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Title

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

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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.

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Keywords:

Carbon stock − nitrogen stocks – vegetation community – soils – Arctic – long-lived compartment − 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. 2021a) 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. 2021b).

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

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limit the decrease in soil temperature during winter, promoting permafrost thaw and thermokarst processes (Johansson et al. 2013). Subsequently, 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.

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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 (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

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123 southwest of the Báddosdievvá hill (68°31′N, 18°86′E; 600 m a.s.l, ~25 ha) with shallow soils
124 on top of metamorphic bedrocks (Agnan et al. 2019). Each site was divided into different
125 habitats based on vegetation composition, micro-topography, and the presence of free water to
126 encompass within-site heterogeneity (see Fig. 1 for photographs of ecosystems and habitats).

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

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

144 **Vegetation characterisation and sampling**

145 Vegetation composition was characterised, and vegetation and soil samples were
146 collected in both ecosystems at the peak of the growing season, at the beginning of August
147 2021 and 2022. Sampling was conducted in accordance with all applicable laws, guidelines

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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, twenty quadrats were distributed across the wet-heath (n = 5), humid-heath (n = 5), and dry-heath habitat (n = 10) continuum to 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) were 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*, *E. 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). 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 ten 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.*

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173 *vitis-idaea*) to separate the total aboveground biomass into short- (leaves) and long-lived
174 (branches) compartments. More information regarding allometric equations can be found in
175 Supplementary I.

176 Trees were inventoried in two randomly placed 10 m × 10 m plots in the birch forest
177 next to the heathland. Trees were categorised into small living trees (<1.3 m), tall living trees
178 (>1.3 m), snags (>1.3 m), and stumps (<1.3 m) based on height. Ground level diameter and
179 diameter at breast height (DBH; i.e., 1.3 m above ground level, only for living trees) were
180 measured. Multiple stems from polycormous individuals were considered distinct individuals
181 for biomass estimations.

182 **Soil sampling and characterisation**

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

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197 homogeneous, was sampled independently for elemental content and moisture content
198 measurements.

199 Each soil sample was analysed for C and N content, and soil moisture content was
200 measured by the mass difference after drying at 60 °C for over 48 h. Bulk soil density was
201 estimated for surface and deep horizons using a photogrammetry method for some selected
202 habitats in August 2022 (Coulouma et al. 2021). Briefly, this method consists in carefully
203 digging three holes in each horizon and modelling the volume of each hole from a series of 20
204 pictures taken from different angles before and after the digging. Volume estimations were
205 performed using CloudCompare 2.12.4 (http://www.cloudcompare.org/) after 3-D modelling
206 each hole using PhotoScan 1.2.6 (Agisoft LLC, St. Petersburg, Russia), and the extracted soil
207 was weighed after >48 h drying at 105 °C. Masses and volumes were corrected for coarse
208 mineral particles after sieving at 2 mm (considering a standard mineral particle density of
209 2.6 g cm^{-3}), and bulk soil densities were computed. The photogrammetric method for bulk
210 density measurements is not applicable to saturated soil profiles because it needs the soil to
211 keep its structure and the water table not to be higher than soil level. Thus, those bulk density
212 estimations were limited to the palsa, humid-heath, dry-heath and forest understorey habitats,
213 and bulk densities of bog and wet-heath habitats were attributed to each horizon based on
214 similarity in soil characteristics with measured horizons (depth, soil moisture, and lithogenic
215 influence), and were used to compute soil stocks. For three sampled points, no deep horizon
216 could be properly identified and were not sampled. The mean soil characteristics and stocks
217 of their habitat's deep horizons were later attributed to those missing horizons for statistical
218 analysis.

219 **Sample preparation and elemental content measurements**

220 Biomass samples were dried at 60 °C for at least 48 h and ground to <250 µm using a
221 grinder (ultra-centrifugal mill ZM200, Retsch, Haan, Germany). Leaves and branches of

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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 8010EB, 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 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

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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 (PCA) 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 (PC) for vegetation cover and soil characteristics, respectively, were considered and retained for clustering. Optimal number of clusters was visually determined using average

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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 (HSD) 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 principal components explained 60.7% of the data variance. Figure 2 shows the biplot of variables (species covers) and observations (vegetation quadrats) for the first 2 principal axes. The first principal component (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 principal components (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-

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297 means clustering on the three principal components identified four different dominant
298 vegetation groups (hereafter referred to as "types"), associated with contrasting dominant
299 species cover across the two ecosystems and the seven habitats (Fig. 2B): a first type
300 characterised by a developed dwarf shrub cover (DS) of *B. nana*, *E. nigrum*, and *V. vitis-*
301 *idaea*; a second type with important aquatic graminoid covers (AG) of *C. rostrata* and *E.*
302 *angustifolium*; a third type characterised by sphagnum and small graminoid (*E. vaginatum;*
303 SG); and a fourth type with a mixed cover (MC) of dwarf shrubs, sphagnum and small
304 graminoids. These types mostly included all quadrats from the same type of habitat, but
305 grouped together habitat types from different ecosystems (e.g., dry-heath and palsa, wet-heath
306 and bog).

307 **Aboveground vegetation stocks and distribution between plant compartments**

308 Aboveground biomass varied from 283.1 + 26.3 g_{DW} m^{-2} in MC to 306.1 ± 35.1 g_{DW}
309 m^{-2} in DS but did not significantly differ across the dominant vegetation types (global
310 average of 297 ± 18.0 g_{DW} m^{-2}; $F = 0.08$, $p > 0.5$). Similarly, carbon stocks associated with
311 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
312 global average of 148.6 ± 9.8 g_C m^{-2}, but no significant differences were detected between the
313 different dominant vegetation types ($F = 0.60$, $p > 0.5$; Fig. 3A). In contrast, nitrogen stocks
314 did vary significantly between dominant vegetation types, from 3.0 ± 0.3 g_N m^{-2} in DS to 4.3
315 ± 0.2 g_N m^{-2} in AG ($F = 3.20$, $p = 0.033$; Fig. 3C, capital letters), as a result of aquatic
316 graminoid species presenting higher nitrogen content than small graminoids, mosses, and
317 dwarf-shrub overall biomass (t-tests, $p < 0.01$). Moreover, C and N stock distribution between
318 compartments differed significantly between dominant vegetation types ($X^2 > 110$, $p < 0.001$
319 for both C and N): less than 2% of the total carbon and 1% of total nitrogen was stored in
320 long-lived compartments in both AG and SG, compared to 30 and 18% in MC and more than
321 40 and 25% in DS, for C and N respectively (Fig. 3A and 3C, lowercase letters).

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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 5-times higher, respectively, with 515.0 ± 27.3 g_C m^{-2} and 17.0 ± 0.89 g_N m^{-2} on average (Fig. 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 principal components explained 67.9% of the total variance and were both kept for visual representation (Fig. 4). The first principal component (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 principal component (17.1%) grouped C and N content of the surface horizon (Fig. 4A). K-means clustering using the first two principal components distinguished two groups of soil profiles (hereafter referred to as 'types'). These soil profiles 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

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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).

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 ($X^2 = 2.82$, $p > 0.1$ and $X^2 = 1.6$, $p = 0.09$). 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 principal components explained 89.9% of the total variance. The first principal component (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),

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clearly separating the two soil profile types (Fig. 6B). The second principal component (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 (not shown). Across the three principal components, 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, 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 g g_{DW}^{-1} 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

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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 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

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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 to 1.7 and 2.1 to 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-

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446 accumulative soil profiles in which anaerobic conditions caused by soil waterlogging limit
447 organic matter degradation (Olid et al. 2020). In contrast, the mineral-profile type represents
448 soils for which the organic horizon development is limited by unsaturated soil conditions that
449 promote organic matter degradation, and where the mineral horizon accounts for a higher
450 proportion of the sampled profile depth. This functional difference is particularly evident for
451 C and N stocks, which were on average 5-times higher in the organic profiles (Fig. 5), despite
452 the fact that both profile types have the same soil mass per surface unit, which is in part due to
453 the shallow depths of the mineral soils in this field study. The emergence of this difference is
454 particularly interesting given that the estimation of soil stocks was limited to the active layer
455 in the peat bog and therefore does not include the entire soil profile down to the parent
456 material. These results also suggest that, similarly to vegetation, soil stocks could be
457 approached at a larger scale than habitats using soil characteristics such as soil moisture,
458 which result from both large-scale and small-scale topography, and have been related to
459 organic matter accumulation and soil profile development (Donnelly et al. 1990; Fang et al.
460 2022). However, the organic-profile type exhibited a high variability in C and N stocks that
461 tended to separate palsa soil profiles with higher stocks from bog and wet-heath soil profiles
462 with lower stocks (see Supplementary III). This variability seems to indicate that the current
463 soil characteristics of these habitats, such as moisture content, do not fully reflect past soil
464 functions that resulted in these C and N stocks.

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

466 Despite the expected correlation between vegetation composition (four different
467 dominant covers) and soil characteristics (two soil profile types) as shown by the co-inertia
468 analysis, the co-occurrence of these features varied within the study area. For example, palsa
469 and dry-heath habitats that both presented shrub-dominated covers (vegetation classification,
470 Fig. 2) belonged to organic- and mineral-profile types, respectively (soil classification, Fig.

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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 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

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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. 2021a) 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

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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

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plant communities (Mekonnen et al. 2021a) 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, 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.

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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 in order to improve our understanding of the potential magnitude of the Arctic environment transformation.

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Author contribution

HP, XR, YA, AA, MC-R and MA designed the study; HP, XR, YA, AA, VV and MA gathered the samples; HP and VV analysed the samples; HP analysed the data; HP wrote the manuscript that was revised by all co-authors.

Competing interests

The authors declare there are no competing interests.

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598 **Data Availability**

599 Data access can be requested at https://doi.org/10.5281/zenodo.8199206. Data will be

600 fully available in open-access once the article published.

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Figures

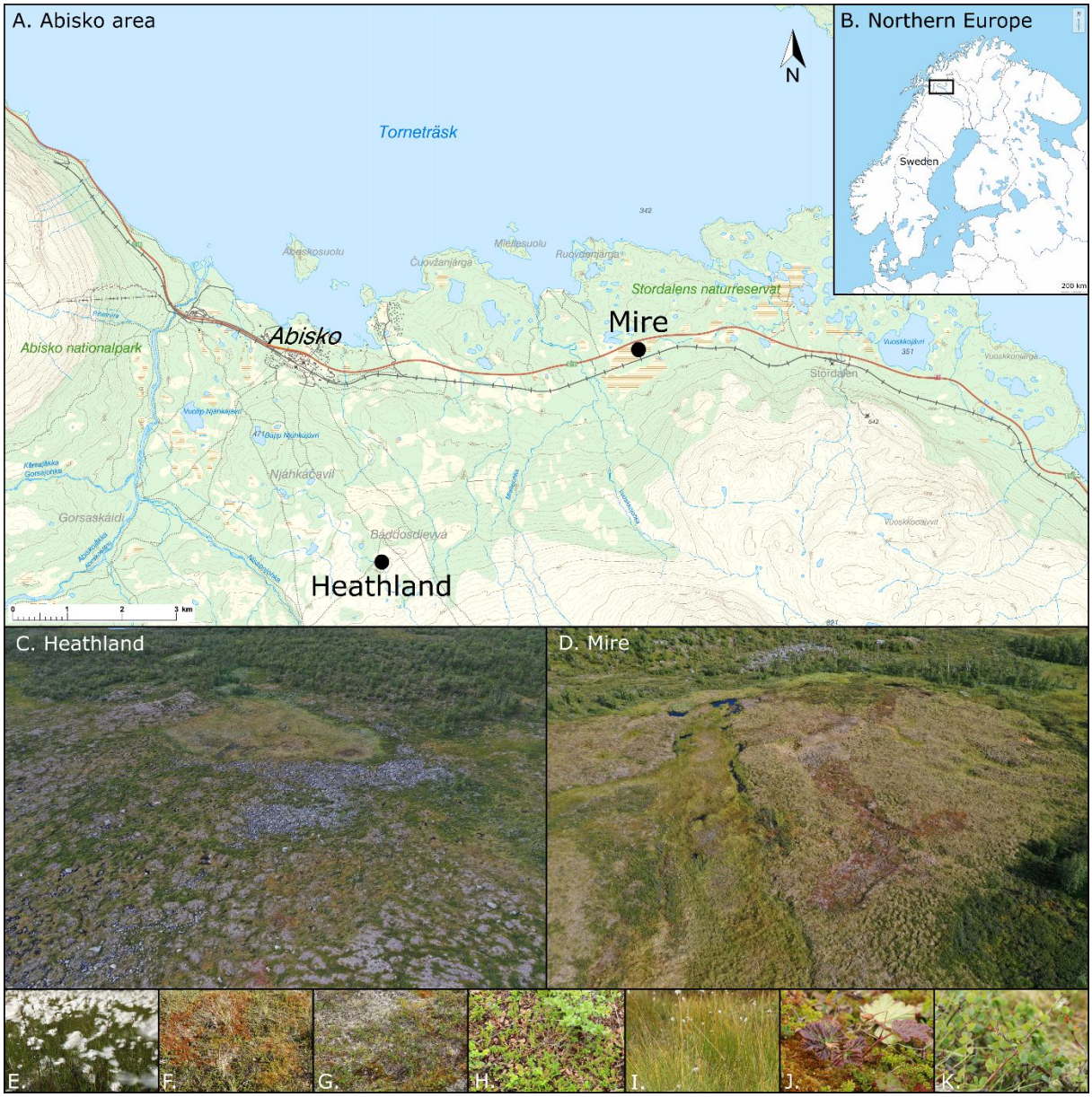


Figure 1: Location of the two study sites (mire and heathland) near Abisko (A), in Northern Sweden (B). Aerial photographs of the mire (C) and the heathland (D) ecosystems and close-up photographs of the ground-level vegetation of their different habitats: wet-heath (E), humid-heath (F), dry-heath (G) 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).

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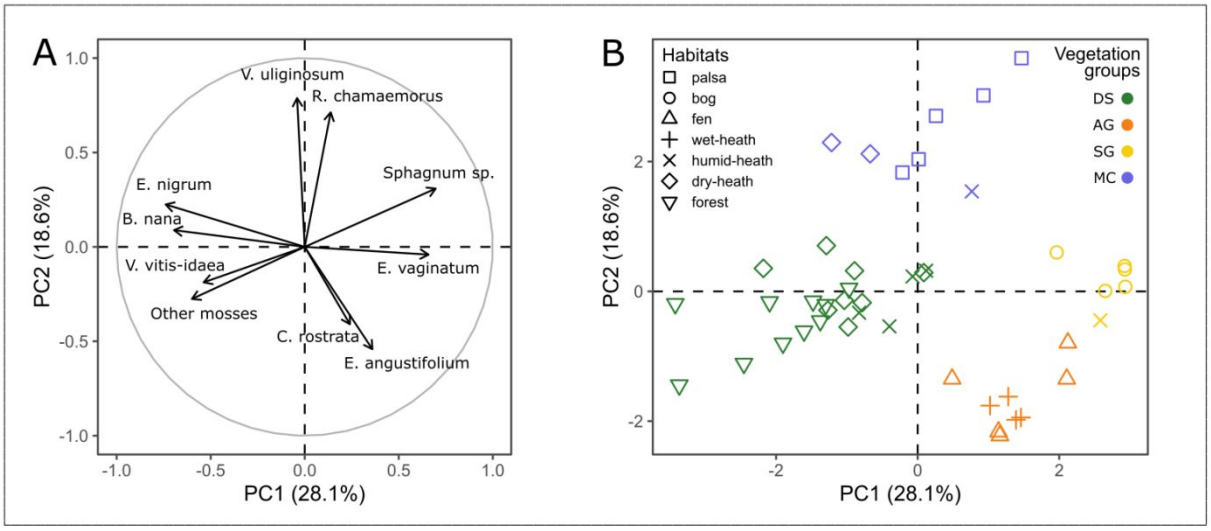


Figure 2: Principal component analysis of dominant species cover across different mire and heathland habitats in the Abisko area, Sweden: representation of principal component (PC) 1 vs 2 (A) and representation of observations by habitat (symbols) and dominant vegetation groups (colours) determined using 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.

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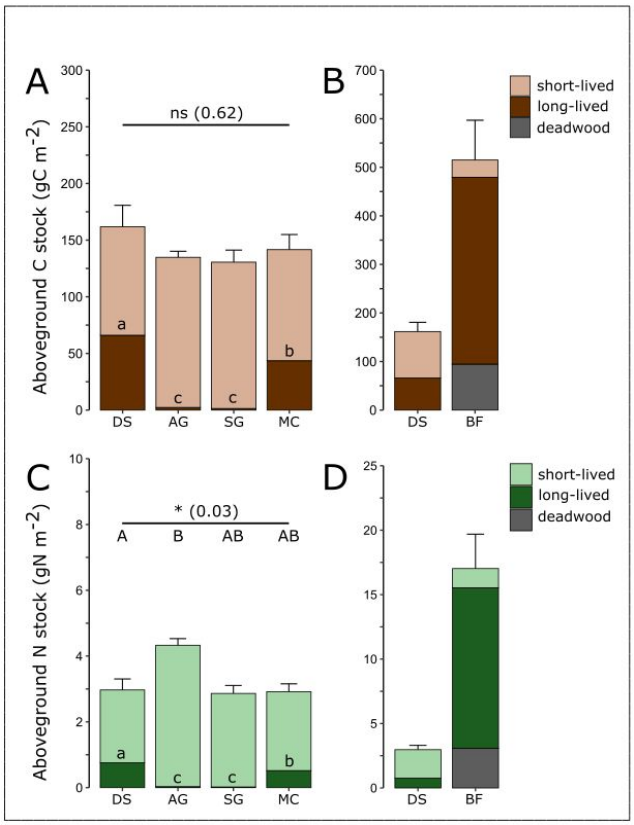
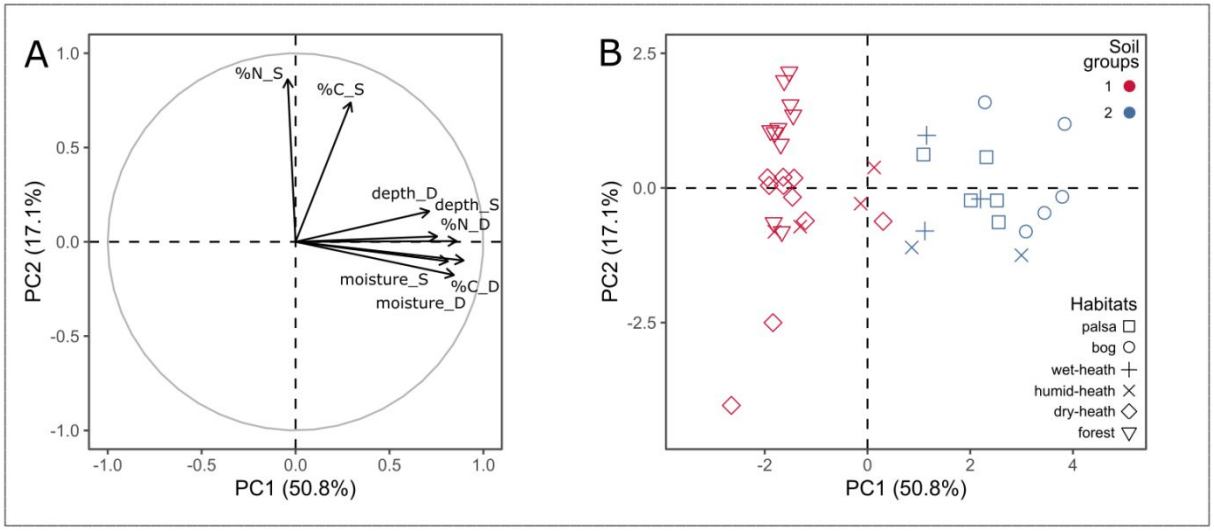


Figure 3: Carbon (A, B) and nitrogen (C, D) total stocks and their distributions between short-lived and long-lived compartments for the different dominant vegetation types identified using K means clustering (Figure 4B) in the Abisko area, Sweden, for ground-level vegetation (A, C) and dwarf shrub vegetation type (representing the birch forest understorey) vs birch tree layer (B, 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.

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884

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

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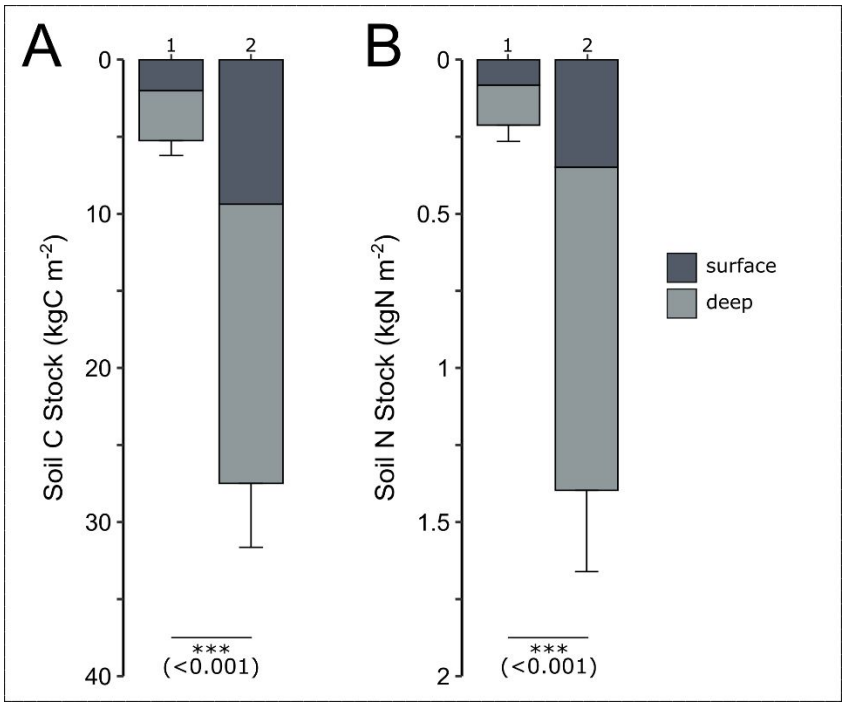


Figure 5: Carbon (A) and nitrogen (B) stock distributions between surface and deep horizons for the two different soil profile types identified using K means clustering (Figure 4B) in the Abisko area, Sweden. Error bars represent standard errors of the mean.

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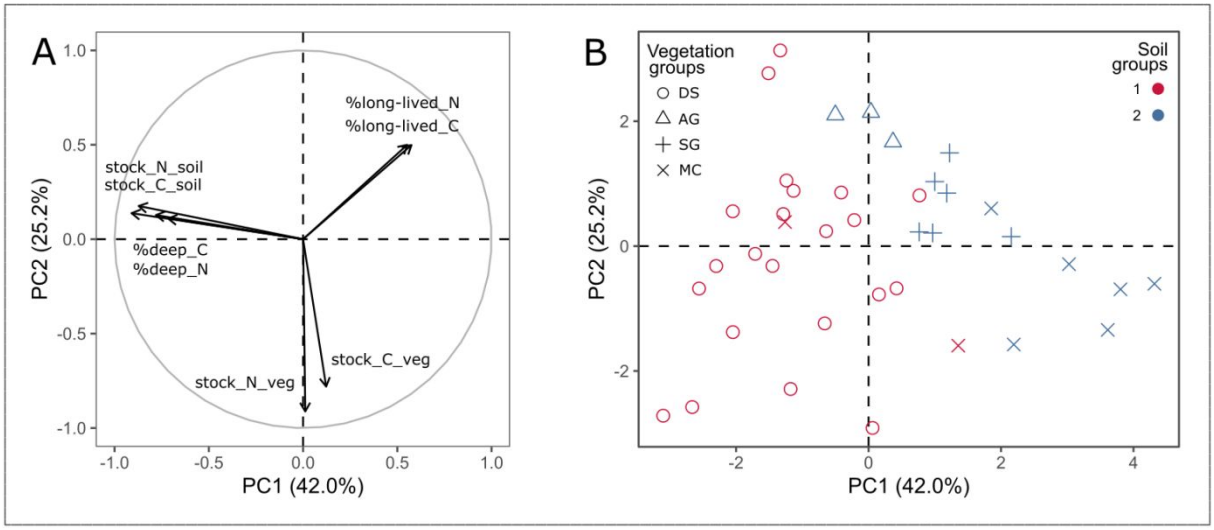


Figure 6: Principal component analysis of carbon and nitrogen stocks in the aboveground vegetation and the soil profile of different mire and heathland habitats in the Abisko area, Sweden: representation of principal component 1 vs 2 (A) and representation of observations by vegetation groups (symbols) 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.

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