation or denitrification that control N stocks and bioavailability (Mooshammer et al. 2014; Bellenger et al. 2020; Du et al. 2020; Oulehle et al. 2021). Responses of these processes to environmental change might enhance or mitigate the proposed progressive N limitation that can occur when primary productivity increases (Luo et al. 2004), although recent work has also highlighted strong plant adaptations to low-nitrogen conditions (Martin et al. 2022). Future work should contribute to a more mechanistic and fine-scale understanding of these processes and of organic matter (e.g., litter and dissolved organic matter), water (e.g., surface and subsurface), and energy fluxes in these ecosystems to better predict environmental responses to climate change in Arctic ecosystems.

Conclusion

In this work, we investigated the influence of variation in vegetation cover composition on vegetation and soil C and N stocks in different Arctic habitats. Our results highlight that shrub or graminoid dominance in the vegetation at the local scale does not necessarily lead to variations in aboveground C stocks but rather in N stocks, especially between aquatic graminoid cover with higher N content and shrub cover with lower N content. The difference between

these vegetation covers primary lies in the distribution of aboveground biomass stocks between short-lived and long-lived compartments, with shrub-dominated habitats presenting higher long-lived woody biomass, which could induce a significant slowdown of C and N cycling in these habitats. However, such a slowdown could be mitigated by more favourable conditions for microbial decomposition of organic matter in soils. In the more graminoid-dominated environments, however, the increase in short-lived C and N stocks and the decomposition-limiting conditions (soil water saturation) could also represent a global slowdown of C and N cycling in these habitats. Finally, this work reveals the independence between aboveground biomass and soils stocks for both C and N at the local scale, potentially highlighting a decoupling between vegetation cover and soil profile changes. Future research should consider the simultaneous changes in biomass distribution and environmental conditions in relation to elemental cycling to improve our understanding of the potential magnitude of the Arctic environment transformation.

Acknowledgements

The authors acknowledge the main support of this project by the French national grant EC2CO/Biohefect—INCEPTION and the METIS laboratory for additional financial support. HMGP particularly thanks the IPV Doctoral Program for financial support. The authors thank the Swedish Polar Research Secretariat and SITES for the support of the work done at the Abisko Scientific Research Station. SITES is supported by the Swedish Research Council's grant 4.3-2021-00164. The research leading to these results has received funding from the European Union's Horizon 2020 project INTERACT, under grant agreement No. 730938. The authors gratefully thank Margareta Johansson for access to the Storflaket mire. The authors also thank both CISE and ALYSE platforms (Institut d'Ecologie et des Sciences de l'Environnement de Paris, Paris, France, and Institut de Recherche pour le Développement, Bondy, France) and Magloire Madeng Yogo for elemental analysis and analytic support, and Olivier Huttel for his support in computing soil densities with the photogrammetry method. The authors thank Antoine Séjourné for the aerial photographs of mire and heathland sites. Finally, the authors thank Romain Barnard and the anonymous reviewers for their helpful comments on the manuscript.

Article information

History dates

Received: 15 September 2023
Accepted: 24 September 2024
Accepted manuscript online: 4 October 2024
Version of record online: 15 January 2025

Copyright

© 2025 The Authors. This work is licensed under a Creative Commons Attribution 4.0 International License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

Data availability

Data access can be requested at https://doi.org/10.5281/zenodo.8199206. Data will be fully available in open-access once the article published.

Author information

Author ORCIDs

Hugo M.G. Potier https://orcid.org/0000-0001-6486-0649
Xavier Raynaud https://orcid.org/0000-0002-9065-2867
Yannick Agnan https://orcid.org/0000-0002-9349-6310
Alienor Allain https://orcid.org/0000-0002-5786-8754
Maryse Castrec-Rouelle https://orcid.org/0000-0002-6020-9610

Author notes

Present address for Hugo M.G. Potier: PatriNat (OFB-MNHN-CNRS-IRD) Muséum National d'Histoire Naturelle de Paris 75005 Paris France.

Author contributions

Conceptualization: HMGP, XR, YA, MC, MAA
Data curation: HMGP, XR, YA, AA, VV, MC, MAA
Funding acquisition: MC, MAA
Investigation: HMGP, XR, YA, AA, VV, MC, MAA
Methodology: HMGP, XR, YA, VV, MC, MAA
Project administration: MC, MAA
Supervision: XR, MC, LA, MAA
Validation: VV
Visualization: HMGP
Writing – original draft: HMGP
Writing – review & editing: HMGP, XR, YA, AA, MC, VV, LA, MAA

Competing interests

The authors declare there are no competing interests.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/as-2023-0049.

References

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

Agnan, Y., Courault, R., Alexis, M.A., Zanardo, T., Cohen, M., Sauvage, M., and Castrec-Rouelle, M. 2019. Distribution of trace and major elements in subarctic ecosystem soils: sources and influence of vegetation. Science of The Total Environment, **682**: 650–662. doi:10.1016/j.scitotenv.2019.05.178.

Allain, A., Alexis, M.A., Bridoux, M.C., Humbert, G., Agnan, Y., and Rouelle, M. 2023. Fingerprinting the elemental composition and chemodiversity of vegetation leachates: consequences for dissolved

Arctic Science Downloaded from cdnsciencepub.com by 91.86.0.77 on 12/05/25

Arctic Science Downloaded from cdnsciencepub.com by 91.86.0.77 on 12/05/25

organic matter dynamics in Arctic environments. Biogeochemistry, **164**: 73–98, doi:10.1007/s10533-022-00925-9.

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

Baillargeon, N., Pold, G., Natali, S.M., and Sistla, S.A. 2022. Lowland tundra plant stoichiometry is somewhat resilient decades following fire despite substantial and sustained shifts in community structure. Arctic, Antarctic, and Alpine Research, **54**: 525–536. doi:10.1080/15230430.2022.2121246.

Bellenger, J.P., Darnajoux, R., Zhang, X., and Kraepiel, A.M.L. 2020. Biological nitrogen fixation by alternative nitrogenases in terrestrial ecosystems: a review. Biogeochemistry, **149**: 53–73. doi:10.1007/s10533-020-00666-7.

Berner, L.T., Beck, P.S.A., Bunn, A.G., and Goetz, S.J. 2013. Plant response to climate change along the forest–tundra ecotone in northeastern Siberia. Global Change Biology, **19**: 3449–3462. doi:10.1111/gcb.12304.

Berner, L.T., Massey, R., Jantz, P., Forbes, B.C., Macias-Fauria, M., Myers-Smith, I., et al. 2020. Summer warming explains widespread but not uniform greening in the Arctic tundra biome. Nature Communications, **11**: 1–12. doi:10.1038/s41467-020-18479-5.

Camill, P., Lynch, J.A., Clark, J.S., Adams, J.B., and Jordan, B. 2001. Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Ecosystems, **4**: 461–478. doi:10.1007/s10021-001-0022-3.

Christensen, T.R., Johansson, T., Åkerman, H.J., Mastepanov, M., Malmer, N., Friborg, T., et al. 2004. Thawing sub-arctic permafrost: effects on vegetation and methane emissions. Geophysical Research Letters, **31**. doi:10.1029/2003GL018680.

Cornelissen, J.H.C., Bodegom, P.M. van, Aerts, R., Callaghan, T.V., Logtestijn, R.S.P. van, Alatalo, J., et al. 2007. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. Ecology Letters, **10**: 619–627. doi:10.1111/j.1461-0248.2007.01051.x.

Coulouma, G., Feurer, D., Vinatier, F., and Huttel, O. 2021. Assessing new sensor-based volume measurement methods for high-throughput bulk density estimation in the field under various soil conditions. European Journal of Soil Science, **72**: 2049–2061. doi:10.1111/ejss.13115.

Cribari-Neto, F., and Zeileis, A. 2010. Beta regression in R. Journal of Statistical Software, **34**: 1–24. doi:10.1201/9781315119403-7.

Daubenmire, R. 1959. A canopy coverage method of vegetation analysis. Northwest Science, 43–64.

Donnelly, P.K., Entry, J.A., Crawford, D.L., and Cromack, K. 1990. Cellulose and lignin degradation in forest soils: response to moisture, temperature, and acidity. Microbial Ecology, **20**: 289–295. doi:10.1007/BF02543884.

Dorrepaal, E., Cornelissen, J.H.C., Aerts, R., Wallén, B., and Van Logtestijn, R.S.P. 2005. Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? Journal of Ecology, **93**: 817–828. doi:10.1111/j.1365-2745.2005.01024.x.

Drake, J.E., Gallet-Budynek, A., Hofmockel, K.S., Bernhardt, E.S., Billings, S.A., Jackson, R.B., et al. 2011. Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO2. Ecology Letters, **14**: 349–357. doi:10.1111/j.1461-0248.2011.01593.x.

Dray, S., and Dufour, A.B. 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software, **22**: 1–20. doi:10.18637/jss.v022.i04.

Du, E., Terrer, C., Pellegrini, A.F.A., Ahlström, A., van Lissa, C.J., Zhao, X., et al. 2020. Global patterns of terrestrial nitrogen and phosphorus limitation. Nature Geoscience, **13**: 221–226. doi:10.1038/s41561-019-0530-4.

Engelhardt, B.M., Weisberg, P.J., and Chambers, J.C. 2012. Influences of watershed geomorphology on extent and composition of riparian vegetation. Journal of Vegetation Science, **23**: 127–139. doi:10.1111/j.1654-1103.2011.01328.x.

Eskelinen, A., Stark, S., and Männistö, M. 2009. Links between plant community composition, soil organic matter quality and microbial communities in contrasting tundra habitats. Oecologia, **161**: 113–123. doi:10.1007/s00442-009-1362-5. PMID: 19452173.

Fang, X., Lin Zhu, Y., Di Liu, J., Ping Lin, X., Zhao Sun, H., Hao Tan, X., et al. 2022. Effects of moisture and temperature on soil organic carbon decomposition along a vegetation restoration gradient of subtropical China. Forests, **13**: 1–17. doi:10.3390/f13040578.

Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., et al. 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO2. Proceedings of the National Academy of Sciences, **104**: 14014–14019. doi:10.1073/pnas.0706518104.

Fouché, J., Christiansen, C.T., Lafrenière, M.J., Grogan, P., and Lamoureux, S.F. 2020. Canadian permafrost stores large pools of ammonium and optically distinct dissolved organic matter. Nature Communications, **11**: 1–11. doi:10.1038/s41467-020-18331-w.

Fouché, J., Bouchez, C., Keller, C., Allard, M., and Ambrosi, J.P. 2021. Seasonal cryogenic processes control supra-permafrost pore water chemistry in two contrasting cryosols. Geoderma, **401**: 115302. doi:10.1016/j.geoderma.2021.115302.

Hedenås, H., Olsson, H., Jonasson, C., Bergstedt, J., Dahlberg, U., and Callaghan, T.V. 2011. Changes in tree growth, biomass and vegetation over a 13-year period in the Swedish sub-Arctic. Ambio, **40**: 672–682. doi:10.1007/s13280-011-0173-1.

Heijmans, M.M.P.D., Magnússon, R., Lara, M.J., Frost, G.V., Myers-Smith, I.H., van Huissteden, J., et al. 2022. Tundra vegetation change and impacts on permafrost. Nature Reviews Earth & Environment, **3**: 68–84. doi:10.1038/s43017-021-00233-0.

Holmes, M.E., Crill, P.M., Burnett, W.C., McCalley, C.K., Wilson, R.M., Frolking, S., et al. 2022. Carbon accumulation, flux, and fate in Stordalen Mire, a permafrost peatland in transition. Global Biogeochemical Cycles, **36**: 1–17. doi:10.1029/2021GB007113.

Holtmeier, F., and Broll, G. 2007. Treeline advance—driving processes and adverse factors. Landscape Online, **1**: 1–33. doi:10.3097/LO.200701.

Hugelius, G., Tarnocai, C., Broll, G., Canadell, J.G., Kuhry, P., and Swanson, D.K. 2013. The northern circumpolar soil carbon database: spatially distributed datasets of soil coverage and soil carbon storage in the northern permafrost regions. Earth System Science Data, **5**: 3–13. doi:10.5194/essd-5-3-2013.

IPCC, 2021. Climate Change 2021: the physical science basis. *In* Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. *Edited by* V. Masson-Delmotte, P. Zhai, A. Pirani, S.L. Connors, C. Péan, and S. Berger, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 2391p. doi:10.1017/9781009157896.

Jobbagy, E.G., and Jackson, R.B. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications, **10**: 423. doi:10.2307/2641104.

Johansson, M., Callaghan, T.V., Bosiö, J., Åkerman, H.J., Jackowicz-Korczynski, M., and Christensen, T.R. 2013. Rapid responses of permafrost and vegetation to experimentally increased snow cover in sub-arctic Sweden. Environmental Research Letters, **8**: 035025. doi:10.1088/1748-9326/8/3/035025.

Johansson, T., Malmer, N., Crill, P.M., Friborg, T., Åkerman, J.H., Mastepanov, M., and Christensen, T.R. 2006. Decadal vegetation changes in a northern peatland, greenhouse gas fluxes and net radiative forcing. Global Change Biology, **12**: 2352–2369. doi:10.1111/j.1365-2486.2006.01267.x.

Jonasson, S., Michelsen, A., and Schmidt, I.K. 1999. Coupling of nutrient cycling and carbon dynamics in the Arctic, integration of soil microbial and plant processes. Applied Soil Ecology, **11**: 135–146. doi:10.1016/S0929-1393(98)00145-0.

Kassambara, A., and Mundt, F. 2022. factoextra: extract and visualize the results of multivariate data analyses. R package version 1.0.7. Available from https://CRAN.R-project.org/package=factoextra; https://github.com/kassambara/factoextra/issues [accessed 15 September 2024].

Keuper, F., van Bodegom, P.M., Dorrepaal, E., Weedon, J.T., van Hal, J., van Logtestijn, R.S.P., and Aerts, R. 2012. A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands. Global Change Biology, **18**: 1998–2007. doi:10.1111/j.1365-2486.2012.02663.x.

Arctic Science Downloaded from cdnsciencepub.com by 91.86.0.77 on 12/05/25

Van Der Kolk, H.J., Heijmans, M.M.P.D., Van Huissteden, J., Pullens, J.W.M., and Berendse, F. 2016. Potential Arctic tundra vegetation shifts in response to changing temperature, precipitation and permafrost thaw. Biogeosciences, **13**: 6229–6245. doi:10.5194/bg-13-6229-2016.

Kropp, H., Loranty, M.M., Natali, S.M., Kholodov, A.L., Rocha, A.V., Myers-Smith, I., et al. 2021. Shallow soils are warmer under trees and tall shrubs across Arctic and Boreal ecosystems. Environmental Research Letters, **16**: 015001. doi:10.1088/1748-9326/abc994.

López-Blanco, E., Langen, P.L., Williams, M., Christensen, J.H., Boberg, F., Langley, K., and Christensen, T.R. 2022. The future of tundra carbon storage in Greenland—sensitivity to climate and plant trait changes. Science of the Total Environment, **846**: 157385. doi:10.1016/j.scitotenv.2022.157385.

Loranty, M.M., Abbott, B.W., Blok, D., Douglas, T.A., Epstein, H.E., Forbes, B.C., et al. 2018. Reviews and syntheses: changing ecosystem influences on soil thermal regimes in northern high-latitude permafrost regions. Biogeosciences, **15**: 5287–5313. doi:10.5194/bg-15-5287-2018.

Luo, Y., Su, B., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U., et al. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. Bioscience, **54**: 731–739. doi:10.1641/0006-3568(2004)054[0731:PNLOER]2.0.CO;2.

Ma, S., He, F., Tian, D., Zou, D., Yan, Z., Yang, Y., et al. 2018. Variations and determinants of carbon content in plants: a global synthesis. Biogeosciences, **15**: 693–702. doi:10.5194/bg-15-693-2018.

Martin, A.C., Macias-Fauria, M., Bonsall, M.B., Forbes, B.C., Zetterberg, P., and Jeffers, E.S. 2022. Common mechanisms explain nitrogen-dependent growth of Arctic shrubs over three decades despite heterogeneous trends and declines in soil nitrogen availability. New Phytologist, **233**: 670–686. doi:10.1111/nph.17529.

Matthews, G. 1993. The carbon content of trees. *In* Forestry Commission technical paper 4.

Mekonnen, Z.A., Riley, W.J., Berner, L.T., Bouskill, N.J., and Torn, M.S. 2021a. Arctic tundra shrubification: a review of mechanisms and impacts on ecosystem carbon balance. Environmental Research Letters, **16**: 053001. doi:10.1088/1748-9326/abf28b.

Mekonnen, Z.A., Riley, W.J., Grant, R.F., Salmon, V.G., Iversen, C.M., Biraud, S.C., et al. 2021b. Topographical controls on hillslope-scale hydrology drive shrub distributions on the Seward Peninsula, Alaska. Journal of Geophysical Research: Biogeosciences, **126**: 1–16. doi:10.1029/2020JG005823.

Mooshammer, M., Wanek, W., Hämmerle, I., Fuchslueger, L., Hofhansl, F., Knoltsch, A., et al. 2014. Adjustment of microbial nitrogen use efficiency to carbon:nitrogen imbalances regulates soil nitrogen cycling. Nature Communications, **5**: 1–7. doi:10.1038/ncomms4694.

Olid, C., Klaminder, J., Monteux, S., Johansson, M., and Dorrepaal, E. 2020. Decade of experimental permafrost thaw reduces turnover of young carbon and increases losses of old carbon, without affecting the net carbon balance. Global Change Biology, **26**: 5886–5898. doi:10.1111/gcb.15283.

Oulehle, F., Goodale, C.L., Evans, C.D., Chuman, T., Hruška, J., Krám, P., et al. 2021. Dissolved and gaseous nitrogen losses in forests controlled by soil nutrient stoichiometry. Environmental Research Letters, **16**: 064025. doi:10.1088/1748-9326/ac007b.

Paletto, A., Agnelli, A.E., and De Meo, I. 2021. Carbon stock in deadwood: the Mountain Birch (*Betula pubescens* subsp. czerepanovii) forests in the Khibiny Mountains (Russia). Journal of Sustainable Forestry, **40**: 385–400. doi:10.1080/10549811.2020.1767144.

Peterson, K.M., and Billings, W.D. 1980. Tundra vegetational patterns and succession in relation to microtopography near Atkasook, Arctic and Alpine Research, **12**: 473–482. doi:10.1080/00040851.1980.12004207.

Pold, G., Baillargeon, N., Lepe, A., Rastetter, E.B., and Sistla, S.A. 2021. Warming effects on arctic tundra biogeochemistry are limited but habitat-dependent: a meta-analysis. Ecosphere, **12**. doi:10.1002/ecs2.3777.

Preston, C.M., Trofymow, J.A.T., and Intersite, C. 2000. Variability in litter quality and its relationship to litter decay in Canadian forests. Canadian Journal of Botany, **78**: 1269–1287. doi:10.1139/b00-101.

R Core Team 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/ [accessed 15 September 2024].

Sandström, F., Petersson, H., Kruys, N., and Ståhl, G. 2007. Biomass conversion factors (density and carbon concentration) by decay classes for dead wood of *Pinus sylvestris*, *Picea abies* and *Betula* spp. in boreal forests of Sweden. Forest Ecology and Management, **243**: 19–27. doi:10.1016/j.foreco.2007.01.081.

Schimel, J.P., Bilbrough, C., and Welker, J.M. 2004. Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. Soil Biology and Biochemistry, **36**: 217–227. doi:10.1016/j.soilbio.2003.09.008.

Semenchuk, P.R., Elberling, B., Amtorp, C., Winkler, J., Rumpf, S., Michelsen, A., and Cooper, E.J. 2015. Deeper snow alters soil nutrient availability and leaf nutrient status in high Arctic tundra. Biogeochemistry, **124**: 81–94. doi:10.1007/s10533-015-0082-7.

Shaver, G.R., and Chapin, F.S. 1991. Production: biomass relationships and element cycling in contrasting arctic vegetation types. Ecological Monographs, **61**: 1–31. doi:10.2307/1942997.

Shaver, G.R., Billings, W.D., Chapin, F.S., Giblin, A.E., Nadelhoffer, K.J., Oechel, W.C., and Rastetter, E.B. 1992. Global change and the carbon balance of Arctic ecosystems. Bioscience, **42**: 433–441. doi:10.2307/1311862.

Sjögersten, S., Ledger, M., Siewert, M., de la Barreda-Bautista, B., Sowter, A., Gee, D., et al. 2023. Optical and radar Earth observation data for upscaling methane emissions linked to permafrost degradation in sub-arctic peatlands in northern Sweden. Biogeosciences, **20**: 4221–4239. doi:10.5194/bg-20-4221-2023.

Starr, M., Hartman, M., and Kinnunen, T. 1998. Biomass functions for mountain birch in the Vuoskojärvi Integrated Monitoring area. Boreal Environment Research, **3**: 297–303.

Sulman, B.N., Salmon, V.G., Iversen, C.M., Breen, A.L., Yuan, F., and Thornton, P.E. 2021. Integrating Arctic plant functional types in a land surface model using above- and belowground field observations. Journal of Advances in Modeling Earth Systems, **13**: 1–24. doi:10.1029/2020MS002396.

Targulian, V.O., and Krasilnikov, P.V. 2007. Soil system and pedogenic processes: self-organization, time scales, and environmental significance. Catena, **71**: 373–381. doi:10.1016/j.catena.2007.03.007.

Weintraub, M.N., and Schimel, J.P. 2005. Nitrogen cycling and the spread of shrubs control changes in the carbon balance of arctic tundra ecosystems. Bioscience, **55**: 551. doi:10.1641/0006-3568(2005)055[0551:E]2.0.CO;2.

Wilson, R.M., Hough, M.A., Verbeke, B.A., Hodgkins, S.B., Tyson, G., Sullivan, M.B., et al. 2022. Plant organic matter inputs exert a strong control on soil organic matter decomposition in a thawing permafrost peatland. Science of The Total Environment, **820**: 152757. doi:10.1016/j.scitotenv.2021.152757.

Zhang, T. 2005. Influence of the seasonal snow cover on the ground thermal regime: an overview. Reviews of Geophysics, **43**. doi:10.1029/2004RG000157.