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Strong Changes in Soil Nutrient Stocks in Northern Forests Over Four Decades

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ABSTRACT

Northern forests are currently taking up large quantities of carbon due to tree growth. Yet, it is not known how the stocks of soil nutrients have responded to this increase in biomass. Therefore, we analyzed thousands of forest soils in Sweden over the last four decades. We found strong increases in the concentrations and stocks of plant-available magnesium, calcium, and manganese in the organic layer of the soils. Specifically, the concentrations of plant-available magnesium, calcium, and manganese in the organic layer increased by 38%, 21%, and 100%, respectively, over the four decades. These increases were related to soil texture and the magnesium concentration of the soil parent material as well as to the dominant tree species. The increase in nutrients in the organic layer might be caused by an uplift of nutrients from the mineral subsoil to the organic layer due to plant nutrient uptake in the subsoil and litter fall and they might also be driven by decreased leaching of nutrients from the organic layer due to decreased acid deposition. Concurrently, the nitrogen content of the organic layer decreased over the four decades. In conclusion, our results show that stocks and concentrations of plant-available cations in the organic layer of Swedish forest soils increased despite increases in tree biomass and regular tree harvests. Our study indicates that there is a low risk for base cation deficiency and that nitrogen will remain the limiting nutrient for tree growth in northern forests.

1 | Introduction

Forests in northern Europe produce large quantities of biomass and form a considerable carbon (C) pool in the Earth system (Gauthier et al. 2015). The amount of standing tree biomass has increased in northern forests over the past decades (Gauthier et al. 2015; SLU 2024; Laudon et al. 2024). This increase in the tree biomass in northern forests contributes to the terrestrial C sink, which has captured a substantial proportion of the anthropogenic C emissions over the past decades (Denning 2022; Friedlingstein et al. 2023; Sitch et al. 2024). Yet, it is not known if and for how long the capacity of the soils to provide enough nutrients to sustain high tree growth will last (Akselsson et al. 2007, 2008; Augusto et al. 2017; Karltun et al. 2022). Therefore, it is important to understand nutrient dynamics and temporal trends in northern forest soils. Specifically in Swedish forests, the standing wood volume increased by about 50% from 1950 to 2010 (SLU 2024). The increase in standing wood volume has started to decline only over the past few years, for reasons that are not yet fully understood (Laudon et al. 2024; SLU 2024). This recent decline in forest growth in Sweden could be related to a deterioration of nutrient contents of trees which has been observed in European forests over the last decades (Jonard et al. 2015), but it might also be related to climatic stresses, insect outbreaks, or competition among trees.

Increased tree growth and tree harvest might cause a decline in the concentrations of plant-available nutrients of the soil organic layer (Akselsson et al. 2007, 2008; Achat et al. 2015). Such a decline in plant-available nutrients in the topsoil seems particularly likely to occur in Sweden where clear-cut forestry is

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dominating forest management since the middle of the 20th century (Akselsson et al. 2007, 2008). Moreover, whole-tree harvest increased in Sweden over the last decades causing the removal of fine woody litter and needles that are comparatively nutrient-rich (Akselsson et al. 2019).

Yet, it could also be that increased tree growth enhances solubilization of nutrients in the subsoil (solubilization refers to the combination of weathering and desorption of ions). An increase in root biomass and rooting depth might increase nutrient solubilization rates due to increased root respiration and root turnover in deeper parts of the soil (Brantley et al. 2011; Hasenmueller et al. 2017; Finlay et al. 2020). Increased solubilization of nutrients in the subsoil might lead to increased plant nutrient uptake (Clarholm and Skyllberg 2013; Marschner and Rengel 2023). Elevated plant nutrient uptake, in turn, enriches the plant biomass and plant litter with nutrients, resulting in nutrient uplift from the subsoil to the organic layer (Jobbágy and Jackson 2001, 2004; Lucas 2001; Clarholm and Skyllberg 2013). This might particularly be the case for nutrients such as magnesium (Mg) and calcium (Ca) that are mainly taken up by plants passively with the pore water, driven by transpiration, that is, by mass flow, independently of the tree nutrient demand, leading to so-called luxury uptake (Barber 1995; Jobbágy and Jackson 2001, 2004; Clarholm and Skyllberg 2013; Marschner and Rengel 2023). Thus, Mg and Ca might be enriched in the soil organic layer in response to an increase in tree biomass, in particular in forests dominated by tree species with high transpiration rates, and hence a high water uptake, as shown for Swedish forests (Clarholm and Skyllberg 2013). Nutrient uplift from the subsoil to the organic layer is likely most pronounced for nutrients that are taken up passively (i.e., independently of the tree nutrient demand) since these nutrients might remain for a shorter period in the tree biomass than nutrients that are actively taken up in an energy-consuming process driven by plant nutrient demand (Vergutz et al. 2012).

Next to changes in standing wood volume, there have also been major changes in atmospheric element deposition in northern forests during the last decades (Lövblad et al. 2004; Hansen et al. 2013; Ferm et al. 2019; Karlsson et al. 2024). Deposition of sulfur (S) increased until the 1970s and remained high until the end of the 1980s when it fell sharply to levels five times lower than during the deposition peak. The mobile SO_4^{2-} ion increased leaching of base cations, leading to elevated acidity in Swedish forest soils (Eriksson et al. 1992). Furthermore, deposition of nitrogen (N) increased significantly in the period 1970 to 1989 in the south and mostly southwestern part of Sweden, and it decreased significantly from 1990 to 2009 in the south of Sweden (Hansen et al. 2013; Karlsson et al. 2024). The substantial atmospheric N input to the ecosystems at the end of the last millennium might be relevant for forest nutrition since tree growth in northern forests is mainly limited by N (Hyvönen et al. 2008; Sponseller et al. 2016; Högberg et al. 2017). Yet, it is not known how the N stock of the forest soils has changed over the last decades in response to tree growth and harvest as well as changes in atmospheric deposition.

The objective of this study was to understand nutrient dynamics in Swedish forest soils during four decades from 1983 to 2022. We tested two hypotheses.

H1. *The concentrations and stocks of exchangeable base cations in the organic layer declined over the four decades (from* 1983 *to* 2022*) because of increased tree biomass (and thus, increased tree nutrient uptake) and regular tree harvest.*

H2. *The total N concentration and stock of the organic layer declined during the four decades (from* 1983 *to* 2022*) due to a reduction in atmospheric N deposition during this period and increased tree N uptake caused by increased tree biomass.*

To test these hypotheses, we analyzed soil data from four repeated soil inventories spanning the period between 1983 and 2022.

2 | Material and Methods

2.1 | Structure of the Inventory, Data, and Sample Collection

All data analyzed here was collected in Sweden for the Swedish Forest Soil Inventory (SFSI) and the Swedish National Forest Inventory (NFI). The SFSI monitors the state of the Swedish forest soils and covers all of Sweden except for arable land and urban areas. The SFSI is conducted in collaboration with the NFI. The SFSI visits about 20,000 permanent plots distributed all over Sweden over a 10-year period. During each year, plots in all parts of Sweden are visited (about 2000 per year). After 10 years, the same plots are visited again, and we refer to a 10-year sampling period as one inventory. Yet, in the first inventory, all plots were visited during a 5-year period. The first inventory was conducted from 1983 to 1987, the second inventory was conducted from 1993 to 2002, the third one from 2003 to 2012, and the fourth inventory from 2013 to 2022.

The SFSI has a grid design. Circular plots with a 10 m radius are located in quadratic clusters on a triangular grid (Ranneby et al. 1987), which is denser towards the south of the country to account for the greater fragmentation of the landscape and a more diverse geology in the south of Sweden. Each quadratic cluster encompasses eight circular plots (or four in the south-western region). At each of these circular plots, forest characteristics including tree stem diameter at breast height and tree species composition are classified by the NFI at the same time as the soil is examined. The dominant tree species is determined based on basal area. The stem diameter is recorded for all trees with a stem diameter > 1 mm at breast height (1.3 m). Trees with a diameter ≥ 100 mm are calipered at breast height (1.3 m) in plots with a 10 m radius, trees with a diameter from 40 to 99 mm are calipered in plots with a radius of 3.5 m and small trees with a diameter ≤ 40 mm are calipered on two subplots with a radius of 1 m (Fridman et al. 2014). Based on the diameter of all living trees that have reached breast height and the number of these trees per area, the standing wood volume (including bark) is calculated (Fridman et al. 2014).

The organic layer is described according to Hesselmann (1926) and sampled volumetrically in a 3.14 m^2 subplot at 50% of all permanent plots (about 10,000 plots). The sample is taken throughout the entire depth of the organic layer (excluding the annual litter) to a maximum of 30 cm. For this purpose, 1–9 volumetric

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samples are taken and combined to gain a sample with a volume of at least 1.5 L using a 10 cm diameter corer. Nitrogen concentrations and pH of the organic layer are determined in all samples, while base cations and aluminum (Al) are only determined in the samples of the plots, where also the mineral soil is sampled (see below).

Field-based description of the soil profile and soil classification according to the World Reference Base for Soil Resources (IUSS Working Group WRB 2015) is carried out on all plots, while soil sampling of the mineral soil is carried out on a subset of plots (about 4500 plots visited during one inventory). For this purpose, a small soil profile is dug in the subplot. When a plot is revisited after 10 years, a new soil profile is prepared at a pre-determined location a few meters away from the old soil profile. The texture of the mineral soil is determined in the field at a depth of 20 cm in the mineral soil according to the following texture groups: gravel, coarse sand, sand, fine sand, coarse silt, fine silt, and clay, using the so-called finger test (Vos et al. 2016). Samples for analysis of the minerals soil are taken from the profile wall. The sampling depths of the mineral soil have changed during the four inventories. During the last two inventories, the soil was collected at fixed depth intervals measured from the top of the mineral soil: 0–10, 10–20, and 55–65 cm.

2.2 | Sample Preparation and Soil Chemical Analyses

In the laboratory, all soil samples are dried to constant weight at 35°C. The mineral soil samples are homogenized and sieved (< 2 mm), and roots that remain on the sieve are removed. The organic layer samples are disintegrated in a grinder and separated into a fine (< 2 mm) and a coarse fraction (> 2 mm). The samples are weighed, and the stock of the organic layer is calculated based on the weight of the < 2 mm fraction of the organic layer. Chemical analyses are carried out on the fine soil fraction (< 2 mm).

The total N concentration is analyzed using an elemental analyzer (TruMac CN, LECO). The pH is determined in water (at a soil: water ratio of 1:2.5 w/v) using a Pt electrode (Aquatrode Plus Pt1000, Metrohm). Exchangeable cations (Ca, Mg, Na, K, and Mn) are extracted in 1 M ammonium acetate buffered at pH 7.0. Exchangeable Al is extracted in 1 M KCl. Both cations and aluminum are quantified by inductively coupled plasma optical emission spectroscopy (ICP-OES; Avivo 200, Perkin Elmer). The exchangeable cations (Ca, Mg, Na, K, and Mn) determined here represent the easily plant-available ions. Element stocks are calculated by multiplying the organic layer stock with its element concentration. In the first inventory, total N was analyzed using a Kjeldahl procedure after wet oxidation in H_2SO_4, and base cations were quantified using atomic absorption spectrometry (Nilsson 1988). A re-analysis of archived samples using the current analytical techniques showed that the results are directly comparable for the organic layer.

The total element contents of the soil parent material were determined in the first inventory at 1896 plots. For this purpose, samples were collected in the soil profiles in the interval 45 to 55 cm from the soil surface corresponding to the C or B/C horizons. The samples were ground, sieved (< 2 mm), ignited, and fused with lithium metaborate. Subsequently, total element contents were determined by ICP (Olsson et al. 1993).

2.3 | Selection of Plots and Basic Plot Description

For the present study, we selected all plots at which the organic layer stock was determined between 1983 and 2022. From this dataset, we excluded plots with the humus form mull, mull-like moder, and peat because in these plots, the samples are taken according to a different protocol for the SFSI (together these plots form about 38% of all plots). Furthermore, we excluded plots that did not have an organic layer (4% of all plots). Thus, in the dataset analyzed here, there are the four humus forms: mor type 1 (mor dominated by the Of horizon), mor type 2 (mor dominated by the Oh horizon), peaty mor, and moder. The total number of observations (across all four inventories) selected for this study is 33,500.

Across the whole dataset, 44% of the soils were classified as Podzols, 36% were Regosols, 10% were Leptosols, 4.5% were Gleysols, 2% were Histosols, and < 1% were Umbrisols and Cambisols. These 2% of Histosols are in the dataset (even though the humus form peat is excluded) because an organic layer on bedrock with a depth > 10 cm is classified as a Histosol according to the World Reference Base for Soil Resources (although the organic layer form is not peat). Furthermore, across the whole dataset, 41% of the plots were dominated by Scots pine (*Pinus sylvestris* L.), 30% of the plots were dominated by Norway spruce (*Picea abies* L. Karst.), 15% of the plots by birch (*Betula pendula*, Roth), and 4.3% and 2.9% by beech (*Fagus sylvatica* L.) and European aspen (*Populus tremula L.*), respectively (based on the basal area of all trees that reach breast height).

For the mineral soil, we only analyzed samples from the last two inventories, during which the mineral soil was sampled in the same depth increments (see above). We did not analyze the mineral soil samples from previous inventories due to different sampling intervals among inventories.

2.4 | Calculations and Data Analyzes

Since there is a steep temperature gradient from the south to the north of Sweden along which soil properties vary considerably (Spohn and Stendahl 2022, 2023), we divided all plots into four latitudinal zones, with equal numbers of plots. This division into latitudinal zones was done before the sample selection for this study. We call these four latitudinal zones High North (≥ 63.7° N), North (≥ 60.6° N and < 63.73° N), South (≥ 58.2° N and < 60.6° N), and Low South (< 58.2° N). The latitudinal ranges of these four zones are as follows: High North: 12.4 to 24.1° E, North: 12.1 to 20.3° E, South: 11.1 to 19.3° E, and Low South: 11.5 to 19.3° E.

To assess differences over time, we compared the four full inventories. This is the most conservative way to analyze this dataset since during each inventory (i.e., one 10-year period) the

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same plots are visited. We refrain from analyzing changes over periods shorter than one full inventory period to avoid misinterpretation of data that might emerge from variation among plots sampled in different years. By integrating data collected over a 10-year period, we also minimize the potential effect that interannual variation in temperature and rainfall might have on the results (due to potential effects of the soil water content on the sampling depth of the organic layer). To minimize the effect of these outliers on the results we calculated the changes over time based on the medians rather than the means. We present most of the results in boxplots, in which the 25% and 75% percentile define the box and the 10% and 90% percentiles are depicted by the bars.

We tested for significant differences in soil chemical properties among the four inventories by Kruskal–Wallis test followed by Dunn post hoc test (using the R package FSA, version 0.9.4), whereby $p < 0.050$ was considered to indicate statistically significant differences. We used the same statistical method to test for significant differences in soil properties among forests dominated by different tree species. We chose the Kruskal–Wallis test because it allows us to test whether groups differ significantly regarding observations that are not normally distributed. In addition, we used the Student's *t*-test to compare two groups of soils of one inventory, for instance, soils with coarse and fine texture or soils with high and low Mg concentration of the parent material. Coarse-textured soils are those that have a texture coarser than fine silt, while fine-textured soils are those that have the texture fine silt or clay. Further, the soils were divided depending on whether their parent material had a magnesium-oxide (MgO) content larger or smaller than the median MgO concentration of the parent material. All data analyses were conducted using R (version 4.4.1, R Core Team 2021).

3 | Results

The stem diameter increased significantly by 37% across all of Sweden over the four decades (Figure 1A), and it increased significantly in all four latitudinal zones of Sweden (Table 1). The stem diameter differed among the latitudinal zones, and the median stem diameter in the northernmost latitudinal zone was only 60% of that in the southernmost zone (Table 1). In addition, the wood volume per area increased over the four decades (Figure 1B).

The median organic layer stock was highest in the first inventory (1980s) and lowest in the third inventory (2003 to 2012) across the whole of Sweden (Figure 1C). In the two southern latitudinal zones, the organic layer decreased significantly over the four decades (by 18% in the southernmost latitudinal zone and by 13% in the second most southern zone; Table 1). The median organic layer stock was more than twice as large in the southernmost (Table 1) than in the northernmost latitudinal zone (Table 1).

The total N concentration of the organic layer decreased from the third to the fourth inventory across all of Sweden (Figure 2A). The total N stock of the organic layer was highest in the second inventory (1993 to 2002), and lowest in the fourth inventory, that is, 2013–2022 (Figure 2B). The total N stock decreased by 6% from the first to the last inventory (Figure 2B).

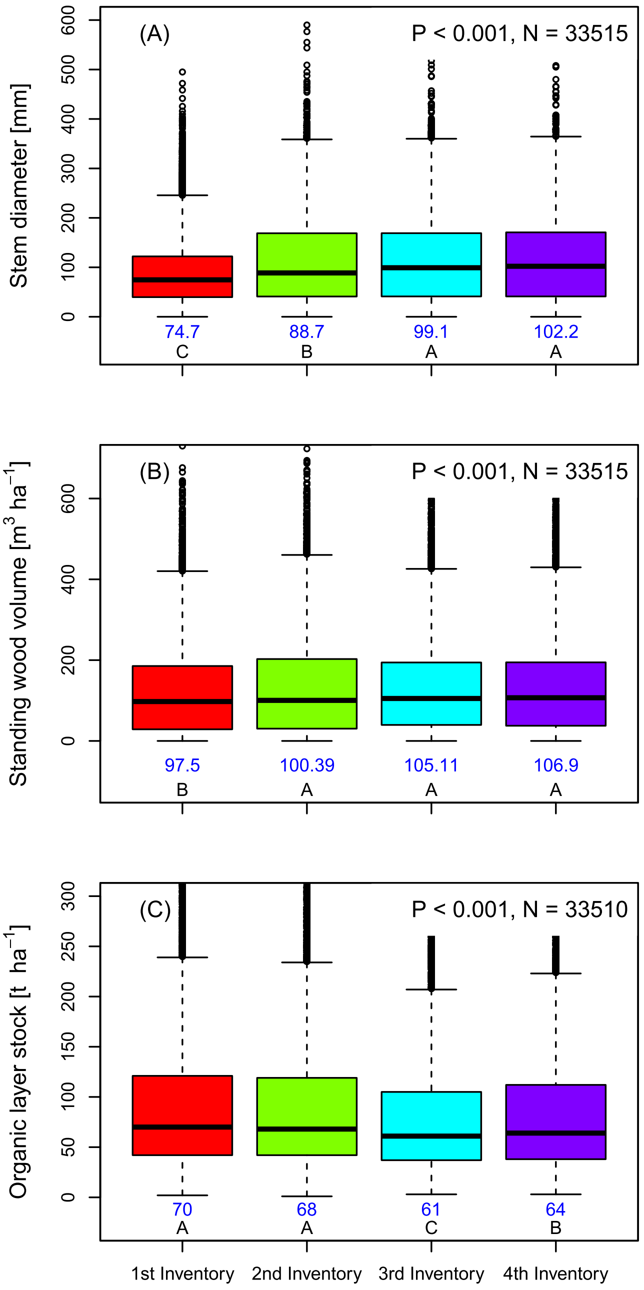

FIGURE 1 | The tree stem diameter at breast height (A), standing wood volume (B), and the stock of the organic layer (C) in Swedish forests in the four inventories conducted between 1983 and 2022. Different capital letters indicate significant ($p < 0.05$) differences among the four inventories according to the Dunn test. The blue numbers depict the medians. The number of observations (N) is given in the upper right corner of each panel. A few outliers are beyond the plotted range.

The plant-available Mg concentration of the organic layer increased continuously and significantly from the first to the last inventory across all of Sweden by 38% (Figure 2C). The median plant-available Mg concentration increased continuously in all four latitudinal zones (Table 1). The increase was 62% in the southernmost (Table 1) and 28% in the northernmost latitudinal zone (Table 1). The plant-available Mg stock of the organic layer increased continuously and significantly from the first to the last inventory across all of Sweden, and the increase amounted to 25% (Figure 2D).

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TABLE 1 | Medians of stem diameter, standing wood volume, soil organic layer stock, total nitrogen of the organic layer as well as plant-available magnesium, calcium, manganese, and potassium concentrations of the organic layer in the four latitudinal zones in the four inventories.

		Inventory					
Variable	**Latitudinal zone**	**First (1983–1987)**	**Second (1993–2002)**	**Third (2003–2012)**	**Fourth (2013–2022)**	***p***	**N**
Stem diameter (mm)	High North	56.5^{C}	64.2^{B}	81.7^{A}	78.2^{A}	<0.001	9157
	North	75.2^{C}	83.7^{B}	89.0^{A}	93.6^{A}	<0.001	9146
	South	86.6^{C}	105.6^{B}	120.1^{AB}	130.3^{A}	<0.001	7919
	Low South	93.1^{B}	117.0^{A}	133.9^{A}	133.9^{A}	<0.001	7293
Standing wood volume ($m^{3}\,ha^{-1}$)	High North	60.0^{B}	65.0^{B}	73.0^{A}	73.7^{A}	<0.001	9157
	North	97.5	86.2	99.6	101.1	0.056	9146
	South	118.6^{B}	117.2^{B}	135.7^{A}	147.0^{A}	<0.001	7919
	Low South	148.8^{B}	160.9^{A}	156.3^{A}	162.4^{B}	<0.001	7293
Organic layer stock ($t\,ha^{-1}$)	High North	49^{AB}	48^{AB}	46^{B}	52^{A}	0.030	9156
	North	54	53	52	55	0.052	9142
	South	89^{A}	84^{B}	74^{C}	77^{C}	<0.001	7919
	Low South	112^{A}	97^{B}	90^{C}	92^{C}	<0.001	7293
Total nitrogen ($g\,kg^{-1}$)	High North	10.4^{D}	11.3^{B}	11.7^{A}	10.8^{C}	<0.001	9157
	North	10.3^{D}	11.3^{B}	11.6^{A}	10.7^{C}	<0.001	9146
	South	11.0^{C}	12.4^{A}	12.7^{A}	11.9^{B}	<0.001	7918
	Low South	11.3^{C}	14.0^{A}	13.6^{A}	12.9^{B}	<0.001	7293
Magnesium ($mmol\,kg^{-1}$)	High North	13.0^{CB}	13.6^{C}	14.9^{B}	16.6^{A}	<0.001	2817
	North	11.7^{C}	12.2^{CB}	12.9^{B}	14.0^{A}	<0.001	2922
	South	11.1^{D}	11.9^{C}	13.5^{B}	14.7^{A}	<0.001	2397
	Low South	10.1^{D}	13.0^{C}	13.5^{B}	16.5^{A}	<0.001	2276
Calcium ($mmol\,kg^{-1}$)	High North	50.3	48.7	49.7	50.3	0.181	2818
	North	49.2	52.0	50.1	52.8	0.094	2922
	South	42.5	43.7	42.6	44.3	0.278	2397
	Low South	28.1^{B}	33.2^{AB}	34.8^{A}	36.7^{A}	<0.001	2276
Manganese ($mmol\,kg^{-1}$)	High North	1.8	2.4	2.4	2.7	0.222	2668
	North	2.1^{B}	2.7^{AB}	2.7^{AB}	3.1^{A}	0.003	2707
	South	1.1	1.4	1.5	1.6	0.172	2218
	Low South	0.9^{B}	1.1^{AB}	1.1^{A}	1.3^{A}	<0.001	2109
Potassium ($mmol\,kg^{-1}$)	High North	23.4^{A}	$19.1S^{C}$	20.0^{B}	20.2^{B}	<0.001	2743
	North	23.0^{A}	18.8^{B}	18.7^{B}	19.4^{B}	<0.001	2790
	South	15.8^{A}	13.7^{B}	14.0^{B}	14.7^{A}	<0.001	2269
	Low South	12.3^{A}	12.0^{B}	12.3^{AB}	12.7^{A}	<0.001	2115

Note: Different capital letters indicate significant ($p < 0.05$) differences among the four inventories, tested separately for each variable and latitudinal zone by the Dunn test. *p* indicates the *p* value of the Kruskal–Wallis test, and N indicates the number of observations.

The plant-available Ca concentration of the organic layer increased continuously from the first to the fourth inventory across all of Sweden by 21% (Figure 2E). In the southernmost latitudinal zone, the increase over the four inventories was 31% (Table 1), while no significant increase occurred in the other latitudinal zones ($p > 0.05$; Table 1). The plant-available Ca stock

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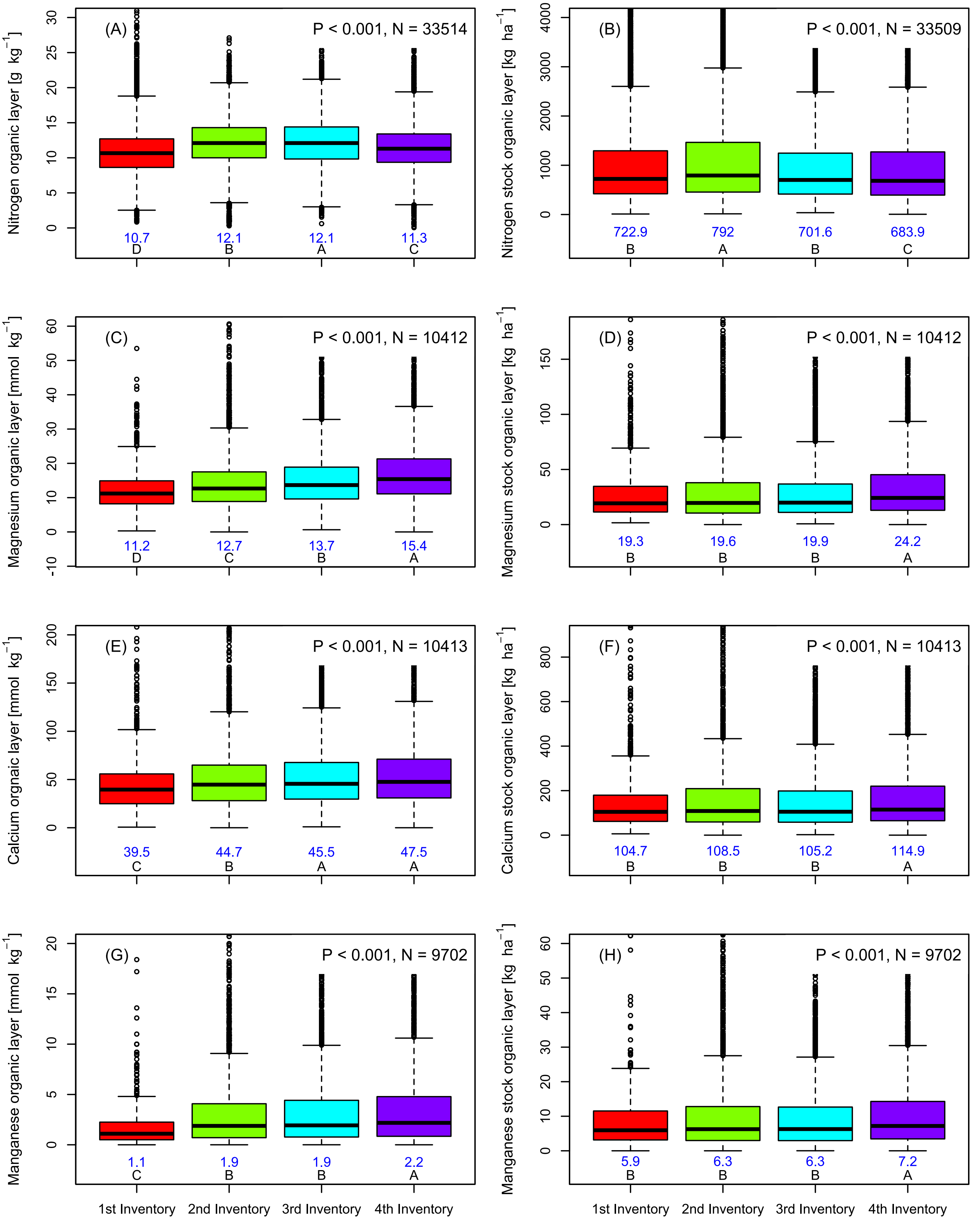

FIGURE 2 | The concentrations and stocks of total nitrogen (A, B), plant-available magnesium (C, D), plant-available calcium (E, F), and plant available manganese (G, H) in the four inventories conducted between 1983 and 2022. Different capital letters indicate significant ($p < 0.05$) differences among the four inventories according to the Dunn test. The blue numbers depict the medians. The number of observations (N) is given in the upper right corner of each panel. A few outliers are beyond the plotted range.

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of the organic layer increased significantly from the first to the last inventory across all of Sweden, albeit not continuously. The increase in the medians of the Ca stock was 10% over the four decades (Figure 2F).

The plant-available manganese (Mn) concentration of the organic layer increased significantly over the four inventories by 100% (Figure 2G), while the Mn stock increased by 22% (Figure 2H). The Mn concentration also increased significantly in two latitudinal zones, by 55% and 67% (Table 1). In contrast, the plant-available potassium concentration of the organic layer did not differ significantly among the first and the fourth inventory (Figure S1A). The exchangeable sodium (Na) concentration of the organic layer decreased continuously and significantly from the first to the fourth inventory by 51% (Figure S1B). The aluminum concentration did not differ significantly among the last three inventories (Figure S1C). The median pH of the organic layer was 3.8 in the last three inventories, and 4.0 in the first inventory (Figure S1D).

The plant-available Mg concentration of the organic layer increased more strongly in the fine-textured soils than in the coarse-textured soils from the first to the fourth inventory (Figure 3A). Similarly, the plant-available Ca concentration increased more strongly in the fine-textured soils than in the coarse-textured soils from the first to the fourth inventory (Figure S2). Furthermore, the plant-available Mg concentration was significantly higher in the organic layer of soils with a high, as compared to a low Mg concentration of the soil parent material across all of Sweden, in all four inventories. The Mg concentration of the organic layer increased more strongly in soils with high Mg concentration compared to those with low Mg concentration in the parent material from the first to the fourth inventory (Figure 3B). In addition, the plant-available Mg concentration of the organic layer was positively correlated with the total MgO concentration of the soil parent material across all of Sweden in each of the four inventories (Figure 3C; R^2 between 0.08 and 0.09, and $p < 0.001$ for each inventory).

The plant-available Mg concentration of the organic layer increased significantly over the four inventories in pine, spruce, and birch forests (Figure 4). The Mg concentration increased more over the four decades in spruce and birch forests than in pine forests (by 2.2, 5.4, and 4.0 $\mathrm{mmol\,kg^{-1}}$, in pine, spruce and birch forests, respectively). Consequently, pine forests had a significantly lower Mg concentration in the organic layer than spruce and birch forests, in the last three inventories (Figure 4). In addition, the Ca concentration increased more over the four decades in spruce and birch forests than in pine forests (by 1.4, 11.1, and 10.7 $\mathrm{mmol\,kg^{-1}}$, in pine, spruce and birch forests, respectively; Figure S3). Consequently, pine forests had a significantly lower Ca concentration in the organic layer than spruce and birch forests, in the last two inventories (Figure S3).

In the mineral soil, the concentrations of plant-available Mg, Ca, and Mn increased with increasing soil depth (Figure 5), indicating that roots that reach into the subsoil experience a higher nutrient availability than roots that grow in the mineral topsoil. In the uppermost 10 cm of the soils, the plant-available Mg concentration was significantly lower in the fourth than in the third inventory (Figure 5A).

Pine, spruce and birch forests had on average similar concentrations of Mg and Ca in the soil parent material (Figure S4C,D). In addition, pine, spruce, and birch forests had on average similar textures (Figure S4B). Plant-available Mg, Ca, and Mn concentrations in the different soil depth increments were only very weakly correlated with latitude, if at all (Table S1). Furthermore, fine-textured and coarse-textured soils were both distributed all over the country and had a very similar median latitude (60.5° and 61.1° N, respectively; Figure S5).

4 | Discussion

4.1 | Increases in Calcium, Magnesium, and Manganese

We found a substantial increase in plant-available Mg, Ca, and Mn in the organic layer of forest soils in Sweden over four decades. Specifically, the concentrations of plant-available Mg, Ca, and Mn in the organic layer increased by 38%, 21%, and 100%, respectively. The concentrations of plant-available cations increased more strongly than the respective element stocks (Figure 2C–H). This indicates that the increases in plant-available nutrients were not simply caused by elevated plant litter inputs to the organic layer, resulting from increased tree biomass. Instead, our findings indicate that the organic layer was enriched with exchangeable Mg, Ca, and Mn. There seem to be two main reasons for these changes, which are not mutually exclusive and likely both contributed to the observed increases in exchangeable cations in the organic layer. First, the decrease in acid deposition during the last decades has likely reduced leaching of base cations from the organic layer to the mineral soil. Second, increased tree growth likely caused increased uplift of nutrients due to increased tree nutrient uptake in the mineral soil and litterfall (Figure 6). In addition, increased decomposition of the organic layer in the south of Sweden (indicated by the decrease in the organic layer stock, Table 1) might have released base cations from the organic matter, contributing to the increase in exchangeable base cations in the south of Sweden over the four decades.

The exposure to acid rain at the end of the 20th century led to leaching of base cations from the organic layer (Eriksson et al. 1992), and the reduction in acid deposition during the last decades (Hansson et al. 2013; Ferm et al. 2019; Karlsson et al. 2024, 2025) very likely reduced leaching of base cations from the organic layer. This might have contributed to the increase in the base cation stocks and concentrations. However, atmospheric Mg deposition has decreased during the last decades, specifically in the south of Sweden (Karlsson et al. 2025). Thus, reduced leaching of base cations might not be the only reason for the increase in base cations in the organic layer. Instead, nutrient uplift from the mineral soil to the organic layer by trees has likely also contributed to the increase in exchangeable base cations in the organic layer.

We found that the increase in the concentrations of exchangeable Mg, Ca, and Mn in the organic layer was related to the texture of the mineral soil as well as to the nutrient contents of the soil parent material (Figure 3, Figure S2). This indicates that the exchangeable base cations that accumulate in the organic layer

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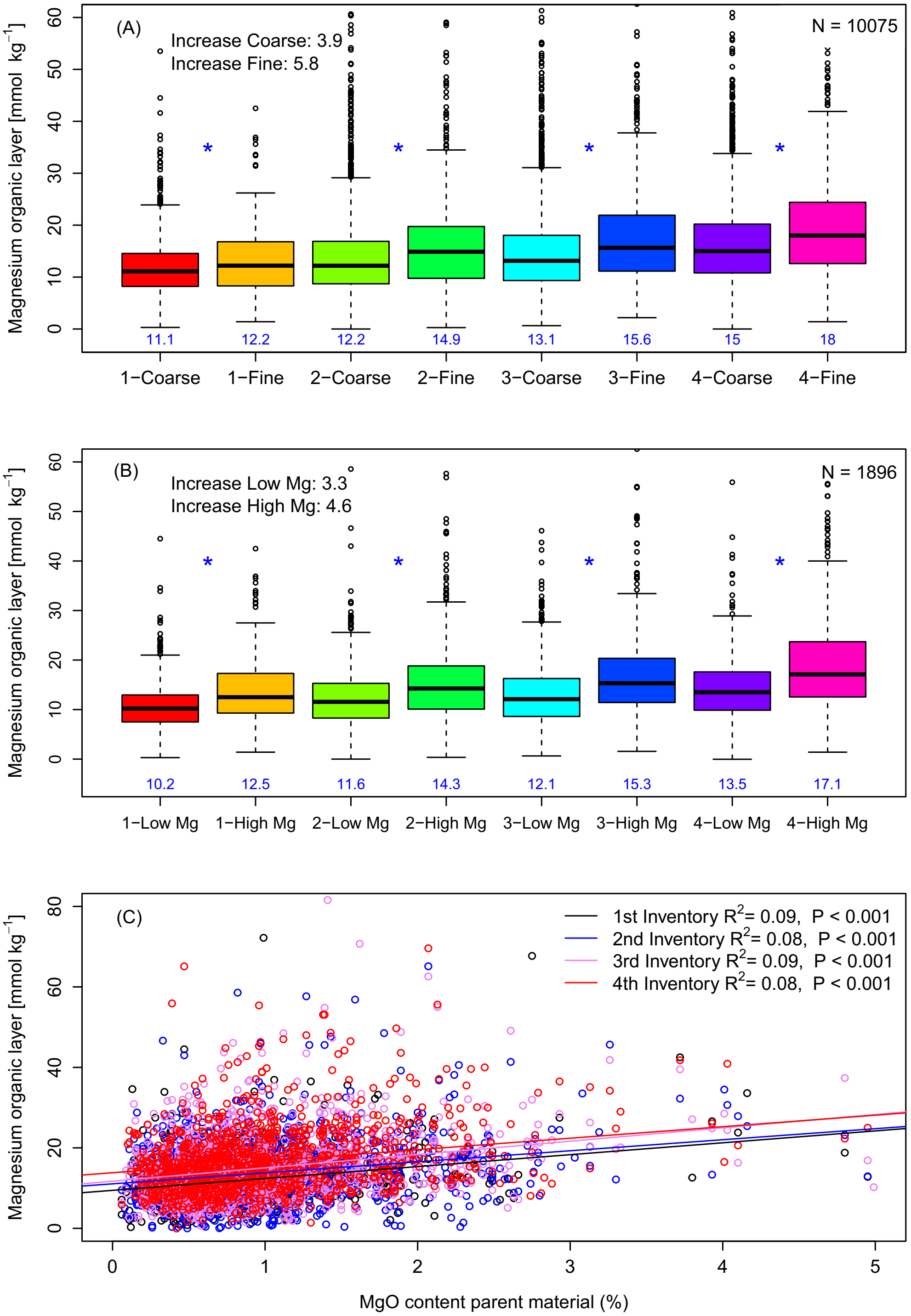

FIGURE 3 | The plant-available magnesium concentration of the organic layer in the four inventories depending on the texture of the mineral soil (A) and the total magnesium-oxide (MgO) concentration of the parent material (B, C). The blue asterisks indicate a significant ($p<0.05$) difference among the two texture classes (fine and coarse) and the two classes of total magnesium-oxide in the soil parent material (low and high), tested separately by student's *t*-test for each inventory. The blue numbers (in panel A, B) depict the medians, and the increase in magnesium concentration from the first to the fourth inventory is indicated. A few outliers are beyond the plotted range.

might be derived from the mineral soil and the soil parent material. The increase in tree size (Figure 1A) likely led to increased uptake of nutrients in the mineral soil because the trees got larger but also because they rooted deeper. The uptake of nutrients through so-called mass flow increases with the concentration of the nutrients in the soil solution (Barber 1995; Marschner and Rengel 2023). The concentrations of plant-available Mg, Ca, and Mn in the mineral soil increase with increasing soil depth (Figure 5), which makes it likely that passive nutrient uptake is higher if the roots grow in deeper soil horizons.

The increase in the Mg and Ca concentrations of the organic layer differed among forests dominated by different tree species (Figure 4, Figure S3). These differences indicate that uplift of

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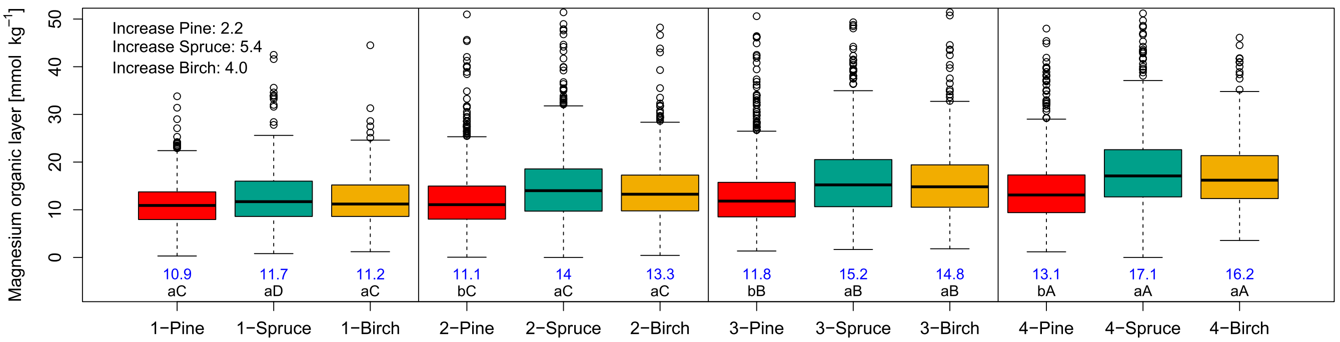

FIGURE 4 | The plant-available magnesium concentration of the organic layer depending on dominant tree species (pine, spruce, and birch) in the four inventories (1–4). Different lowercase letters indicate significant ($p < 0.05$) differences among different tree species in one inventory. Different capital letters indicate significant ($p < 0.05$) differences among the inventories for one specific tree species according to the Dunn test. The blue numbers depict the medians. The increase in the magnesium concentration from the first to the fourth inventory is indicated in black. A few outliers are beyond the plotted range.

the nutrients from the mineral soil to the organic layer is related to the trees. Plant nutrient uplift that increases the nutrient concentration of the topsoil is known to occur in various ecosystems (Jobbágy and Jackson 2001; Lucas 2001; McCulley et al. 2004; Clarholm and Skyllberg 2013; Uhlig et al. 2017; Han et al. 2021). For instance, eucalypt trees strongly enriched the topsoil with Mn over a period of 50 years in Argentina (Jobbágy and Jackson 2004). In addition, uplift of Mg and Ca from the subsoil to the organic layer by trees is known to occur in Swedish forest soils (Clarholm and Skyllberg 2013). In the following we will discuss the different aspects summarized in this section in more detail.

4.2 | Atmospheric Deposition

Atmospheric deposition of cations can strongly contribute to the nutrition of forest trees (Van Der Heijden et al. 2014, 2015). The fluxes of atmospheric Mg deposition in Sweden were in the range of 0.3–2.8 kg ha^{-1} year^{-1}, while the fluxes of atmospheric Ca deposition were in the range of 0.5–3.5 kg ha^{-1} year^{-1} during the last decades (Lövblad et al. 2004; Karlsson et al. 2025). The atmospheric Mg deposition has decreased during the last decades, specifically in the south of Sweden, by about 50% (Karlsson et al. 2025). Yet, the fluxes of atmospheric Mg and Ca deposition are large enough to strongly affect the concentrations of exchangeable Mg and Ca in the organic layer, particularly if leaching is low. Leaching of cations was elevated during times of high atmospheric acid deposition (Eriksson et al. 1992), and it has very likely decreased during the last decades due to a decline in acid deposition (Hansson et al. 2013; Ferm et al. 2019; Karlsson et al. 2024, 2025). Thus, it might be that atmospheric deposition of Mg, Ca, and Mn in combination with a decrease in leaching contributed strongly to the increase in exchangeable base cations in the organic layer (Figure 6). This would require a very strong reduction in leaching that compensated for the decrease in atmospheric deposition of base cations.

4.3 | Weathering and the Mineral Soil

We found that the increases in plant-available Mg in the organic layer were related to the properties of the mineral soil, such as soil texture, and the Mg content of the parent material (Figure 3). These findings make it seem probable that the Mg accumulating in the organic layer is derived from the soil parent material. The plant-available Mg and Ca concentrations were significantly higher in the organic layer of fine-textured than coarse-textured soils (Figure 3A, Figure S5). Fine-textured soils usually have higher nutrient concentrations due to a higher clay mineral content (as shown for Swedish forest soils in Spohn and Stendahl 2022, Spohn and Stendahl 2023), and the fine particles are more prone to weathering due to a larger specific surface area than coarse particles.

Our results show that the amount of Mg in the organic layer increased on average over the whole of Sweden by 4.9 kg ha^{-1} from the first to the fourth inventory, that is, during a mean time of 33 years (Figure 2D). Assuming, for a moment, that all Mg transported to the organic layer is derived from weathering of the parent material, and that all weathered Mg goes to the organic layer, the Mg weathering rate would thus be 0.15 kg Mg ha^{-1} year^{-1} (equaling 6.1 mol Mg ha^{-1} year^{-1}). Given that on average only 0.6% of the parent material consists of Mg (Table S2), 24.7 kg of parent material ha^{-1} year^{-1} need to weather to release this amount of Mg (assuming that Mg is homogeneously distributed in the parent material). However, it is unlikely that all Mg that is released from the parent material is transported to the organic layer. Thus, the increase in the weathering (or solubilization) rate caused by elevated tree biomass is likely higher since a part of the Mg is leached out of the soil, and another part is taken up by the plants and remains there.

Likewise, the amount of Ca in the organic layer increased on average over the whole of Sweden by 10.2 kg ha^{-1} from the first inventory to the fourth inventory. Assuming that all Ca transported to the organic layer is derived from weathering of the parent material (and that all weathered Ca goes to the organic layer), the Ca weathering rate would thus be 0.31 kg Ca ha^{-1} year^{-1} (equaling 7.7 mol ha^{-1} year^{-1}). Given that on average only 1.3% of the parent material consists of Ca (see Table S2), we can estimate that 23.8 kg of parent material ha^{-1} year^{-1} need to weather to release this amount of Ca. Thus, there is a good match of the amounts of soil parent material that need to weather to release both Mg and Ca in the quantities in which they were enriched in the organic layer over the four decades.

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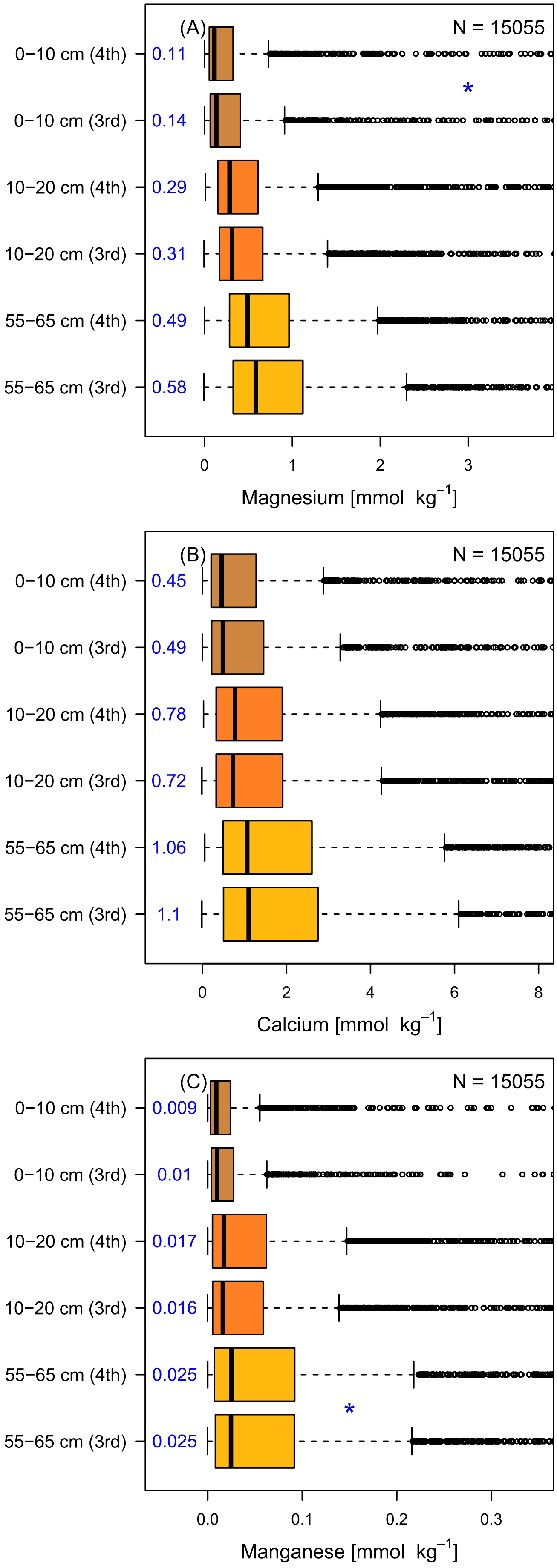

FIGURE 5 | Concentrations of plant-available magnesium (A), calcium (B), and manganese (C) in the mineral soil (at a depth of 0–10, 10–20 and 55–65 cm) in the third and fourth inventory (conducted between 2003 and 2022). The blue asterisks indicate a significant ($p < 0.05$) difference between the third and fourth inventory, tested by student's *t*-test separately for each depth increment and element. The blue numbers depict the medians. A few outliers are beyond the plotted range.

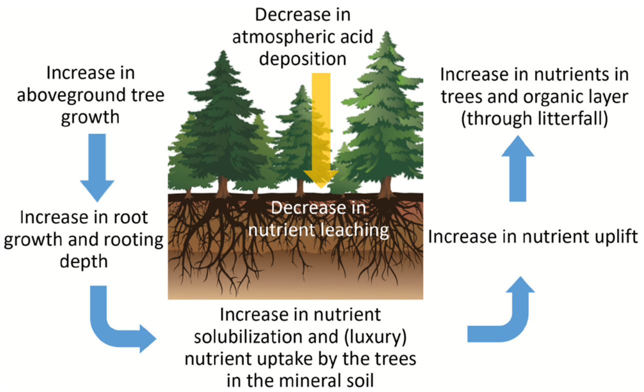

FIGURE 6 | Conceptual figure showing processes that contribute to the increase in exchangeable base cations (Mg, Ca, and Mn) in the organic layer.

The estimated weathering rate for Mg, Ca, and K together is on average about 300 mol_c $\text{ha}^{-1}\text{year}^{-1}$ in Swedish forest soils (Akselsson et al. 2019). This flux is much larger than the increase in Mg and Ca in the organic layer, which equals 12.2 mol_c $\text{ha}^{-1}\text{year}^{-1}$ and 15.4 mol_c $\text{ha}^{-1}\text{year}^{-1}$, respectively, according to our results (see above). Thus, the weathering rate seems to be large enough to replenish the exchangeable Mg, Ca, and Mn pools despite increased plant nutrient uptake caused by increased tree growth. Given that the release of Mg, Ca, and K through weathering is about 20 times larger than the increase in the base cation stocks of the organic layer, weathering is also large enough to provide nutrients to increase the cation pools of the trees, which are several times larger than those of the organic layer and have been increasing due to the increase in standing tree biomass (Karltun et al. 2022). Thus, the increase in base cations has been large enough for increased cation accumulation both in the organic layer and in the biomass.

The fact that the concentrations of exchangeable Mg, Ca, and Mn in the mineral soil differed only little between the third and the fourth inventory (Figure 5) is likely due to the high weathering rate, which constantly replenishes the pool of plant-available cations. The reason for the high weathering rate is mainly the low age of the soils, which only started to develop at the end of the last ice age, that is, 9000 to 14,000 years ago. Due to their low age, the soils are relatively shallow, contain a high volume of stones, and the weathering rate of their parent material is high. Thus, removal of base cations (due to plant uptake or leaching) does not lead to substantial decreases in the pools of exchangeable cations.

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4.4 | Effects of Tree Species on Changes in Base Cations

We found that the concentrations of plant-available Mg and Ca in the organic layer increased more in spruce and birch forests than in pine forests from the first to the fourth inventory (Figure 4, Figure S3). These findings suggest that the increase in nutrient concentrations is related to the characteristics of the tree species. There are multiple reasons for a higher Mg, Ca, and Mn uplift in spruce and birch forests than in pine forests, including differences in transpiration, root distribution, and release of weathering agents by the trees, as detailed in the following.

First, lower Mg and Ca uplift in the pine forests compared to forests dominated by spruce and birch might be due to differences in transpiration, and thus plant water uptake since Mg and Ca are largely taken up passively with the water, through so-called mass flow (Barber 1995; Marschner and Rengel 2023). Pine transpires less than spruce. For instance, transpiration was up to 25% smaller in pine than in spruce stands in Sweden during summer (Cienciala et al. 1998). Furthermore, broadleaf trees generally transpire more than conifers since canopy transpiration is related to the leaf area index (e.g., Ewers et al. 2002). Thus, it seems likely that the higher Mg and Ca uplift in spruce and birch forests is primarily caused by higher canopy transpiration rates in these forests compared to pine, leading to higher passive uptake of nutrients by so-called mass flow.

Second, the differences in nutrient uplift among forests dominated by different tree species are likely also related to differences in fine root biomass and root distribution. This is supported by a higher fine root biomass of spruce than that of pine (Finér et al. 2007; Hansson et al. 2013; Kalliokoski et al. 2008). Furthermore, birch typically has a lower root biomass in the organic layer but a higher root biomass in the mineral soil than pine (Kalliokoski et al. 2008; Hansson et al. 2013). Thus, the fine root biomass and its distribution in soil might be an important factor that explains the differences in nutrient uplift among forests dominated by different tree species.

Third, it is well possible that increased weathering is only a side effect of elevated root biomass because root respiration leads to the formation of carbonic acid in the soil pore water, and organic inputs from the roots stimulate microbial respiration and production of organic acids, which also promote weathering (Hasenmueller et al. 2017). Thus, without actively mining the soil for nutrients, plant roots foster weathering, simply through respiration and root turnover. However, it could be that specific tree species allocate substantial amounts of C and energy to processes fulfilling primarily the function of releasing nutrients from the soil parent material (Finlay et al. 2020). Allocation of C and energy to weathering might be driven by the trees' requirement for nutrients, such as for example phosphorus (P) (Jonard et al. 2015). Future studies should measure the P concentration of the organic layer and of trees to investigate whether there are indications that P is becoming critical for tree nutrition in northern forests.

4.5 | Changes in Sodium and Potassium

We found a decrease in the concentration of exchangeable Na in the organic layer during the four inventories (Figure S1B). The reason for this seems to be the strong enrichment of Mg and Ca in the organic layer since Na competes less successfully for binding sites in soils than the two bivalent metal cations Mg and Ca (Brady et al. 2008). Thus, the increase in the concentrations of the two bivalent metal cations Mg and Ca likely caused a loss of exchangeable Na from the organic layer over the four decades. In addition, it could be that a decrease in Na deposition in the 1990s (Lövblad et al. 2004) contributed to the decrease in the exchangeable Na concentration.

Contrary to Na, the K concentration of the organic layer did not differ significantly between the first and the last inventory (Figure S1A). The capacity of K to compete for sorption sites in soil is not much larger than that of Na (Brady et al. 2008). Yet, K is taken up actively by plants in large quantities against the concentration gradient between the root cells and the soil pore water, in contrast to Na, Mg, and Ca (Marschner and Rengel 2023). The active K uptake by trees and the intensive cycling of K between the plants and the soil likely keep K in the ecosystem and prevent it from leaching out of the organic layer (Spohn and Sierra 2018) in response to Mg and Ca enrichments. The concentration of K differed more strongly among the latitudinal zones than the concentrations of Mg, Ca, and Mn, and it decreased with decreasing latitude (Table 1, Table S3). The reason for the low K concentration in the south of Sweden is likely the fact that K is needed in large quantities by the plants and that plant growth is largest in the south of Sweden (Table 1).

4.6 | Nitrogen Dynamics

We found that the N stock of the organic layer was highest in the second inventory, that is, in the 1990s and at the beginning of the current millennium, across all of Sweden (Figure 2B). The high N stock is likely the result of atmospheric N deposition that was highest in the late 1980s and early 1990s (Hansson et al. 2013; Ferm et al. 2019; Karlsson et al. 2024). The N stocks were significantly lower in the last inventory than in the first inventory. The decrease in the N stock might be caused by the increase in tree biomass over the past decades (SLU 2024; Laudon et al. 2024), which likely resulted in elevated plant N uptake. This is supported by the magnitude of the changes; the N stocks of the organic layer decreased on average by 108 $\mathrm{kg\,ha^{-1}}$ from the second to the fourth inventory (Figure 2), while the wood volume increased on average by 6.5 $\mathrm{m^3\,ha^{-1}}$ during the same time (Figure 1).

Our findings indicate that the current N consumption exceeds the current N inputs in Swedish forests. Thus, it seems that trees in Swedish forests, and particularly in forests in southern Sweden are now in part nourished from past atmospheric N deposition, thus on an N legacy derived mainly from air pollution of the last decades of the last millennium. The decrease in the N stock indicates that plant N uptake offsets N inputs to the organic layer (atmospheric inputs and N_2 fixation) during the last inventory (2013–2022). Thus, the current tree N uptake and N removal with harvest likely aggravate N limitation of forest growth in Sweden over the long term.

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4.7 | Latitudinal Differences

The increase in the plant-available Mg concentration of the organic layer over the four decades was much larger in the south than in the north of Sweden (62% in the southernmost and 28% in the northernmost latitudinal zone; Table 1), despite substantial decreases in atmospheric Mg deposition, particularly in the south of Sweden (Karlsson et al. 2025). Furthermore, the Mn concentration of the organic layer also increased most strongly in the southernmost latitudinal zone (by 55%; Table 1). The Ca concentration increased only in the southernmost zone (by 31%), but not significantly in the other latitudinal zones (Table 1). The fact that the increase in the nutrient contents was stronger in the south than in the north of Sweden is likely related to the larger tree biomass and the larger absolute increase in tree biomass in the south during the four decades (Table 1) as well as to the stronger reduction in atmospheric acid deposition in the south of Sweden. In addition, it might be that the elevated decomposition of the organic layer in the south of Sweden (indicated by the decreased organic layer stock, Table 1) released cations from the non-exchangeable pool, increasing the pool of exchangeable cations in the organic layer.

The organic layer stock decreased significantly in the two southern latitudinal zones (Table 1). This is particularly noteworthy given the increase in wood volume and stem diameter in the south of Sweden (Figure 1, Table 1), which could be expected to cause an increase in the organic layer stock due to elevated plant detritus inputs into the organic layer; yet the opposite is the case. It could be that the decrease in the organic layer in the south of Sweden is related to climate change, and specifically to milder and shorter winters that allow for organic matter decomposition during a larger part of the year. In addition, it could be that the decrease in the organic layer stock in the south of Sweden is a legacy effect of the high atmospheric N inputs in the south of Sweden at the end of the last millennium. One could also speculate that the strong increase in the Mn concentration in the south of Sweden stimulated decomposition of organic matter in the organic layer because Mn affects the activity of manganese peroxidases (Zhang et al. 2024). This is supported by a negative correlation between the plant-available Mn concentration and the carbon stock of the organic layer of Swedish forest soils (Stendahl et al. 2017). Yet, in the last inventory, the organic layer stock across the whole of Sweden was slightly elevated compared to the previous inventory. This might suggest that the increase in tree biomass started to positively affect the organic layer stock during the last years.

5 | Conclusions

We studied nutrient dynamics in northern forests over four decades (1983–2022). Our results show a strong increase in the concentrations of plant-available Mg, Ca, and Mn in the organic layer of Swedish forest soils over four decades despite strong forest growth. There are likely two main reasons for these changes that are not mutually exclusive and that likely both have contributed to the observed increases in exchangeable cations. First, the decrease in acid deposition during the last decades has likely reduced leaching of base cations from the organic layer. Second, increased tree growth has likely caused increased uplift of nutrients from the mineral soil to the organic layer due to tree nutrient uptake in the mineral soil and litterfall. In addition, increased decomposition in the south of Sweden likely released base cations from the organic matter, contributing to the increase in exchangeable base cations in the south of Sweden. In contrast to Mg, Ca, and Mn, the N content of the organic layer decreased over the last decades, after it was comparatively high in the 1990s, which is most likely due to changes in atmospheric N deposition and tree N uptake, the latter resulting from an increase in tree biomass. Against the common concern that strong tree growth and regular harvests deplete soil nutrients, we found that the stocks of Mg, Ca, and Mn in the organic layer increased over the last four decades. Our study indicates that there is a low risk for base cation deficiency and that N will remain the limiting nutrient for tree growth in northern forests.

Author Contributions

M.S. developed and framed research questions, analyzed data, and wrote the paper. E.K. used to lead the SFSI and contributed to the manuscript. J.S. leads the SFSI and contributed to the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The R code and the data to reproduce all figures and tables of this study can be found in Zenodo (https://doi.org/10.5281/zenodo.17578630).

References

Achat, D. L., C. Deleuze, G. Landmann, N. Pousse, J. Ranger, and L. Augusto. 2015. "Quantifying Consequences of Removing Harvesting Residues on Forest Soils and Tree Growth–A Meta-Analysis." *Forest Ecology and Management* 348: 124–141.

Akselsson, C., S. Belyazid, J. Stendahl, et al. 2019. "Weathering Rates in Swedish Forest Soils." *Biogeosciences* 16, no. 22: 4429–4450.

Akselsson, C., O. Westling, M. Alveteg, G. Thelin, A. M. Fransson, and S. Hellsten. 2008. "The Influence of N Load and Harvest Intensity on the Risk of P Limitation in Swedish Forest Soils." *Science of the Total Environment* 404, no. 2–3: 284–289.

Akselsson, C., O. Westling, H. Sverdrup, et al. 2007. "Impact of Harvest Intensity on Long-Term Base Cation Budgets in Swedish Forest Soils." *Acid Rain-Deposition to Recovery* 7, no. 1: 201–210.

Augusto, L., D. L. Achat, M. Jonard, D. Vidal, and B. Ringeval. 2017. "Soil Parent Material—A Major Driver of Plant Nutrient Limitations in Terrestrial Ecosystems." *Global Change Biology* 23, no. 9: 3808–3824.

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Barber, S. A. 1995. *Soil Nutrient Bioavailability: A Mechanistic Approach*. Wiley.

Brady, N. C., R. R. Weil, and R. R. Weil. 2008. *The Nature and Properties of Soils*. Vol. 13, 662–710. Prentice Hall.

Brantley, S. L., J. P. Megonigal, F. N. Scatena, et al. 2011. "Twelve Testable Hypotheses on the Geobiology of Weathering." *Geobiology* 9, no. 2: 140–165.

Cienciala, E., J. Kucera, M. G. Ryan, and A. Lindroth. 1998. "Water Flux in Boreal Forest During Two Hydrologically Contrasting Years; Species Specific Regulation of Canopy Conductance and Transpiration." In *Annales Des Sciences Forestières*, vol. 55. EDP Sciences.

Clarholm, M., and U. Skyllberg. 2013. "Translocation of Metals by Trees and Fungi Regulates pH, Soil Organic Matter Turnover and Nitrogen Availability in Acidic Forest Soils." *Soil Biology and Biochemistry* 63: 142–153.

Denning, A. S. 2022. "Where Has All the Carbon Gone?" *Annual Review of Earth and Planetary Sciences* 50, no. 1: 55–78.

Eriksson, E., E. Karltun, and J. E. Lundmark. 1992. "Acidification of Forest Soils in Sweden." *Ambio* 21: 150–154.

Ewers, B. E., D. S. Mackay, S. T. Gower, D. E. Ahl, S. N. Burrows, and S. S. Samanta. 2002. "Tree Species Effects on Stand Transpiration in Northern Wisconsin." *Water Resources Research* 38, no. 7: 8–11.

Ferm, M., L. Granat, M. Engardt, et al. 2019. "Wet Deposition of Ammonium, Nitrate and Non-Sea-Salt Sulphate in Sweden 1955 Through 2017." *Atmospheric Environment: X* 2: 100015.

Finér, L., H. S. Helmisaari, K. Lõhmus, et al. 2007. "Variation in Fine Root Biomass of Three European Tree Species: Beech (*Fagus sylvatica* L.), Norway Spruce (*Picea abies* L. Karst.), and Scots Pine (*Pinus sylvestris* L.)." *Plant Biosystems* 141, no. 3: 394–405.

Finlay, R. D., S. Mahmood, N. Rosenstock, et al. 2020. "Reviews and Syntheses: Biological Weathering and Its Consequences at Different Spatial Levels–From Nanoscale to Global Scale." *Biogeosciences* 17, no. 6: 1507–1533.

Fridman, J., S. Holm, M. Nilsson, P. Nilsson, A. H. Ringvall, and G. Ståhl. 2014. "Adapting National Forest Inventories to Changing Requirements–the Case of the Swedish National Forest Inventory at the Turn of the 20th Century." *Silva Fennica* 48, no. 3: 1–29.

Friedlingstein, P., M. O'Sullivan, M. W. Jones, et al. 2023. "Global Carbon Budget Earth Syst." *Scientific Data* 15: 5301–5369.

Gauthier, S., P. Bernier, T. Kuuluvainen, A. Z. Shvidenko, and D. G. Schepaschenko. 2015. "Boreal Forest Health and Global Change." *Science* 349, no. 6250: 819–822.

Han, E., F. Li, U. Perkons, et al. 2021. "Can Precrops Uplift Subsoil Nutrients to Topsoil?" *Plant and Soil* 463: 329–345.

Hansen, K., G. Pihl Karlsson, M. Ferm, et al. 2013. "Trender i Kvävenedfall Över Sverige 1955–2011."

Hansson, K., H. S. Helmisaari, S. P. Sah, and H. Lange. 2013. "Fine Root Production and Turnover of Tree and Understorey Vegetation in Scots Pine, Silver Birch and Norway Spruce Stands in SW Sweden." *Forest Ecology and Management* 309: 58–65.

Hasenmueller, E. A., X. Gu, J. N. Weitzman, et al. 2017. "Weathering of Rock to Regolith: The Activity of Deep Roots in Bedrock Fractures." *Geoderma* 300: 11–31.

Hesselmann, H. 1926. "Studier Över Barrskogens Humustäcke, Dess Egenskaper Och Boroende av Skogsvården." *Meddelanden Från Statens Skogsförsöksanstalt* 22: 169–552.

Högberg, P., T. Näsholm, O. Franklin, and M. N. Högberg. 2017. "Tamm Review: On the Nature of the Nitrogen Limitation to Plant Growth in Fennoscandian Boreal Forests." *Forest Ecology and Management* 403: 161–185.

Hyvönen, R., T. Persson, S. Andersson, B. Olsson, G. I. Ågren, and S. Linder. 2008. "Impact of Long-Term Nitrogen Addition on Carbon Stocks in Trees and Soils in Northern Europe." *Biogeochemistry* 89: 121–137.

IUSS Working Group WRB. 2015. "World Reference Base for Soil Resources 2014, update 2015, International Soil Classification System for Naming Soils and Creating Legends for Soil Maps, World Soil Resources Reports No. 106, FAO, Rome."

Jobbágy, E. G., and R. B. Jackson. 2001. "The Distribution of Soil Nutrients With Depth: Global Patterns and the Imprint of Plants." *Biogeochemistry* 53: 51–77.

Jobbágy, E. G., and R. B. Jackson. 2004. "The Uplift of Soil Nutrients by Plants: Biogeochemical Consequences Across Scales." *Ecology* 85, no. 9: 2380–2389.

Jonard, M., A. Fürst, A. Verstraeten, et al. 2015. "Tree Mineral Nutrition Is Deteriorating in Europe." *Global Change Biology* 21, no. 1: 418–430.

Kalliokoski, T., P. Nygren, and R. Sievänen. 2008. "Coarse Root Architecture of Three Boreal Tree Species Growing in Mixed Stands." *Silva Fennica* 42, no. 2: 189–210.

Karlsson, G. P., C. Akselsson, S. Hellsten, and P. E. Karlsson. 2024. "Atmospheric Deposition and Soil Water Chemistry in Swedish Forests Since 1985 – Effects of Reduced Emissions of Sulphur and Nitrogen." *Science of the Total Environment* 913: 169734.

Karlsson, G. P., C. Akselsson, S. Hellsten, V. Kronnäs, P. E. Karlsson, and V. Klemetz. 2025. "Försurning Och Övergödning i Det Svenska Skogslandskapet: Resultat Från Krondroppsnätet Till Och Med 2023/24."

Karltun, E., J. Stendahl, J. Iwald, and S. Löfgren. 2022. "Forest Biomass Accumulation Is an Important Source of Acidity to Forest Soils: Data From Swedish Inventories of Forests and Soils 1955 to 2010." *Ambio* 51, no. 1: 199–208.

Laudon, H., A. A. Mensah, J. Fridman, T. Näsholm, and S. Jämtgård. 2024. "Swedish Forest Growth Decline: A Consequence of Climate Warming?" *Forest Ecology and Management* 565: 122052.

Lövblad, G., C. Persson, T. Klein, et al. 2004. "The Deposition of Base Cations in the Nordic Countries." IVL Svenska Miljöinstitutet.

Lucas, Y. 2001. "The Role of Plants in Controlling Rates and Products of Weathering: Importance of Biological Pumping." *Annual Review of Earth and Planetary Sciences* 29, no. 1: 135–163.

Marschner, P., and Z. Rengel. 2023. "Nutrient Availability in Soils." In *Marschner's Mineral Nutrition of Plants*, 499–522. Academic Press.

McCulley, R. L., E. G. Jobbágy, W. T. Pockman, and R. B. Jackson. 2004. "Nutrient Uptake as a Contributing Explanation for Deep Rooting in Arid and Semi-Arid Ecosystems." *Oecologia* 141: 620–628.

Nilsson, S. I. 1988. "Acidity Properties in Swedish Forest Soils—Regional Patterns and Implications for Forest Liming." *Scandinavian Journal of Forest Research* 3, no. 1–4: 417–424.

Olsson, M., K. Rosén, and P. A. Melkerud. 1993. "Regional Modelling of Base Cation Losses From Swedish Forest Soils due to Whole-Tree Harvesting." *Applied Geochemistry* 8: 189–194.

R Core Team. 2021. "A Language and Environment for Statistical Computing R Foundation for Statistical Computing."

Ranneby, B., T. Cruse, B. Hägglund, H. Jonasson, and J. Swärd. 1987. "Designing a New National Forest Survey for Sweden." *Studia Forestalia Suecica* 177: 1–28.

Sitch, S., M. O'sullivan, E. Robertson, et al. 2024. "Trends and Drivers of Terrestrial Sources and Sinks of Carbon Dioxide: An Overview of the TRENDY Project." *Global Biogeochemical Cycles* 38, no. 7: e2024GB008102.

SLU. 2024. "Skogsdata 2024." Umea.

13652486, 2025, 11, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.70615 by Swedish University Of Agricultural Sciences, Wiley Online Library on [08/12/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Spohn, M., and C. A. Sierra. 2018. “How Long Do Elements Cycle in Terrestrial Ecosystems?” *Biogeochemistry* 139: 69–83.

Spohn, M., and J. Stendahl. 2022. “Carbon, Nitrogen, and Phosphorus Stoichiometry of Organic Matter in Swedish Forest Soils and Its Relationship With Climate, Tree Species, and Soil Texture.” *Biogeosciences* 19, no. 8: 2171–2186.

Spohn, M., and J. Stendahl. 2023. “Spatial Patterns of Nitrogen Isotope Ratios in Forest Soils Are Related to Latitude and Soil Phosphorus Concentration.” *Biogeochemistry* 165, no. 1: 43–56.

Sponseller, R. A., M. J. Gundale, M. Futter, et al. 2016. “Nitrogen Dynamics in Managed Boreal Forests: Recent Advances and Future Research Directions.” *Ambio* 45: 175–187.

Stendahl, J., B. Berg, and B. D. Lindahl. 2017. “Manganese Availability Is Negatively Associated With Carbon Storage in Northern Coniferous Forest Humus Layers.” *Scientific Reports* 7, no. 1: 15487.

Uhlig, D., J. A. Schuessler, J. Bouchez, J. L. Dixon, and F. von Blanckenburg. 2017. “Quantifying Nutrient Uptake as Driver of Rock Weathering in Forest Ecosystems by Magnesium Stable Isotopes.” *Biogeosciences* 14, no. 12: 3111–3128.

Van Der Heijden, G., E. Dambrine, B. Pollier, B. Zeller, J. Ranger, and A. Legout. 2015. “Mg and ca Uptake by Roots in Relation to Depth and Allocation to Aboveground Tissues: Results From an Isotopic Labeling Study in a Beech Forest on Base-Poor Soil.” *Biogeochemistry* 122: 375–393.

Van Der Heijden, G., A. Legout, B. Pollier, J. Ranger, and E. Dambrine. 2014. “The Dynamics of Calcium and Magnesium Inputs by Throughfall in a Forest Ecosystem on Base Poor Soil Are Very Slow and Conservative: Evidence From an Isotopic Tracing Experiment (26 Mg and 44 ca).” *Biogeochemistry* 118: 413–442.

Vergutz, L., S. Manzoni, A. Porporato, R. F. Novais, and R. B. Jackson. 2012. “Global Resorption Efficiencies and Concentrations of Carbon and Nutrients in Leaves of Terrestrial Plants.” *Ecological Monographs* 82, no. 2: 205–220.

Vos, C., A. Don, R. Prietz, A. Heidkamp, and A. Freibauer. 2016. “Field-Based Soil-Texture Estimates Could Replace Laboratory Analysis.” *Geoderma* 267: 215–219.

Zhang, Y., S. E. Hobbie, W. H. Schlesinger, B. Berg, T. Sun, and J. Zhu. 2024. “Exchangeable Manganese Regulates Carbon Storage in the Humus Layer of the Boreal Forest.” *Proceedings of the National Academy of Sciences of the United States of America* 121, no. 13: e2318382121.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** The concentrations of plant available potassium (A), sodium (B), and aluminum (C) as well as the pH (D) of the organic layer in the four inventories conducted between 1983 and 2022. Different capital letters indicate significant ($p < 0.05$) differences among the four inventories. The blue numbers depict the medians. The number of observations (N) is given in the upper right corner of each panel. A few outliers are beyond the plotted range. **Figure S2:** The plant-available calcium concentration of the organic layer in the four inventories depending on the texture of the soil. The blue asterisks indicate a significant ($p < 0.05$) difference between the two texture classes (fine and coarse) tested separately by student's *t*-test for each inventory. The blue numbers depict the medians, and the increase in the calcium concentration from the first to the fourth inventory is indicated in black. A few outliers are beyond the plotted range. **Figure S3:** The plant-available calcium concentration of the organic layer depending on dominant tree species (pine, spruce, and birch) in the four inventories (1–4). Different lowercase letters indicate significant ($p < 0.05$) differences among different tree species in one inventory (given only when significant difference were found). Different capital letters indicate significant ($p < 0.05$) differences among the inventories for one specific tree species. The blue numbers depict the medians, and the increase in the calcium concentration from the first to the fourth inventory is indicated in black. A few outliers are beyond the plotted ran. **Figure S4:** Latitude, texture group, and the magnesium and calcium content of the parent material of forests dominated by either pine, spruce or birch. The blue numbers depict the medians. Different capital letters indicate significant ($p < 0.05$) differences among the tree species. **Figure S5:** Latitude of fine-textured and coarse-textured soils. The blue numbers depict the medians. **Table S1:** Summary of linear models of exchangeable concentrations of magnesium, calcium, and manganese as a function of latitude. **Table S2:** Mass percentage of the main components of the soil parent material. The numbers show means ± standard deviations calculated across the parent material of 1896 soils located all over Sweden. **Table S3:** Results of a 2-way ANOVA. Shown are the *p* values of the independent variables and their interactions. N is the number of observations.

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