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Forest inventory tree core archive reveals changes in boreal wood traits over seven decades

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ABSTRACT

Boreal forests play an important role in the global carbon (C) cycle, and there is great interest in understanding how they respond to environmental change, including nitrogen (N) and water limitation, which could impact future forest growth and C storage. Utilizing tree cores archived by the Swedish National Forest Inventory, we measured stemwood traits, including stable N and C isotope composition which provides valuable information related to N availability and water stress, respectively, as well as N and C content, and C/N ratio over 1950–2017 in two central Swedish counties covering an area of ca. 55,000 sq. km ($n = 1038$). We tested the hypothesis that wood traits are changing over time, and that temporal patterns would differ depending on alternative dendrochronological reconstruction methods, i.e. the commonly applied "single tree method" (STM) or a conceptually stronger "multiple tree method" (MTM). Averaged across all MTMs, our data showed that all five wood traits for *Picea abies* and *Pinus sylvestris* changed over time. Wood $\delta^{15}N$ strongly declined, indicating progressive nitrogen limitation. The decline in $\delta^{13}C$ tracked the known atmospheric $\delta^{13}CO_2$ signal, suggesting no change in water stress occurred. Additionally, wood N significantly increased, while C and C/N ratios declined over time. Furthermore, wood trait patterns sometimes differed between dendrochronological methods. The most notable difference was for $\delta^{15}N$, where the slope was much shallower for the STM compared to MTMs for both species, indicating that mobility of contemporary N is problematic when using the STM, resulting in substantially less sensitivity to detect historical signals. Our study indicates strong temporal changes in boreal wood traits and also indicates that the field of dendroecology should adopt new methods and archiving practices for studying highly mobile element cycles, such as nitrogen, which are critical for understanding environmental change in high latitude ecosystems.

1. Introduction

Boreal forests play an important role in the global carbon (C) cycle due to their capacity to take up and store a considerable amount of global C (Pan et al., 2011; DeLuca and Boisvenue, 2012; Lucas et al., 2016). As the world's largest vegetation type, this circumpolar forest belt covers about 11 % of the Earth's land surface, and stores roughly 272 ± 23 petagrams (1 Pg = 1 billion metric tons) of C, accounting for 32 % of the total terrestrial C stocks (Pan et al., 2011). Since the start of the Industrial Era, anthropogenic activities such as fossil fuel combustion, cement production, and land use changes (Canadell et al., 2007) have caused atmospheric carbon dioxide (CO_2) to rise dramatically. Presently, approximately 11 Pg C of CO_2 are emitted to the atmosphere annually (Friedlingstein et al., 2022) and according to some IPCC (2013) models, atmospheric CO_2 levels are predicted to more than double by the end of the century. Present-day boreal forests not only grow in an atmosphere with >50 % higher CO_2 concentrations compared to pre-industrial levels (NOAA, 2022), but increasing atmospheric CO_2 is also responsible for rising global surface temperatures and associated changes in precipitation (IPCC, 2007) that alter the land-atmosphere vapor pressure deficit, VPD (Yuan et al., 2019), the driving force of water loss through evaporation and transpiration (Rawson et al., 1977). Additionally, the Progressive Nitrogen Limitation (PNL) hypothesis (Hungate et al., 2003; Luo et al., 2004) predicts that increased CO_2 levels may lead to the enrichment of plants with C relative to N (higher C/N ratio) leading to reduced N cycling and availability to forests (Luo et al., 2004). Numerous models predict future climate change will continue to enhance C uptake; however, these predictions are highly uncertain

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(Hungate et al., 2003; Koca et al., 2006; Fang et al., 2014; Ehlers et al., 2017) because they may not consider the development of resource limitations that could gradually constrain forest growth through time (Pretzsch et al., 2018), or changes in the C concentration of major forest C compartments, such as wood.

Given their important role in the global C cycle, there is great interest in evaluating how boreal forests are responding to environmental and management changes. One monitoring tool used to assess forest growth, C stocks, and forest response to change is the systematic collection of stemwood cores by national forest inventories in many forested countries. Trees serve as long-term biological indicators that record the environmental factors that limit or enhance growth in a given period of time (Speer, 2010). So, while tree cores are often collected to measure annual growth increment, they are also used to evaluate a variety of other traits, including wood N content, C content, C/N ratio, as well as N and C isotope values.

Classical dendrochronological protocols involve reconstructing time from individual trees (hereafter referred to as the "single tree method", STM; Fig. 1), which are often selected from extreme sites where stress is greatest, in order to maximize climatic signals found in the annual growth rings (Fritts, 1976). The STM is relevant to address certain types of dendrochronological questions; however, it may have limitations when used in other contexts such as assessing forest-level responses to environmental change. For example, tree cores are increasingly being promoted as tools to provide spatial and temporal resolution of key wood traits related to forest C and N cycling (e.g. wood C and N content; Evans et al., 2022). Stable isotope values can further serve as powerful tools for understanding biogeochemical cycles by integrating element flux processes that play out over spatial and temporal scales (Bahn et al., 2012). Wood δ^{13}C values serve as an indicator for intrinsic water use efficiency (iWUE), with values deviating positively from the atmospheric signal indicating increasing water stress (Saurer et al., 2014). Additionally, the δ^{15}N of plant tissues is indicative of N availability (Poulson et al., 1995; Craine et al., 2018; Mason et al., 2022a), where decreasing δ^{15}N values are considered indicative of slowing or tightening of the N cycle, suggesting lower N availability to plants (McLauchlan et al., 2007; Craine et al., 2018). When chronologies are established from single trees (STM) within forests, both the age of the tree and the forest has changed through time. This may be problematic because the competitive ability of trees for resources, such as N or water, is known to change as trees age (Forrester, 2019); further, nutrient limitation is known to intensify during forest successional time (Bond-Lamberty et al., 2006; DeLuca et al., 2008; Gundale et al., 2011; Gundale et al., 2012). Thus, the STM approach may introduce substantial bias when a project goal is to infer about the average forest's response to long-term environmental change at the landscape scale. An alternative to the STM is to utilize national forest inventory (NFI) archival collections to create tree ring chronologies from multiple trees collected at different points in time from trees of the same age class (i.e. a "multiple tree method", MTM; Fig. 1), which would allow tree age to be held constant, and thus would eliminate biases caused by the above-mentioned ecological processes (Martínez-Sancho et al., 2020). Yet, while the MTM may be conceptually better, a potential drawback of the method is that it might introduce substantial noise associated with incorporating greater site-to-site variation, making temporal trends more difficult to detect.

To address this knowledge gap, we investigated whether five stemwood traits: δ^{15}N, δ^{13}C, N content, C content, and C/N ratios have changed over the period of 1950 to 2017 over a large land area (ca. 55,000 sq. km) in central Sweden. Further, we evaluated whether temporal patterns differed depending on which dendrochronological reconstruction method we employed, i.e. STM vs. MTM. Regarding the MTM, we also evaluated whether patterns differed across three different age classes of trees (Fig. 1). Our project utilized a unique tree core archive resource collected as part of the Swedish NFI, established in 1923 (Thorell and Östlin, 1931) and evolved to include over 30,000 permanent plots measured at 5-year intervals and 910,000 temporary sampling plots measured since 1953, all with corresponding data

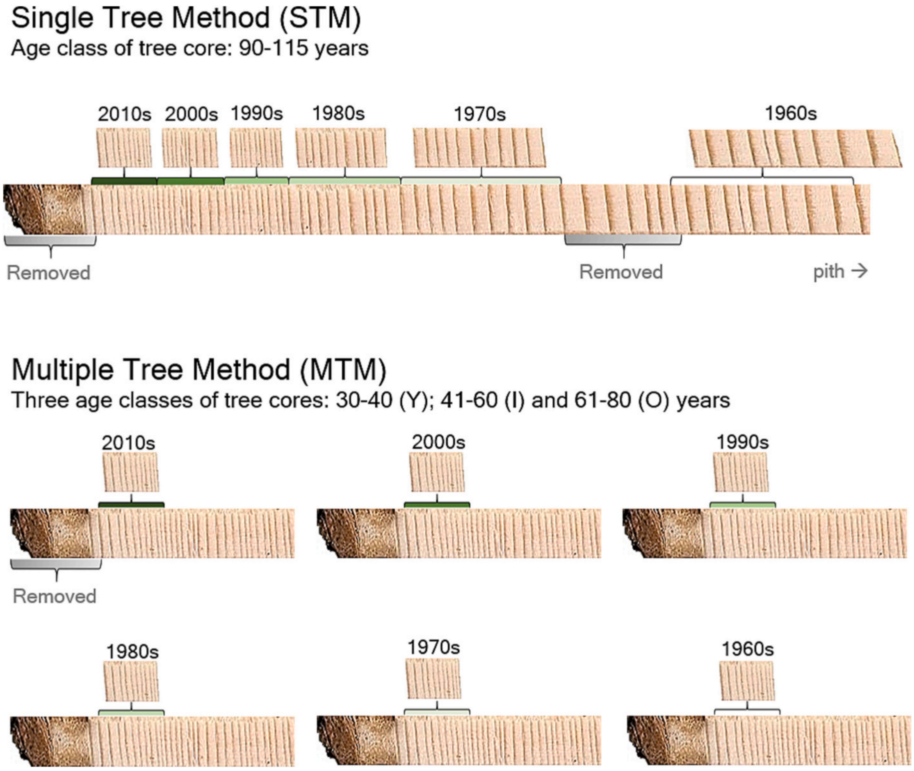

Fig. 1. Representation of sampling for the four alternative methods: STM and MTM-Y, MTM-I, and MTM-O. * Bark, cambium and most recent growth ring were removed from all cores for both methods.

maintained in the NFI database (Fridman et al., 2014). The present-day NFI tree core archive contains systematically collected and archived wood cores from 1961 onward. We isolated and analyzed contemporary and historical cores at the decade scale (10-year segments) from the archive to test the following hypotheses. First, we hypothesized that wood traits: δ^{15}N, δ^{13}C, N and C content, and C/N ratios, would change over time. Specifically, we hypothesized that wood δ^{15}N and N content would decrease with time as a result of PNL, and C content and C/N ratios would increase in association with rising atmospheric CO_2 concentrations. With respect to wood δ^{13}C, we hypothesized a decrease through time, but expected this negative slope to be less steep than the well-known decrease in atmospheric δ^{13}C, which would contribute to increasing iWUE as a response to water stress. Secondly, we hypothesized that the four methods (STM and three age classes of MTM) would differ in their representation of time, with the further expectation that method differences would be more pronounced for N versus C traits, due to greater mobility of N that could obscure historic signals (Nömmik, 1966; Mead and Preston, 1994). To our knowledge, no previous study has directly compared the commonly used STM to the conceptually stronger MTM as an alternative tool for reconstruction of temporal wood trait patterns. Testing these hypotheses will not only provide novel data on how boreal forest properties are changing across a large temporal and spatial scale, but will also provide new insights into the importance of method choice for revealing these patterns.

2. Materials and methods

2.1. Study area and sample selection

The study area includes two counties, Jämtland and Västernorrland (range: 61–65°N, 12–19°E; 0–1796 m.a.s.l.) in central Sweden, and spans an area of 55,687 sq. km. (Fig. 2). This region is characterized by coniferous boreal forest covering coastal, inland, and montane environments. We used 5.15 mm diameter tree core samples collected at breast height (1.3 m), archived by the Swedish NFI as part of its annual surveys. We spatially subdivided the study area by creating a 44-cell grid system; each grid measured 50 × 50 sq. km (Fig. 2), and was either fully or partially within county boundaries. From each 50 × 50 sq. km grid, we selected tree cores from each of the two most abundant and economically important tree species in Sweden: Norway spruce (*Picea abies* L. Karst) and Scots pine (*Pinus sylvestris* L.). Cores were selected from six archived decades, 1960s to the 2010s, which allowed us to evaluate a date range from 1950 to 2017 (described further below). Tree cores were randomly selected from the NFI archive database using the following criteria: i) dominant or co-dominant trees; ii) mesic, well-drained sites; and iii) sites with 20 % slope or less ($n = 1038$). We prepared each core by removing the outer bark and cambium, as well as the most recent annual ring to avoid including an incomplete year of growth due to variability in the timing of core collection during the growing season (Fig. 1). We then sectioned the target 10-year growth segment(s) using a No.11 stainless steel surgical blade under a stereo microscope with a 20× magnification, which had an accuracy of 0.01 mm. No false rings were observed. For the purposes of this study, we compared four alternative collection methods: one STM and three MTMs (Fig. 1). The STM consisted of archived tree cores that were collected from 90 to 115 year old trees that were cored in the most recent decade (2010s); thereby, all six representative decade segments in a given grid location were derived from a single tree core. Alternatively, for the MTM, a different tree core was removed from the archive to represent each decade in each grid such that the tree age could be held constant (Fig. 1). We employed this approach for three different tree age classes: 30–40 (young, Y), 41–60 (intermediate, I) and 61–80 (old, O) years old, hereafter referred to as MTM-Y, MTM-I, and MTM-O, respectively. To obtain sufficient tree cores for the STM method, we gathered cores originally collected in 2016–2018 and for each of the MTM age classes, we used cores that were originally collected in 2016–2018, 2006–2008, 1996–1998, 1986–1988, 1977 and 1961 (Table 1). Samples were then categorized according to the 'average growth year' of the decadal period. For example, for a core collected in 2017, analysis was done for increment period 2006–2016, and was assigned an 'average growth year' of 2011. For decades where cores were utilized from multiple collection years (i.e., 2016–2018), the middle of those three years (i.e., 2017) was used for classification. In order to create an identical time series between the STM and MTMs, we removed a five-year section of tree rings (1961–1965) from the STM to correspond with the offset in sampling years for the 1960s (1961) and 1970s (1977; Fig. 1).

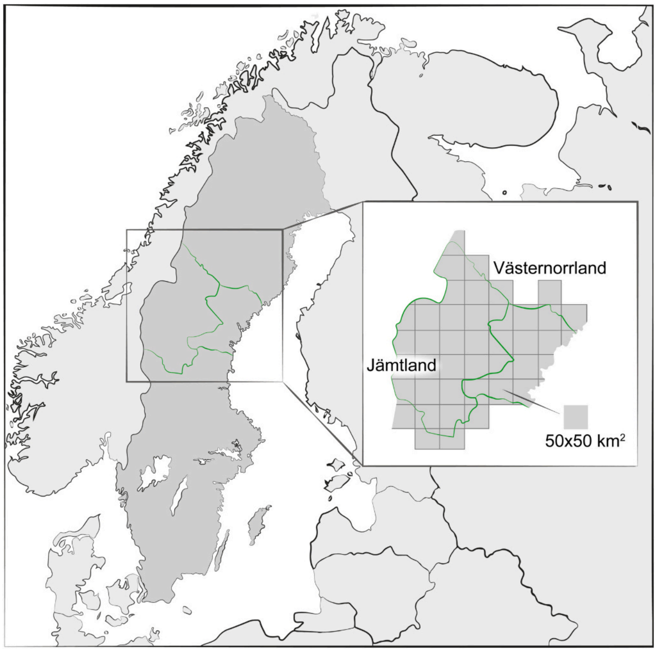

Fig. 2. A map of the study area, Jämtland and Västernorrland counties in central Sweden. The gray squares represent 50 × 50 sq. km sampling grids. The green lines are the approximate boundaries of the two counties.

2.2. Nitrogen and carbon stable isotope analysis

Measurement of nitrogen (δ^{15}N) and carbon (δ^{13}C) isotope ratios, and N and C content were analyzed at the Central Appalachians Stable Isotope Facility (CASIF), University of Maryland Center for Environmental Science (UMCES) Appalachian Laboratory (Frostburg, MD, USA) with a Carlo Erba NC2500 elemental analyzer (CE Instruments Ltd., Wigan, UK) interfaced with a Thermo Finnigan Delta V+ isotope-ratio mass spectrometer (IRMS, Waltham, MA, USA). The Carlo Erba NC2500 Elemental Analyzer with Costech zero-blank autosampler modifications permits for analysis of N and C isotopes in solid organic samples with <0.5 % N such as wood (Elmore et al., 2016; R. Paulman, personal communication, 2023). For each core, a radial slice was precisely sectioned to represent each 10-year segment. Approximately 10 and 1 mg of wood from the core segment was weighed for analysis of δ^{15}N and δ^{13}C, respectively. For δ^{15}N analysis, a Carbosorb trap was used to remove CO_2 in advance of removing water vapor with $MgClO_4$; whereas, for δ^{13}C analysis, an $MgClO_4$ trap was used to remove water vapor before the transfer of sample gases to the IRMS. The δ^{15}N and δ^{13}C data were normalized to the Ambient Inhalable Reservoir (AIR) and Vienna Pee Dee Belemnite (VPDB) scales, respectively, using a two-point normalization curve with internal standards, including ground corn, cocoa, and caffeine powder calibrated against international standards, USGS40 and USGS41. Analytical precision (1σ) of an internal wood standard (ground pine powder) analyzed alongside samples was 0.3 ‰ for δ^{15}N and 0.1 ‰ for δ^{13}C; atropine powder was used for determining N and C content values.

Table 1

The number of samples for each method: single tree (STM) and multiple tree (MTM) by method, species (*Pinus sylvestris*, *Picea abies*), average growth year, and sampling years.

Average growth year		1955	1971	1981			1991			2001			2011			
Sampling years		1961	1977	1986	1987	1988	1996	1997	1998	2006	2007	2008	2016	2017	2018	**Total (*n*)**
Method	Species															
STM	*P. sylvestris*	–	–		–			–			–		18	66	36	120
	P. abies	–	–		–			–			–		36	42	48	126
MTM-Y	*P. sylvestris*	8	22	9	8	1	6	10	6	6	9	6	6	11	7	115
	P. abies	12	20	7	2	4	3	7	5	4	4	10	8	5	7	98
MTM-I	*P. sylvestris*	19	26	13	6	2	6	13	3	4	8	9	11	10	6	136
	P. abies	18	32	9	11	7	6	12	4	6	6	8	9	11	4	143
MTM-O	*P. sylvestris*	25	29	8	15	4	12	8	3	5	8	5	4	10	3	139
	P. abies	26	32	13	12	5	13	12	5	4	10	10	6	10	3	161
	Total (*n*)	108	161	59	54	23	46	62	26	29	45	48	98	165	114	**1038**

2.3. *Analysis of stable nitrogen and carbon isotope ratios*

The ratio of heavy to light isotopes of N samples, $^{15}N{:}^{14}N$ and C samples, $^{13}C{:}^{12}C$ samples are expressed in standard delta (δ) notation with reference to a standard of known isotopic ratio.

$$\delta^{15}N = \left(\left[R_{sample}/R_{standard}\right] - 1\right) \times 1000$$

and

$$\delta^{13}C = \left(\left[R_{sample}/R_{standard}\right] - 1\right) \times 1000$$

where R_{sample} and $R_{standard}$ are the ratios of the heavy to light isotopes in the sample and standard, respectively and are expressed in units of parts per thousand or per mil (‰). The chosen standard for N and C are AIR and VPDB, respectively.

2.4. *Carbon isotope discrimination (Δ) and iWUE calculations*

In C3 plants, carbon isotope discrimination (Δ) can serve as an integrated measure of iWUE (Farquhar et al., 1989) and is written as (Farquhar et al., 1982):

$$\Delta = \frac{\delta^{13}C_{AIR} - \delta^{13}C_P}{\left(1 + \left[\frac{\delta^{13}C_P}{1000}\right]\right)} \tag{1}$$

where Δ is carbon discrimination by the plant; $\delta^{13}C_{AIR}$ is the carbon isotope value of the atmosphere (‰); and $\delta^{13}C_P$ is the carbon isotope value of the plant material (‰). The $\delta^{13}C_{AIR}$ values and the CO_2 concentration in the atmosphere, C_a, for the period of 1950–2004 were taken from McCarroll and Loader (2004); this data was then used to derive values for the period 2005–2017 by adding the rate of change over time taken from the linear regression of the data (0.0252 ‰) per year. The derived rate of change for $\delta^{13}C_{AIR}$ was most consistent with the Scripps data for the period 2004–2017 (−0.0244 ‰ per year) and determined suitable for this application. C_a for the period of 2005–2017 was obtained from the National Oceanic and Atmospheric Administration (NOAA) Global Monitoring Laboratory recorded at PAL: Pallas-Sammaltunturi, GAW Station, Finland (67.9733°N, 24.1157°E; 565 masl; Lan et al., 2022), the monitoring station most similar to the study area in terms of latitude and climate. Δ was calculated using the measured $\delta^{13}C_P$ values from tree rings. Furthermore, Δ is also a function of the intercellular and atmospheric CO_2:

$$\Delta = a + (b - a) \times \left(\frac{C_i}{C_a}\right) \tag{2}$$

where a is the isotopic discrimination associated with diffusion of CO_2 from the atmosphere into the intercellular leaf spaces via the stomata (∼4.4 ‰); b is the net fractionation occurring during carboxylation (∼27 ‰); and $\frac{C_i}{C_a}$ are the intercellular (C_i) and atmospheric (C_a) CO_2 concentrations. Intercellular CO_2 concentrations, C_i are obtained based on Eqs. (1) and (2); and iWUE is calculated as follows (Ehleringer et al., 1993):

$$iWUE = \frac{A}{g_s} = C_a \times \left[\left(1 - \frac{C_i}{C_a}\right) \div 1.6\right] \tag{3}$$

where $\frac{A}{g_s}$ is the ratio of net photosynthetic assimilation rate, A to stomatal conductance, g_s for water vapor; and 1.6 is the constant representing the ratio of diffusivity of water vapor and CO_2 in the air.

2.5. *Statistical methods*

Statistical analysis was performed using R v.4.2.2 (R Core Team, 2022). We first performed separate linear regressions for each species (*P. sylvestris* and *P abies*) and wood trait using only the MTM data (i.e. 3 age classes) including the mean for each decade to establish baseline historical patterns from data derived from the conceptually stronger approach; further, we performed linear regressions examining iWUE as a function of time on the MTM data for each species to determine if significant change occurred. We then performed a factorial linear model for each trait and tree species (*P. sylvestris* and *P. abies*) with time, method, and their interaction serving as fixed factors using Type III sum of squares, ANOVA (package 'tidyverse'). Further, we performed separate follow-up two-way ANOVAs with post-hoc pairwise comparisons ($p = 0.05$) to identify differences in regression slopes between the four methods for each species and trait (package 'emmeans'). And lastly, we calculated the root mean squared error, RMSE (package 'rmse') of the different methods for each of the five traits to compare prediction errors.

3. Results

3.1. *Mean temporal response of wood traits*

The MTM data showed a significant main effect of time for both *P. sylvestris* and *P. abies* for all five wood traits measured (Table 2, Fig. 3). Both $\delta^{15}N$ and $\delta^{13}C$ showed a significant decrease over time for both species, and a 95 % confidence interval of our $\delta^{13}C$ slope indicates that the decline was equal to or slightly steeper than the rate of atmospheric $\delta^{13}C$ decline (approximately 0.025 ‰ per year) for *P. sylvestris* (−0.025 to −0.033 ‰) and *P. abies* (−0.028 to −0.037 ‰). There was a significant increase in N content, while C content and C/N ratio showed a significant decrease over time for each of the species. Additionally, iWUE showed a significant increase over time for both *P. sylvestris* and *P. abies* (Fig. 4).

Table 2
Tests of between-subjects effects for traits: δ^{15}N, N content, C content, C/N ratio, and, δ^{13}C for *Pinus sylvestris* and *Picea abies*.

Variable			δ^{15}N (‰)		N (%)		C (%)		C/N ratio		δ^{13}C (‰)	
Source	Species	*df*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Time	*P. sylvestris*	1	**123.435**	**<0.001**	**50.955**	**<0.001**	**81.701**	**<0.001**	**86.289**	**<0.001**	**239.293**	**<0.001**
	P. abies	1	**50.939**	**<0.001**	**33.742**	**<0.001**	**85.629**	**<0.001**	**73.049**	**<0.001**	**208.579**	**<0.001**
Method	*P. sylvestris*	3	**5.467**	**0.0011**	1.827	0.1413	1.079	0.3576	0.796	0.4968	2.049	0.1061
	P. abies	3	**3.323**	**0.0196**	**4.527**	**0.0038**	**7.399**	**<0.001**	**3.788**	**0.0104**	0.240	0.8683
Time: method	*P. sylvestris*	3	**5.293**	**0.0013**	1.802	0.1458	1.0689	0.3620	0.783	0.5040	2.069	0.1034
	P. abies	3	**3.251**	**0.0216**	**4.4123**	**0.0045**	**7.305**	**<0.001**	**0.368**	**0.01215**	0.244	0.8658

P. sylvestris residual $df = 502$; *P. abies* residual $df = 520$. δ^{15}N (‰): *P. sylvestris*: $R^2 = 0.2736$; adjusted $R^2 = 0.2635$; *P. abies*: $R^2 = 0.1247$; adjusted $R^2 = 0.1129$. N content (%): *P. sylvestris*: $R^2 = 0.1164$; adjusted $R^2 = 0.104$; *P. abies*: $R^2 = 0.1346$; adjusted $R^2 = 0.123$. C content (%): *P. sylvestris*: $R^2 = 0.1458$; adjusted $R^2 = 0.1339$; *P. abies*: $R^2 = 0.1876$; adjusted $R^2 = 0.1767$. C/N ratio: *P. sylvestris*: $R^2 = 0.1636$; adjusted $R^2 = 0.1519$; *P. abies*: $R^2 = 0.1953$; adjusted $R^2 = 0.1844$. δ^{13}C (‰): *P. sylvestris*: $R^2 = 0.3364$; adjusted $R^2 = 0.3271$; *P. abies*: $R^2 = 0.296$; adjusted $R^2 = 0.2866$. ***F* and *p* values in bold show significant differences at $p < 0.05$.**

3.2. Comparison of sampling methods

For *P. abies*, four of five traits (δ^{15}N, N and C content and C/N ratio) responded signficantly to the interaction between time and method, while δ^{13}C was unresponsive to a method by time interaction (Fig. 5). For the variable δ^{15}N, this interaction occured because the STM had a signficantly shallower slope than all three MTMs. For N content, the STM exhibited a steeper slope, with values of the first decade starting at a lower value than for the MTMs (see STM, Fig. 5). For C content, the slope of STM was shallower than MTM-Y, MTM-I and MTM-O, which all exhibited a strongly significant decline through time. Regarding the C/N ratio, the STM exhibited a steeper slope and higher starting value during the first decade than all three MTMs.

For *P. sylvestris*, δ^{15}N responded significantly to the interaction between time and method between all four methods; whereas, δ^{13}C, N and C content, or C/N ratio were not affected by method (Fig. 6). For the variable δ^{15}N, this interaction occured because the STM method had a signficantly shallower slope and a much lower starting value compared to all three MTMs.

4. Discussion and conclusions

Our aim was to provide novel data on how wood traits in boreal forests are changing through time, and to evaluate the traditional dendrochronological STM approach against a conceptually stronger MTM approach. We found that all wood traits we measured, δ^{15}N, N and C content, C/N ratio, and δ^{13}C have changed over time (1950–2017) for both *P. sylvestris* and *P. abies* (Fig. 3), and that these patterns sometimes differed between methods (Figs. 5, 6).

4.1. Mean temporal response of wood traits

In support of our first hypothesis, we found a significant decline in wood δ^{15}N for both *P. sylvestris* and *P. abies* ($p < 0.01$; $p < 0.01$, respectively) over the period of 1950–2017. Several previous studies have provided evidence that wood (Poulson et al., 1995; McLauchlan et al., 2007; McLauchlan and Craine, 2012) or foliar (Craine et al., 2009; Craine et al., 2018) δ^{15}N values are declining with time; however, it is notable that the magnitude change we observed using the MTM (ca. 4 ‰ decline over 70 years) is much steeper than previously reported (e.g., Kranabetter et al., 2013; McLauchlan et al., 2017; Oulehle et al., 2022). Several mechanisms have been proposed to explain these temporal declines in δ^{15}N. First, isotopic signature of δ^{15}N of soil and plants are considered to be sensitive to N cycling and availability in forests (Poulson et al., 1995; Högberg, 1997; Craine et al., 2009). Specifically, ecosystems with low mineralization rates have lower N loss rates, e.g. via nitrification, denitrification, and leaching which lead to greater loss of ^{14}N relative to ^{15}N, and are thus associated with lower δ^{15}N values. Reductions in the δ^{15}N signature through time have been interpreted as evidence of the Progressive Nitrogen Limitation (PNL) hypothesis, which results from elevated CO_2 and subsequent ecosystem N limitation (Luo et al., 2004; Mason et al., 2022a). Thus, a tightening of N cycling and reduction in N losses in response to elevated CO_2 (i.e. PNL hypothesis) may explain the decline in δ^{15}N signatures we observed through time. In addition to PNL, another non-mutually exclusive mechanism that could explain the observed decline in wood δ^{15}N values is greater reliance of trees on mycorrhizal fungi for acquiring N in response to elevated CO_2 (Näsholm et al., 2013; Franklin et al., 2014; Hasselquist et al., 2016). Mycorrhizal fungi are known to retain the heavier ^{15}N atom and pass the depleted N onto the plant (Hobbie and Högberg, 2012) resulting in lower δ^{15}N values in plant tissues. Finally, a counter-argument to the PNL explanation for declining δ^{15}N values is that the total amount and δ^{15}N signature of anthropogenic N deposition has declined for approximately three to four decades (Olff et al., 2022). However, we note that the decline in δ^{15}N we observed in our wood data started at least one decade prior to peak atmospheric N deposition rates in Sweden, which occurred in the early 1980s (Lajtha and Jones, 2013; Ferm et al., 2019). We also note that atmospheric N deposition rates in our study area are relatively low (<4 kg N ha^{-1} yr^{-1}), and experimental work in northern Sweden has shown that long-term anthropogenic N inputs at this rate do not alleviate N limitation (Gundale et al., 2014). Finally, nutrient discharge data from Swedish streams has shown long-term declines in inorganic N, including areas far north of our study area, where atmospheric N deposition rates are <1 kg ha^{-1} yr^{-1} (Lucas et al., 2016), indicating that terrestrial N limitation is increasing, independent of temporal trends in N deposition. While changes in atmospheric N deposition may be partly responsible for the declining wood δ^{15}N signatures we observe, these studies suggest other change factors, such as increasing atmospheric CO_2, are likely key drivers of this pattern (Mason et al., 2022a, 2022b).

Contrary to expectations, our data did not show a significant decrease in N content with time for either species, but rather, we observed a significant increase. One potential explanation for this pattern is that rising atmospheric CO_2 has stimulated trees to invest more energy into N uptake via mycorrhizae, which could potentially result in both higher wood N and lower δ^{15}N values. However, several previous studies on stemwood N concentrations have concluded that wood N content may not serve as a useful indicator of ecosystem N availability, but rather is more responsive to internal physiological drivers versus environmental conditions (Poulson et al., 1995; Doucet et al., 2011). Because N accounts for such a small fraction of wood mass (i.e., 0.03–0.10 % N; Cowling and Merrill, 1966), wood N content may inversely respond to changes in other constituents of wood. In fact, several studies have shown that wood N content is unresponsive to fertilizer addition, whereas δ^{15}N values are highly responsive (Schleppi et al., 1999; Hart and Classen, 2003; Balster et al., 2009). Furthermore, Gerhart and McLauchlan (2014) highlighted that wood δ^{15}N and N concentration are not consistently correlated across studies, and concluded that δ^{15}N is a more sensitive measure of temporal changes in N availability.

In addition to N content, an additional unexpected pattern we observed was that wood C content decreased over time, rather than

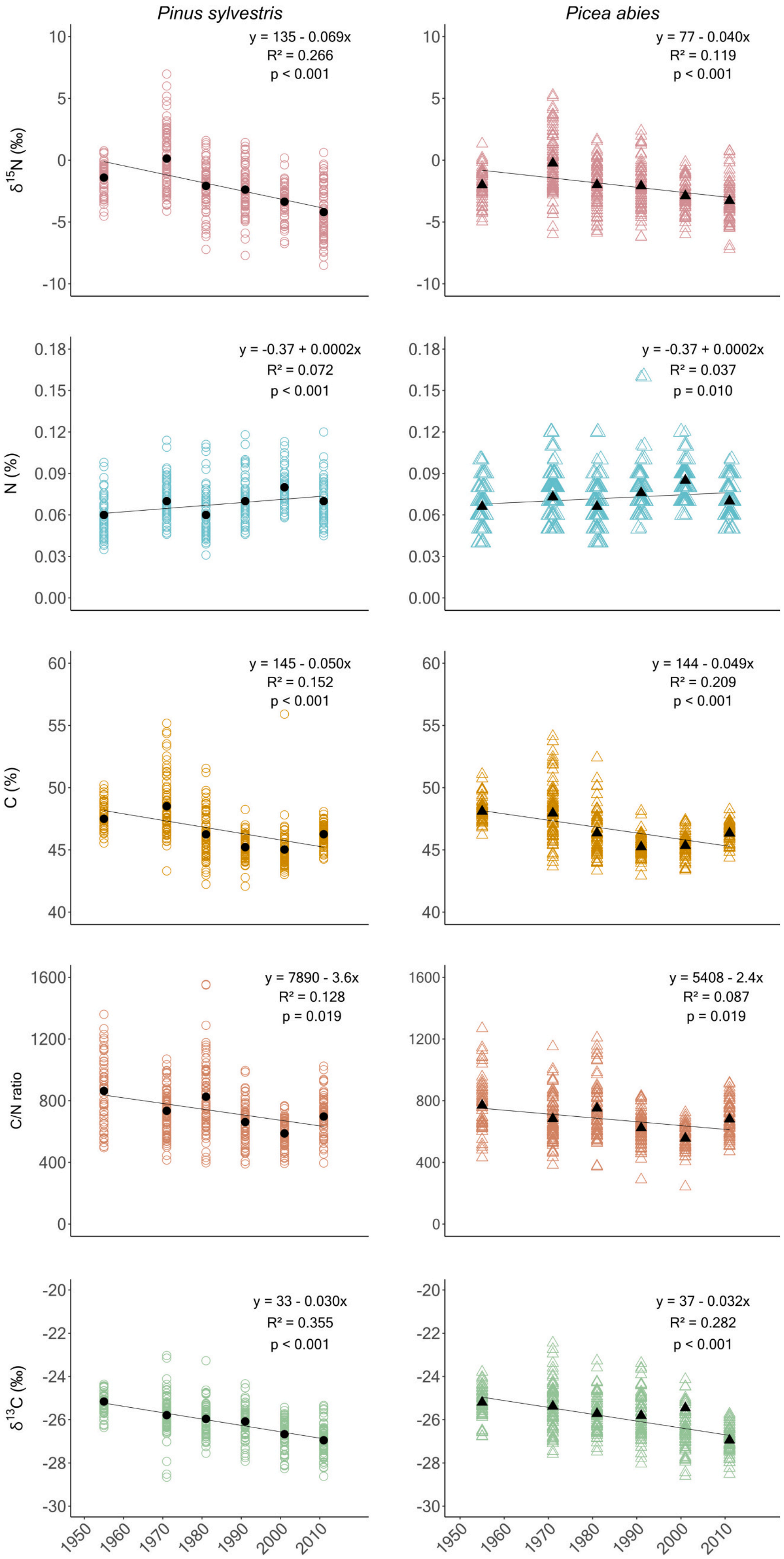

Fig. 3. The composite temporal response of five wood traits, δ^{15}N, N content, C content, C/N ratio, and δ^{13}C for species *Pinus sylvestris* (left-hand panels) and *Picea abies* (right-hand panels) for the three MTMs (young, intermediate and old). Means per decade for each trait and species are indicated by the black symbols. Note: The R ggplot jitter function was applied for N content (*P. abies*) to horizontally offset overlapping data points.

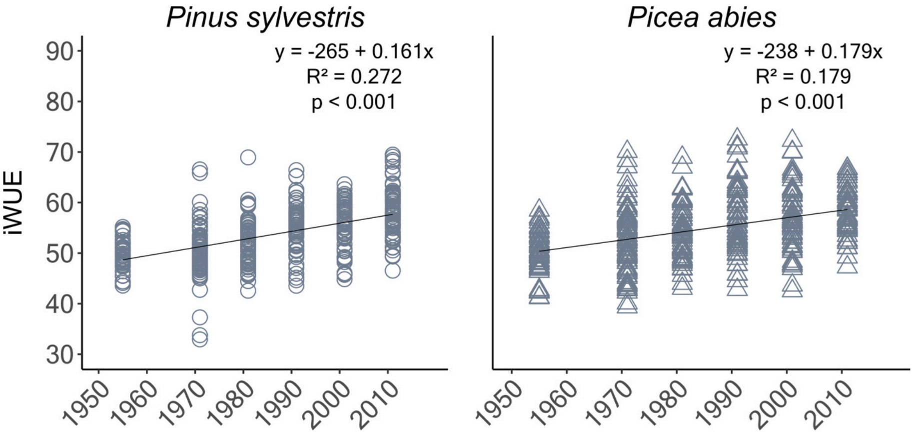

Fig. 4. The composite temporal response of iWUE for *Pinus sylvestris* and *Picea abies* for the three MTMs (young, intermediate and old).

increased, which partially explained the decline in the C/N ratio. The reduction in wood C content, which accounts for nearly 50 % of the mass of wood, may also partially explain the observed increase in N, given that a ca. 7 % change in the most abundant wood element (i.e., C) would cause other elements to become more concentrated. However, the percent increase in N contents we observed were greater than the decrease in wood C contents, at least for *P. sylvestris*. Hence, other factors may also be important for explaining increases in wood N content, such as changes in wood oxygen (O) content. One possible explanation for the decline in wood C content could be a shift towards a higher proportion of latewood versus earlywood in our samples; the former having a lower C content than the latter (Lamlom and Savidge, 2003). In support of this mechanism, several studies have shown that climate change has corresponded with an increase total production of latewood (Arzac et al., 2019), as well as earlier seasonal transition from earlywood to latewood production (Buttò et al., 2021).

Another concurrent change that could potentially explain a decrease in wood C is a reduction in lignin and an increase in cellulose content, which differ in their percent C (ca. 40–45 % and 26–34, respectively; Zobel and van Buijtenen, 1989; Lamlom and Savidge, 2003; Rowell et al., 2012). Finally, N fertilization studies have shown that higher C content in earlywood production (van Buijtenen, 2004) increases in response to N; thus, the long-term reduction in N availability (i.e., PNL) may contribute to a greater portion of lower C content of latewood versus earlywood. Future analysis of the earlywood and latewood transition on individual annual rings, as well as analysis of lignin/cellulose ratio could provide additional clarity on the mechanisms driving the changes in wood N, C, and C/N ratio we observed.

Our data also showed that δ^{13}C values have declined over time for both species, (*P. sylvestris*: $p < 0.01$; *P. abies*: $p < 0.01$); however, this rate of change is consistent with declining δ^{13}C values observed in atmospheric CO_2 worldwide (Mook, 1983; Keeling et al., 1984). Inconsistent with our hypothesis, the rate of change we observed was not significantly less steep than the average decline over time in the δ^{13}C of atmospheric CO_2, (approximately 0.025 ‰ per year) as a result of the addition of δ ^{13}C-depleted fossil fuel-derived CO_2 inputs to the atmosphere (Suppl. Table 1; McCarroll and Loader, 2004; Belmecheri and Lavergne, 2020). Calculations of iWUE are based on atmospheric and plant δ^{13}C values, as well as atmospheric CO_2 concentration (Adams et al., 2020; Mathias and Thomas, 2021), which indicate an increase in iWUE through time in our study area (Fig. 4). This increase in iWUE was entirely driven by the change in the atmospheric CO_2 concentration that has occurred over our analysis period, rather than a change in δ^{13}C fractionation processes during photosynthesis. This suggests that while forests may use water more efficiently per unit of CO_2 acquired, this does not appear to part of a tree stress response (Saurer et al., 2014), as has been observed in some studies of northern temperate forests of North America and Europe (Keenan et al., 2013). Our hypothesis of increased water stress is based on predictions that despite increases in annual precipitation for the period of 1950–2018 (SMHI, 2022), a shift towards less frequent and more intense summer precipitation events are occurring. This may eventually lead to increased run-off and less water retained by forests (IPCC, 2013; Lucas et al., 2016) which could potentially constrain growth and limit C storage. Likewise, climate warming is gradually increasing the land-atmosphere vapor pressure deficit, VPD, which is the driving force of water loss through evaporation and transpiration (Yuan et al., 2019). Increases in VPD have been shown to decrease photosynthetic rates (Fletcher et al., 2007); however, while increasing VPD is emerging as a trend in forests globally (Yuan et al., 2019), our data suggest increasing VPD has not yet crossed a threshold that is clearly impacting the photosynthetic fractionation processes of trees in our study area. In fact, the relative change in total volume growth for our study area (Västernorrland and Jämtland counties) was +3 and +21 %, respectively, between 2005 and 2012; whereas between 2012 and 2016 total volume growth changed by 0 %. This may indicate that volume growth is slowing, potentially due to PNL, but that growth has not yet turned negative as a result of severe drought. In contrast, drought events have been relatively more severe in southern Swedish counties during this period, and annual growth decreased by an average of −8 % during the 2012–2016 period (range −15 to +2 % among the counties in the region; Fridman et al., 2022).

4.2. Difference in methodological sampling approaches

Our analysis indicated that temporal patterns of several traits we measured were sensitive to method choice (i.e. MTM-Y, MTM-I, and MTM-O and STM). We found that δ^{15}N was far more impacted by method choice, whereas δ^{13}C data was not responsive to method choice, which is consistent with our hypothesis. The lack of δ^{13}C response to method is likely due to the non-mobile nature of C once fixed into long-term tissues and compounds, making contamination from contemporary C (e.g. sugars) very minor compared to the pool of C fixed into these long-term pools (Higuchi, 1997). Regarding δ^{15}N, temporal trends never differed between the three different MTMs, whereas the STM almost always differed from the MTMs for both *P. sylvestris* and *P. abies*. We found that all four methods converged on a similar final δ^{15}N value (approx. −4 ‰) in the most recent decade (2010s), while the starting values for the earliest decade (1950s) for the STM and MTMs were much different, −3 ‰ and 0 ‰, respectively. Nitrogen demonstrates high mobility among tree rings of different ages including remobilization of N to active growth regions as well as translocation within stems into older tree rings via ray parenchyma cells (Nömmik, 1966; Mead and Preston, 1994; Schleppi et al., 1999; Tomlinson et al., 2014), thus, the most parsimonious explanation for the relative flatness of the STM slopes is

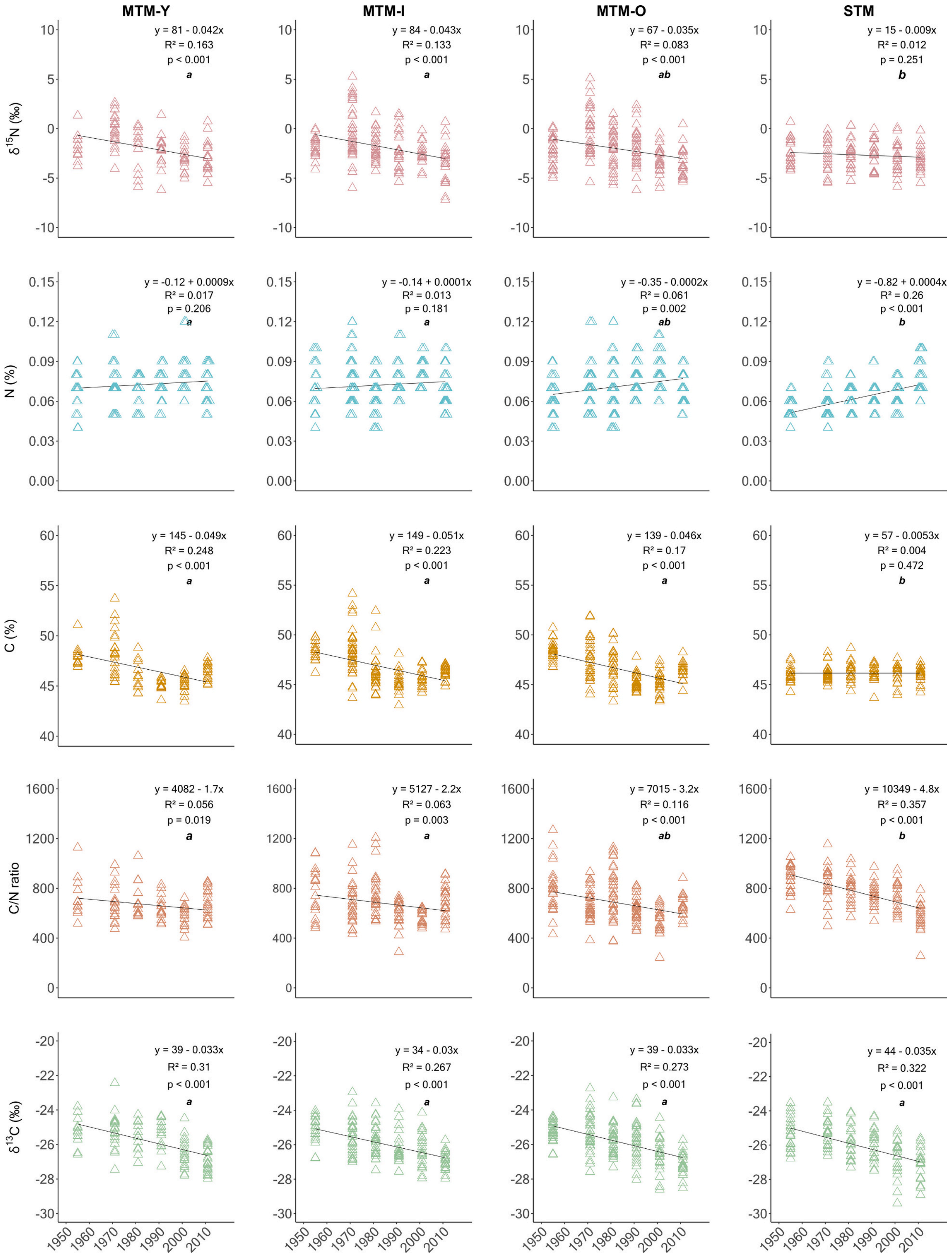

Fig. 5. Linear regression for five wood traits by method: δ^{15}N, N content, C content, C/N ratio, and δ^{13}C over six decades for *Picea abies* with pairwise comparisons of the methods. Pairwise differences between the slopes of each method for each trait (in rows) are indicated by **bold**, *italicized* letters in each panel. Note: The R ggplot jitter function was applied for N content to horizontally offset overlapping data points.

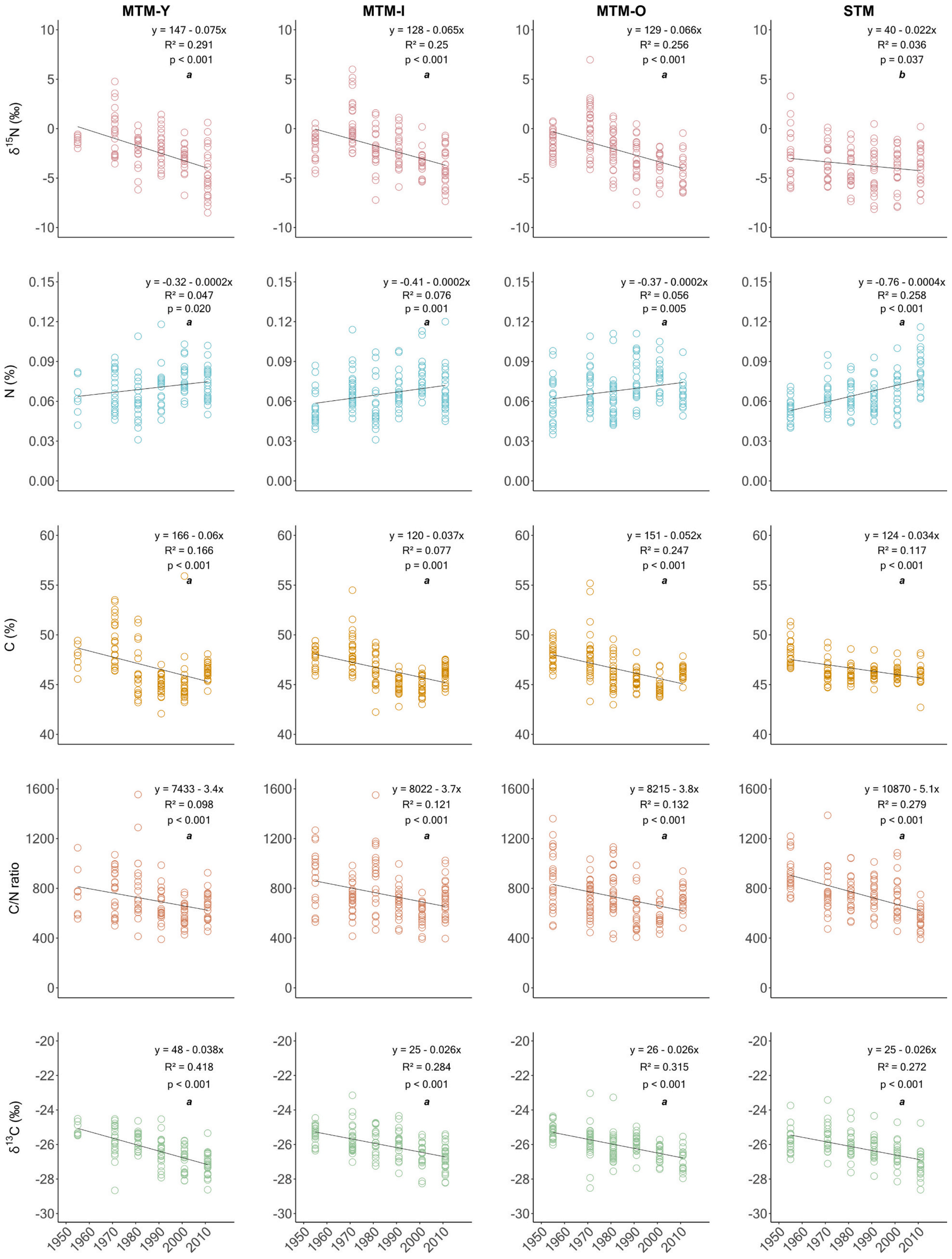

Fig. 6. Linear regression for five wood traits by method: $\delta^{15}N$, N content, C content, C/N ratio, and $\delta^{13}C$ over six decades for *Pinus sylvestris* with pairwise comparisons of the methods. Pairwise differences between the slopes of each method for each trait (in rows) are indicated by **bold**, *italicized* letters in each panel.

that the oldest segments (1950s) are contaminated by contemporarily-acquired N transported in the xylem water (Peuke, 2010) at the time of sampling. Thus, the STM appears to be an inherently limited and insensitive approach to evaluate temporal changes in $\delta^{15}N$, because of the greater opportunity for contemporary physiological and ecological processes to obscure historical signals.

In addition to $\delta^{15}N$, we observed significant differences in temporal patterns among the methods for N, C and C/N ratio, but only for *P. abies*. Interestingly, temporal responses for these three traits exhibited much shallower slopes for MTM than the STM, which contrasts the response described above for $\delta^{15}N$, where responses were stronger for the MTM. This may suggest that *P. abies* wood undergoes stronger changes in wood anatomy or chemistry during aging compared to *P. sylvestris*. Wood C and N content, and C/N ratios can have important implications for ecosystem properties and process, such as estimation of forest C stocks, or as predictors of wood decomposition rates. In regards to forest C, stock estimates often assume a wood C content of 50 % (Doraisami et al., 2022). It is notable that our data suggests a substantially lower and decreasing C content with time, at least for the outer sapwood, which was the focus of our study. While both STM and MTM methods found similar temporal patterns, our comparison of methods suggests that reliance on the classical STM approach would likely exaggerate temporal change in these traits.

While conceptually the MTM is a better approach to evaluate changes in wood traits because it removes the potential influence of tree aging or forest succession on growth and nutrient acquisition, we also considered the potential drawback that using the MTM might have by introducing excessive noise that could make temporal trends difficult to observe. However, our results of the root mean squared error (RMSE) do not show a consistent increase in noise associated with the MTMs across the traits for the two species (Suppl. Table 1). This indicates that there appears to be no major downside for using the MTM approach.

Over 100 countries across Europe, Asia, Africa, and the Americas, accounting for a large amount of the Earth's forested landscape (Suppl. Fig. 1), actively conduct, have capacity in place, or are receiving technical support to develop national forest inventories (Schelhaas et al., 2006; Magnussen et al., 2007; Tomppo et al., 2010; Romijn et al., 2015; UNFAO, n.d.). Clearly, this illustrates the tremendous potential that tree core archiving could provide if incorporated into NFI protocols. Tree cores provide critical benefits to NFIs by providing an unbiased sample, representative of climate and other environmental conditions, which offers insight into the effect of climate on tree growth; and by design, NFIs are well-suited for upscaling, which allows for better and more accurate C accounting (Evans et al., 2022). Wood traits are a tremendous tool for understanding response to climate, and our results show that methodology is clearly important for reconstructing $\delta^{15}N$, which may account for why other studies have found very subtle (Kranabetter et al., 2013; McLauchlan et al., 2017; Oulehle et al., 2022) or no temporal patterns (Tomlinson et al., 2014). Our results show for the first time that the MTM provides a more sensitive window into environmental change for certain biogeochemical cycles that exhibit high intra-wood mobility, i.e. nitrogen, and that systematic archiving of wood cores within already existing NFIs has great potential to provide a long-term record of forest responses to changes in our Earth system.

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Author contributions

All authors developed the experimental design/conceived the study; K.R.B prepared all samples and wrote the first draft of the manuscript; and all authors interpreted and discussed the ideas and results and provided input on each draft of the manuscript.

CRediT authorship contribution statement

Kelley R. Bassett: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Lars Östlund:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Michael J. Gundale:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition. **Jonas Fridman:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Sandra Jämtgård:** Conceptualization, Methodology, Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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References

Adams, M.A., Buckley, T.N., Turnbull, T.L., 2020. Diminishing CO_2-driven gains in water-use efficiency of global forests. Nat. Clim. Chang. 10, 466–471.

Arzac, A., Popkova, M., Anarbekova, A., Olano, J.M., Gutiérrez, E., Nikolaev, A., Shishov, V., 2019. Increasing radial and latewood growth rates of *Larix cajanderi* Mayr. and *Pinus sylvestris* L. in the continuous permafrost zone in Central Yakutia (Russia). Ann. For. Sci. 76, 1–15.

Bahn, M., Buchmann, N., Knohl, A., 2012. Stable isotopes and biogeochemical cycles in terrestrial ecosystems. Biogeosciences 9, 3979–3981.

Balster, N.J., Marshall, J.D., Clayton, M., 2009. Coupling tree-ring $\delta^{13}C$ and $\delta^{15}N$ to test the effect of fertilization on mature Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) stands across the Interior Northwest, USA. Tree Physiol. 29, 1491–1501.

Belmecheri, S., Lavergne, A., 2020. Compiled records of atmospheric CO_2 concentrations and stable carbon isotopes to reconstruct climate and derive plant ecophysiological indices from tree rings. Dendrochronologia 63, 125748.

Bond-Lamberty, B., Gower, S.T., Wang, C., Cyr, P., Veldhuis, H., 2006. Nitrogen dynamics of a boreal black spruce wildfire chronosequence. Biogeochemistry 81, 1–16.

Buttò, V., Khare, S., Drolet, G., Sylvain, J., Gennaretti, F., Deslauriers, A., Morin, H., Rossi, S., 2021. Region-wide temporal gradients of carbon allocation allow for shoot growth and latewood formation in boreal black spruce. Glob. Ecol. Biogeogr. 30, 1657–1670.

Canadell, J.G., Le Quéré, C., Raupach, M.R., Field, C.B., Buitenhuis, E.T., Ciais, P., Conway, T.J., Gillett, N.P., Houghton, R.A., Marland, G., 2007. Contributions to accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks. Proc. Natl. Acad. Sci. U. S. A. 104, 18866–18870.

Cowling, E.B., Merrill, W., 1966. Nitrogen in wood and its role in wood deterioration. Can. J. Bot. 44, 1539–1554.

Craine, J.M., Elmore, A.J., Aidar, M.P.M., Bustamante, M., Dawson, T.E., Hobbie, E.A., Kahmen, A., Mack, M.C., McLauchlan, K.K., Michelsen, A., Nardoto, G.B., Pardo, L. H., Peñuelas, J., Reich, P.B., Schuur, E.A.G., Stock, W.D., Templer, P.H., Virginia, R. A., Welker, J.M., Wright, I.J., 2009. Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. New Phytol. 183, 980–992.

Craine, J.M., Elmore, A.J., Aranibar, J., Bauters, M., Boeck, P., Crowley, B.E., Dawes, M. A., Delzon, S., Fajardo, A., Fang, Y., Fujiyoshi, L., Gray, A., Guerrieri, R., Gundale, M. J., Hawke, D.J., Hietz, P., Jonard, M., Kearsley, E., Kenzo, T., Makarov, M., Marañón-Jiménez, S., McGlynn, T.P., McNeil, B.E., Mosher, S.G., Nelson, D.M., Peri, P.L., Roggy, J.C., Sanders-DeMott, R., Song, M., Szpak, P., Templer, P.H., Van der Colff, D., Wang, L., Werner, C., Xu, X., Yang, Y., Yu, G., Zmudczyńska-Skarbek, K., 2018. Isotopic evidence for oligotrophication of terrestrial ecosystems. Nature Ecology and Evolution 2, 1735–1744.

Deluca, T.H., Boisvenue, C., 2012. Boreal forest soil carbon: distribution, function and modelling. Forestry: An International Journal of Forest Research 85, 161–184.

DeLuca, T.H., Zackrisson, O., Gundale, M.J., Nilsson, M.-C., 2008. Ecosystem feedbacks and nitrogen fixation in boreal forests. Science 320, 1181.

Doraisami, M., Kish, R., Paroshy, N.J., Domke, G.M., Thomas, S.C., Martin, A.R., 2022. A global database of woody tissue carbon concentrations. Scientific Data 9, 284.

Doucet, A., Savard, M.M., Bégin, C., Smirnoff, A., 2011. Is wood pre-treatment essential for tree-ring nitrogen concentration and isotope analysis? Rapid Commun. Mass Spectrom. 25, 469–475.

Ehleringer, J.R., Hall, A.E., Farquhar, G.J. (Eds.), 1993. Stable Isotopes and Plant Carbon-Water Relations. Academic Press.

Ehlers, I., August, A., Betson, T.R., Nilsson, M.B., Marshall, J.D., 2017. Detecting long-term metabolic shifts using isotopomers: CO$_2$-driven suppression of photorespiration in C3 plants over the 20th century. Proceedings of the National Academy of Sciences of the United States 112, 15585–15590.

Elmore, A.J., Nelson, D.M., Craine, J.M., 2016. Earlier springs are causing reduced nitrogen availability in North American eastern deciduous forests. Nature Plants 2, 16133.

Evans, M.E.K., DeRose, R.J., Klesse, S., Girardin, M.P., Heilman, K.A., Alexander, M.R., Arsenault, A., Babst, F., Bouchard, M., Cahoon, S.M.P., Campbell, E.M., Dietze, M., Duchesne, L., Frank, D.C., Giebink, C.L., Gómez-Guerrero, A., Gutiérrez García, G., Hogg, E.H., Metsaranta, J., Ols, C., Rayback, S.A., Reid, A., Ricker, M., Schaberg, P. G., Shaw, J.D., Sullivan, P.F., Villela GaytÁn, S.A., 2022. Adding tree rings to North America's National Forest Inventories: an essential tool to guide drawdown of atmospheric CO$_2$. BioScience 72, 233–246.

Fang, J., Kato, T., Guo, Z., Yang, Y., Hu, H., Shen, H., Zhao, X., Kishimoto-Mo, A.W., Tang, Y., Houghton, R.A., 2014. Evidence for environmentally enhanced forest growth. Proc. Natl. Acad. Sci. U. S. A. 111, 9527–9532.

Farquhar, G., O'Leary, M., Berry, J., 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Aust. J. Plant Physiol. 9, 121–137.

Farquhar, G., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology Plant Molecular Biology 40, 503–537.

Ferm, M., Granat, L., Engardt, M., Pihl Karlsson, G., Danielsson, H., Karlsson, P.E., Hansen, K., 2019. Wet deposition of ammonium, nitrate and non-sea-salt sulphate in Sweden 1955 through 2017. Atmospheric Environment: X 2, 100015.

Fletcher, L., Sinclair, T.R., Allen Jr., L.H., 2007. Transpiration responses to vapor pressure deficit in well-watered 'slow-wilting' and commercial soybean. Environ. Exp. Bot. 61, 145–151.

Forrester, D.I., 2019. Linking forest growth with stand structure: tree size inequality, tree growth or resource partitioning and the asymmetry of competition. For. Ecol. Manag. 447, 139–157.

Franklin, O., Näsholm, T., Högberg, P., Högberg, M.N., 2014. Forests trapped in nitrogen limitation – an ecological market perspective on ectomycorrhizal symbiosis. New Phytol. 203, 657–666.

Fridman, J., Holm, S., Nilsson, M., Nilsson, P., Hedström Ringvall, A., Ståhl, G., 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, 1095.

Fridman, J., Westerlund, B., Mensah, A.A., 2022. Volymtillväxten för träd i Sverige under 00-talet Ett faktaunderlag med anledning av den minskande nettotillväxten. Arbetsrapport/ Sveriges lantbruksuniversitet, Institutionen för skoglig resurshushållning, p. 540.

Friedlingstein, P., O'Sullivan, M., Jones, M.W., Andrew, R.M., Gregor, L., Hauck, J., Le Quéré, C., Luijkx, I.T., Olsen, A., Peters, G.P., Peters, W., Pongratz, J., Schwingshackl, C., Sitch, S., Canadell, J.G., Ciais, P., Jackson, R.B., Alin, S.R., Alkama, R., Arneth, A., Arora, V.K., Bates, N.R., Becker, M., Bellouin, N., Bittig, H.C., Bopp, L., Chevallier, F., Chini, L.P., Cronin, M., Evans, W., Falk, S., Feely, R.A., Gasser, T., Gehlen, M., Gkritzalis, T., Gloege, L., Grassi, G., Gruber, N., Gürses, Ö., Harris, I., Hefner, M., Houghton, R.A., Hurtt, G.C., Iida, Y., Ilyina, T., Jain, A.K., Jersild, A., Kadono, K., Kato, E., Kennedy, D., Klein Goldewijk, K., Knauer, J., Korsbakken, J.I., Landschützer, P., Lefèvre, N., Lindsay, K., Liu, J., Liu, Z., Marland, G., Mayot, N., McGrath, M.J., Metzl, N., Monacci, N.M., Munro, D.R., Nakaoka, S.I., Niwa, Y., O'Brien, K., Ono, T., Palmer, P.I., Pan, N., Pierrot, D., Pocock, K., Poulter, B., Resplandy, L., Robertson, E., Rödenbeck, C., Rodriguez, C., Rosan, T.M., Schwinger, J., Séférian, R., Shutler, J.D., Skjelvan, I., Steinhoff, T., Sun, Q., Sutton, A.J., Sweeney, C., Takao, S., Tanhua, T., Tans, P.P., Tian, X., Tian, H., Tilbrook, B., Tsujino, H., Tubiello, F., van der Werf, G.R., Walker, A.P., Wanninkhof, R., Whitehead, C., Willstrand Wranne, A., Wright, R., Yuan, W., Yue, C., Yue, X., Zaehle, S., Zeng, J., Zheng, B., 2022. Global carbon budget 2022. Earth System Science Data 14, 4811–4900.

Fritts, H.C., 1976. Tree Rings and Climate. Academic Press, London; New York.

Gerhart, L.M., McLauchlan, K.K., 2014. Reconstructing terrestrial nutrient cycling using stable nitrogen isotopes in wood. Biogeochemistry 120, 1–21.

Gundale, M.J., Fajardo, A., Lucas, R.W., Nilsson, M.-C., Wardle, D.A., 2011. Resource heterogeneity does not explain the diversity-productivity relationship across a boreal island fertility gradient. Ecography 34, 887–896.

Gundale, M.J., Hyodo, F., Nilsson, M.-C., Wardle, D.A., 2012. Nitrogen niches revealed through species and functional group removal in a boreal shrub community. Ecology 93, 1695–2005.

Gundale, M.J., From, F., Bach-Holmen, L., Nordin, A., 2014. Nitrogen deposition in boreal forests has a minor impact on the global carbon cycle. Glob. Chang. Biol. 20, 276–286.

Hart, S.C., Classen, A.T., 2003. Potential for assessing long-term dynamics in soil nitrogen availability from variations in δ^{15}N of tree rings. Isot. Environ. Health Stud. 39, 15–28.

Hasselquist, N.J., Metcalfe, D.B., Inselsbacher, E., Stangl, Z., Oren, R., Näsholm, T., Högberg, P., 2016. Greater carbon allocation to mycorrhizal fungi reduces tree nitrogen uptake in a boreal forest. Ecology 97, 1012–1022.

Higuchi, T., 1997. Biochemistry and Molecular Biology of Wood. Springer-Verlag, Timell, T.E., Berlin Heidelberg New York.

Hobbie, E.A., Högberg, P., 2012. Nitrogen isotopes link mycorrhizal fungi and plants to nitrogen dynamics. New Phytol. 196, 367–382.

Högberg, P., 1997. Nitrogen impacts on forest carbon. Nature 447, 781–782.

Hungate, B.A., Dukes, J.S., Shaw, M.R., Luo, Y., Field, C.B., 2003. Nitrogen and climate change. Science 302, 1512–1513.

IPCC, 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

IPCC, 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Keeling, C.D., Carter, A.F., Morek, W.G., 1984. Seasonal, latitudinal and secular variations in the abundance and isotopic ratios of atmospheric CO$_2$. J. Geophys. Res. 88, 10 915-10 933.

Keenan, T., Hollinger, D.Y., Bohrer, G., Dragoni, D., Munger, J.W., Schmid, H.P., Richardson, A.D., 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. Nature 499, 324–327.

Koca, D., Smith, B., Sykes, M.T., 2006. Modelling regional climate change effects on potential natural ecosystems in Sweden. Clim. Chang. 78, 381–406.

Kranabetter, J.M., Saunders, S., MacKinnon, J.A., Klassen, H., Spittlehouse, D.L., 2013. An assessment of contemporary and historic nitrogen availability in contrasting coastal Douglas-fir forests through δ^{15}N of tree rings. Ecosystems 16, 111–122.

Lajtha, K., Jones, J., 2013. Trends in cation, nitrogen, sulfate and hydrogen ion concentrations in precipitation in the United States and Europe from 1978 to 2010: a new look at an old problem. Biogeochemistry 116, 303–334.

Lamlom, S.H., Savidge, R.A., 2003. A reassessment of carbon content in wood: variation within and between 41 North American species. Biomass Bioenergy 25, 381–388.

Lan, X., Dlugokencky, E.J., Mund, J.W., Crotwell, A.M., Crotwell, M.J., Moglia, E., Madronich, M., Neff, D., Thoning, K.W., 2022. Atmospheric Carbon Dioxide Dry Air Mole Fractions from the NOAA GML Carbon Cycle Cooperative Global Air Sampling Network, 1968–2021. Version: 2022-11-21. https://doi.org/10.15138/wkgj-f215.

Lucas, R.W., Sponseller, R.A., Gundale, M.J., Stendahl, J., Fridman, J., Högberg, P., Laudon, H., 2016. Long-term declines in stream and river inorganic nitrogen (N) export correspond to forest change. Ecol. Appl. 26, 545–556.

Luo, Y., Su, B., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U., Hungate, B., McMurtrie, R.E., Oren, R., Parton, W.J., Pataki, D.E., Shaw, M.R., Zak, D.R., Field, C. B., 2004. BioScience 54, 731–739.

Magnussen, S., Smith, B., Uribe, A.S., 2007. National Forest Inventories in North America for monitoring forest tree species diversity. Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology 141, 113–122.

Martínez-Sancho, E., Slámová, L., Morganti, S., Grefen, C., Carvalho, B., Dauphin, B., Rellstab, C., Gugerli, F., Opgenoorth, L., Heer, K., Knutzen, F., von Arx, G., Valladares, F., Cavers, S., Fady, B., Alía, R., Aravanopoulos, F., Avanzi, C., Bagnoli, F., Barbas, E., Bastien, C., Benavides, R., Bernier, F., Bodineau, G., Bastias, C.C., Charpentier, J., Climent, J.M., Corréard, M., Courdier, F., Danusevicius, D., Farsakoglou, A., García Del Barrio, J.M., Gilg, O., González-Martínez, S.C., Gray, A., Hartleitner, C., Hurel, A., Jouineau, A., Kärkkäinen, K., Kujala, S.T., Labriola, M., Lascoux, M., Lefebvre, M., Lejeune, V., Le-Provost, G., Liesebach, M., Malliarou, E., Mariotte, N., Matesanz, S., Michotey, C., Milesim, P., Myking, T., Notivol, E., Pakull, B., Piotti, A., Plomion, C., Pringarbem, M., Pyhäjärvi, T., Raffin, A., Ramírez-Valiente, J.A., Ramskogler, K., Robledo-Arnuncio, J.J., Savolainen, O., Schueler, S., Semerikov, V., Spanu, I., Thévenet, J., Tollefsrud, M.M., Turion, N., Veisse, D., Vendramin, G.G., Villar, M., Westin, J., Fonti, P., 2020. The GenTree Dendroecological collection, tree-ring and wood density data from seven tree species across Europe. Scientific Data 7, 1.

Mason, R.E., Craine, J.M., Lany, N.K., Jonard, M., Ollinger, S.V., Groffman, P.M., Fulweiler, R.W., Angerer, J., Read, Q.D., Reich, P., Templer, P.H., Elmore, A.J., 2022a. Evidence, causes, and consequences of declining nitrogen availability in terrestrial ecosystems. Science 376, 1–11.

Mason, R.E., Craine, J.M., Lany, N.K., Jonard, M., Ollinger, S.V., Groffman, P.M., Fulweiler, R.W., Angerer, J., Read, Q.D., Reich, P.B., Templer, P.H., Elmore, A.J., 2022b. Explanations for nitrogen decline - response. Science 376, 1170.

Mathias, J.M., Thomas, R.B., 2021. Global tree intrinsic water use efficiency is enhanced by increased atmospheric CO$_2$ and modulated by climate and plant functional types. Proc. Natl. Acad. Sci. 1187, e2014286118.

McCarroll, D., Loader, N.J., 2004. Stable isotopes in tree rings. Quat. Sci. Rev. 23, 771–801.

McLauchlan, K.K., Craine, J.M., 2012. Species-specific trajectories of nitrogen isotopes in Indiana hardwood forests, USA. Biogeosciences 9, 867–874.

McLauchlan, K.K., Craine, J.M., Oswald, W.W., Leavitt, P.R., Likens, G.E., 2007. Changes in nitrogen cycling during the past century in a northern hardwood forest. Proceedings of the National Academy of Sciences of the United States 104, 7466–7470.

McLauchlan, K.K., Gerhart, L.M., Battles, J.J., Craine, J.M., Elmore, A.J., Higuera, P.E., Mack, M.C., McNeil, B.E., Nelson, D.M., Pederson, N., Perakis, S.S., 2017. Centennial-scale reductions in nitrogen availability in temperate forests of the United States. Sci. Rep. 7, 7856.

Mead, D.J., Preston, C.M., 1994. Distribution and retranslocation of ^{15}N lodgepole pine over eight growing seasons. Tree Physiol. 4, 389–402.

Mook, W.G., 1983. ^{13}C in atmospheric CO_2. Neth. J. Sea Res. 20, 211–223.

Näsholm, T., Högberg, P., Franklin, O., Metcalfe, D., Keel, S.G., Campbell, C., Hurry, V., Linder, S., Högberg, M.N., 2013. Are ectomycorrhizal fungi alleviating or aggravating nitrogen limitation of tree growth in boreal forests? New Phytol. 198, 214–221.

National Oceanic and Atmospheric Administration (NOAA), National Centers for Environmental Information, 2022. Carbon dioxide now more than 50% higher than pre-industrial levels. https://www.noaa.gov/news-release/carbon-dioxide-now-more-than-50-higher-than-pre-industrial-levels [June 13, 2022].

Nömmik, H., 1966. The uptake and translocation of fertilizer N15 in young trees of scots pine and Norway spruce. *Stockholm: predecessors to SLU > Royal School of Forestry, Sveriges* lantbruksuniversitet. Studia forestalia Suecica 35.

Olff, H., Aerts, R., Bobbink, R., Cornelissen, J.H.C., Erisman, J.W., Galloway, J.N., Stevens, C.J., Sutton, M.A., de Vries, F.T., Wieger Wamelink, G.W., Wardle, D.A., 2022. Explanations for nitrogen decline. Science 376, 1169–1170.

Oulehle, F., Tahovská, K., Ač, A., Kolář, T., Rybníček, M., Čermák, P., Štěpánek, P., Trnka, M., Urban, O., Hruška, J., 2022. Changes in forest nitrogen cycling across deposition gradient revealed by δ^{15}N in tree rings. Environ. Pollut. 304, 119104.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautianen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science 333, 988–993.

Peuke, A.D., 2010. Correlations in concentrations, xylem and phloem flows, and partitioning of elements and ions in intact plants. A summary and statistical re-evaluation of modelling experiments in *Ricinus communis*. J. Exp. Bot. 61, 635–655.

Poulson, S.R., Chamberlain, C.P., Friedland, A.J., 1995. Nitrogen isotope variation of tree rings as a potential indicator of environmental change. Chem. Geol. 125, 307–315.

Pretzsch, H., Biber, P., Schütze, G., Kemmerer, J., Uhl, E., 2018. Wood density reduced while wood volume growth accelerated in central European forests since 1870. For. Ecol. Manag. 429, 589–616.

R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rawson, H.M., Begg, J.E., Woodward, R.G., 1977. The effect of atmospheric humidity on photosynthesis, transpiration and water use efficiency of leaves of several plant species. Planta 134, 5–10.

Romijn, E., Lantican, C.B., Herold, M., Lindquist, E., Ochieng, R., Wijaya, A., Murdiyarso, D., Verchot, L., 2015. Assessing change in national forest monitoring capacities of 99 tropical countries. For. Ecol. Manag. 352, 109–123.

Rowell, R.M., Pettersen, R., Tshabalala, M.A., 2012. Cell wall chemistry. In: Rowell, R.M. (Ed.), Handbook of Wood Chemistry and Wood Composites. CRC Press, Boca Raton, pp. 37–72.

Saurer, M., Spahni, R., Frank, D.C., Joos, F., Leuenberger, M., Loader, N.J., McCarroll, D., Gagen, M., Poulter, B., Siegwolf, R.T.W., Andreu-Hayles, L., Boettger, T., Dorado Liñán, I., Fairchild, I.J., Friedrich, M., Gutierrez, E., Haupt, M., Hilasvuori, E., Heinrich, I., Helle, G., Grudd, H., Jalkanen, R., Levanič, T., Linderholm, H.W., Robertson, I., Sonninen, E., Treydte, K., Waterhouse, J.S., Woodley, E.J., Wynn, P. M., Young, G.H.F., 2014. Spatial variability and temporal trends in water-use efficiency of European forests. Glob. Chang. Biol. 20, 3700–3712.

Schelhaas, M.J., Varis, S., Schuck, A., Nabuurs, G.J., 2006. EFISCEN Inventory Database. European Forest Institute, Joensuu, Finland. http://www.efi.int/portal/virtual_library/databases/efiscen/.

Schleppi, P., Bucher-Wallin, L., Siegwolf, R.T.W., Saurer, M., Muller, N., Bucher, J., 1999. Simulation of increased nitrogen deposition to a montane forest ecosystem: partitioning of the added ^{15}N. Water Air Soil Pollut. 116, 129–134.

Speer, J., 2010. Fundamentals of Tree Ring Research. University of Arizona Press.

Swedish Meteorological and Hydrological Institute (SMHI), 2022. Climate indicator – precipitation. https://www.smhi.se/en/climate/climate-indicators/climate-indicators-precipitation-1.91462 [2023-04-10].

Thorell, K.E., Östlin, E.O., 1931. The National Forest Survey of Sweden. J. For. 29, 585–591.

Tomlinson, G., Siegwolf, R.T.W., Buchmann, N., Schleppi, P., Waldner, P., Weber, P., 2014. The mobility of nitrogen across tree-rings of Norway spruce (*Picea abies* L.) and the effect of extraction method on tree-ring δ^{15}N and δ^{13}C values. Rapid Commun. Mass Spectrom. 27, 1258–1264.

Tomppo, E., Gschwantner, T., Lawrence, M., McRoberts, R.E., Gabler, K., Schadauer, K., Vidal, C., Lanz, A., Ståhl, G., Cienciala, E., 2010. National forest inventories. Pathways for common reporting. European Science Foundation 1, 541–553.

United Nations Food and Agriculture Organization (UN FAO) (n.d.). National Forest Inventory. https://www.fao.org/national-forest-monitoring/areas-of-work/nfi/en/. [2023-05-10].

van Buijtenen, J.P., 2004. Tree breeding practices, genetics and improvement of wood properties. In: Encyclopedia of Forest Sciences. Elsevier Ltd., pp. 1466–1472

Yuan, W., Zheng, Y., Piao, S., Ciais, P., Lombardozzi, D., Wang, Y., Ryu, Y., Chen, G., Dong, W., Hu, Z., Jain, A.K., Jiang, C., Kato, E., Li, S., Lienert, S., Liu, S., Nabel, J.E. M.S., Qin, Z., Quine, T., Sitch, S., Smith, W.K., Wang, F., Wu, C., Xiao, Z., Yang, S., 2019. Increased atmospheric vapor pressure deficit reduces global vegetation growth. Sci. Adv. 5, 1–12.

Zobel, B.J., van Buijtenen, J.P., 1989. Wood variation and wood properties. In: Wood Variation. Springer, Berlin Heidelberg, pp. 1–32.