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An aging population? A century of change among Swedish forest trees

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ABSTRACT

We describe a century of change in Swedish forest using trees sampled for age, diameter, volume and species by the Swedish National Forest Inventory (NFI). Changes in the structure of the tree population since 1923 are described and related to changes in policy. During the first part of the study period, policy aimed at restoring the growing stock and productivity of forest areas, but with methods that changed over time. In the last 30 years, a new forestry policy was introduced, which included restoring the diversity of tree populations, on the assumption that this will also promote biodiversity. Over the last century, and on a national scale, the volume of timber had doubled, tree sizes had increased, older trees had become more common, even more so for broadleaf species in southern Sweden. The volume of today's protected forests has almost tripled, indicating reduced light, water, and nutrients for understory vegetation. We also considered two regional cases. The sparsely populated county of Norrbotten, which was the last region in Sweden to be exploited for forestry in the 1890s, had many old pines and many old but small spruces in 1926. These were reduced in the following decades, first by selective high-grading and then by extensive clear-cutting. After a change in policy around 1990, the negative trends levelled out. In densely populated south-central Sweden, forests have long been used for grazing, timber, fuelwood and charcoal production. During the last century, the volume of timber had tripled, older trees and broadleaves have become more abundant.

1. Introduction

Trees have a finite lifespan. Although the maximum biological age varies between species, a more important factor in determining the age distribution of trees in production forests is the average size considered suitable for harvesting and the time required for trees to grow to that size. Such considerations vary in time and space depending on logistics, market factors and societal constraints (i.e. laws, regulations and policies). Given the slow growth of boreal forests, detailed long-term forest data are helpful in assessing broad patterns of change, the relative importance of different forest management practices, and the extent to which policy changes are achieving their objectives. When developing forest policies, it is also important to analyse historical development of the forest in question, preferably based on sound and detailed data covering as long a period as possible.

In this study, we used a 100-year data set of sample trees from the Swedish National Forest Inventory (NFI; Fridman et al., 2014). Measurements were made using comparable methods and definitions throughout the 100-year period. We focus on (i) tree age (assessed by the number of annual rings), (ii) size (diameter at breast height 1.3 m above ground (DBH) measured by calliper) and (iii) tree volume (calculated based on models using measured height and DBH). This study uses recently digitised data from sample trees dating from the 1920s and data from 1953 onwards, which have been continuously digitised after fieldwork and stored in the NFI database.

To date, most statistics based on data from the Swedish NFI have used field assessments of stand age to capture the age structure of tree populations. Stand age (in the Swedish NFI) refers to the average basal area weighted age of the dominant tree layer and is supported by field age determinations of sample trees and, in the absence of sample trees,

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of subjectively selected representative trees from that layer. Thus, stand age provides a statistical measure of only a part of the tree population. In contrast, the use of individual tree ages provides a deeper understanding of both the age structure and the age dynamics of the tree population. We are only aware of three previous studies using sample tree data from the first NFI (1923–1929). Andersson and Östlund (2004) analysed changes in the density of old trees in the county of Norrbotten, between 1926 and 1997. Axelsson (2001) studied changes in the age of large conifer trees in the county of Dalarna between 1923 and 1990. Preliminary analyses of the sample tree data have been carried out by Elgan and Persson (2022) comparing data from the 1920s and today. The current study is the first attempt to analyse the dynamics of tree populations on longer temporal and larger spatial scales.

Since the first NFI, sample trees have been selected using well-defined sampling schemes (Ståhl, 2024). The probability of inclusion is known for each sample tree, which makes it possible to estimate the total number of trees in the tree population, or a subpopulation thereof, using these sample trees. The probability of inclusion is higher for larger diameter classes which means that the sample tree data provides better information for parts of the tree population. The estimated population at different time periods can be considered as a census of the living tree population. This enables the analysis of the age structure of the tree population over time and to draw conclusions about potential drivers of population change, such as growth, harvesting, and natural mortality.

1.1. Historical factors influencing the Swedish tree population

Forest management in Sweden has undergone significant and rapid changes both before and during the study period. In the 1800s, a frontier of industrial timber exploitation affected Sweden, starting in the south, and ending in the interior of northern Sweden (Björklund, 1998). This was in parallel with timber frontiers moving through northern Finland and Russia (Björklund, 1984) and North America (Williams, 1992). The main driver was an increasing global demand for forest products and increasingly efficient wood processing and logistics. Initially, large and old trees were harvested in Sweden (Östlund et al., 1997, Linder and Östlund, 1998). By 1870, sawn timber exports had reached their peak accounting for half of the value of total exports from Sweden (Pettersson, 2015). Later Sweden also became a major producer and exporter of pulp and paper products which used smaller trees and thus accelerated the depletion of timber resources (Ekelund and Hamilton, 2011). The consequences of exploitative harvesting practices began to become apparent by the end of the 19th century, raising concerns about the future of forestry and the Swedish economy. As a result, a Forest Research Institute was established in 1902, a Forestry Act was passed by Parliament in 1903, and the first steps towards a national forest inventory were taken in 1911 (Fridman and Östlund, 2024).

The establishment of the Forest Research Institute in 1902 laid the foundation for the development of a more science-based forestry. Research led to a scientific understanding of forest regeneration and growth, including the important role of edaphic factors (Jönsson, 2019). As a result, new concepts of rotational forestry emerged, based on more active regeneration after clear-cutting. This included clearing clear-cuts of undergrowth, leaving sufficient seed trees and using prescribed burning or mechanical soil preparation to facilitate seedling establishment and growth. A deeper understanding of the importance of tree genetics made seedling production and replanting after clear-cutting, not only a viable method for regeneration, but also enabled the implementation of tree breeding (Jönsson, 2019). However, it took several decades for these scientific advances to be fully implemented.

The 1903 Act made it compulsory to regenerate forests after logging. Subsequently, more attention was paid to regeneration through the promotion of natural regrowth, planting and seeding. However, the exploitative harvesting of younger forests continued driven by the growing demand for pulpwood, pit prop and fuelwood. Therefore, an amendment to the Forestry Act in 1923 stated that " Younger forest shall not be felled,…, except by thinning appropriate for the development of the forest" (Ekelund and Hamilton, 2011). However, after the economic recession of the late 1920s and during the Second World War, cost considerations discouraged long-term investment in forest renewal and favoured selective harvesting of older forests (Tirén, 1952, Nyblom, 1955, Tillander, 1955, Ebeling, 1959, Stefansson, 1962, Carbonnier, 1978) and natural regeneration. The annual area planted in private forests was reduced to a minimum and rotation forestry, which required active regeneration by planting or seeding was prohibited in the northern state forest districts (Ekelund and Hamilton, 2011). During the Second World War, Sweden substituted wood for coal, which meant a doubling of the harvest of fuelwood (mainly small dimensions) which accounted for 50 % of the annual harvest (SOS, 1948).

Thus, although the practice of selective felling of the larger trees followed by little or no investment in regeneration continued until after the Second World War, the Forestry Act of 1903 and subsequent policy changes succeeded in halting the depletion of forest resources in terms of standing volume and growth rates (Tirén, 1952).

A second major policy change took place around 1950. A new Forestry Act was introduced in 1949, motivated by the need to improve forest management to increase the wood productivity of the forest (Ekelund and Hamilton, 2011). In the early 1950s, logging was gradually mechanised, and Swedish forestry underwent significant changes, especially in the state-owned forests of northern Sweden (Ebeling, 1959, Östlund et al., 1997). Rotation forestry became dominant, the size of harvested areas increased, and substantial investments were made in reforestation. Previously repeatedly high-graded, poorly stocked stands were cleared and replanted.

Mechanisation and the introduction of several new forestry practices in the 1960s and early 1970s (nitrogen fertilisation, radical soil scarification, non-native tree species and herbicide treatment) triggered protests and conflicts that escalated and led to political action and regulation (Simonsson et al., 2015). By the end of the 1980s it had also become clear that a narrow focus on timber production in forestry was having a negative impact on biodiversity and thus also potentially threatening the long-term viability of forests. The Brundtland report "Our Common Future" (1987) and the RIO conference (1992) argued for a broader perspective on sustainable forest management, including greater concern for biodiversity. Therefore, a third major policy shift occurred around 1990 (Simonsson et al., 2015). Then conservation measures such as retention forestry (Franklin, 1989, Simonsson et al., 2015), i.e. intentional leaving living and dead trees, or groups of living trees (Lindhe et al., 2004, Kyaschenko et al., 2022) and also leaving forests to grow old were introduced and became an integral part of practical forest management in Sweden. At the same time, efforts were made to formally protect old-growth forests in reserves of various types (SOU, 1997), resulting in an increase from 1 % of all productive forests being formally protected in 1990 to 6.1 % in 2023 (Table 4.8 in SCB, 2024).

We wanted to investigate how changing forest policies have affected the tree population. Specifically, we examined how three major policy changes have affected the age structure:

- The introduction of the Forestry Act 1903, which made it compulsory to regenerate after clear-cutting and encouraged the use of less intensive high-grading harvesting methods between 1920 and 1950.
- Largescale investment in timber production through increased felling and active regeneration of low stock and old growth forests between 1950 and 1990.
- The introduction of retention forestry and set-asides after 1990.

There are other drivers of change than those mentioned above, such as grazing by domestic and wild animals (Dahlström, 2008, Petersson et al., 2019), substantial fuelwood harvesting during the World War II (Ekelund and Hamilton, 2011), climate change (Brecka et al., 2018, Hedwall et al., 2019, Venäläinen et al., 2020, Hedwall et al., 2021) and

N deposition (Binkley and Högberg, 2016), but we considered that the current data are less likely to shed light on them.

In addition to analysing the entire Swedish tree population, we also considered data from two regions (Fig. 2).

The first was the sparsely populated county of Norrbotten, Sweden's northernmost county (Fig. 2). Here, logging for local use and for tar and potash production had been going on for a long time, but it is unclear to what extent forests were burned to promote grazing for domestic animals (Kempe, 1909, Tirén, 1937, Zackrisson, 1977). Forest exploitation for sawmills started early but productivity was low (Carlgren, 1926). More widespread exploitation began in the late 1800s, driven mainly by a series of administrative and legal changes that facilitated free trade and land ownership (Karlsson and Valinger, 2023). This led to continued efforts to improve rivers for timber rafting (Andersson, 1907, Winberg, 1944, Törnlund and Östlund, 2006), which supplied timber to sawmills established along the coast, later complemented by the pulp industry (which used smaller trees as well as of spruce). At the time of the first NFI 1923–1929, almost all Swedish forests had been high-graded one or more times, except for the most remote parts of Norrbotten county. This makes Norrbotten the only region in Sweden with a significant number of trees older than 300 years at the time of the first NFI (Andersson and Östlund, 2004).

Second, we selected the densely populated region of south-central Sweden (Fig. 2), excluding counties along the coasts with a significant presence of nemoral broadleaved forests and a landscape dominated by agriculture. Forests in the mostly hemiboreal south-central Sweden are more diverse in terms of tree species and more productive than in Norrbotten, allowing for shorter forest rotations. Two pieces of legislation have specifically targeted some broadleaved trees in southern Sweden (*Fagus sylvatica* SFS 1974:434; *Quercus, Tilia, Acer, Fraxinus* SFS 1984:119) to prevent the conversion to coniferous stands. In this area, forests are often mixed with agricultural land, and there is a long history of intensive use of forests for products (fuelwood, timber, charcoal, glassworks, fencing) and for grazing by domestic animals (Segerström and Emanuelsson, 2002, Dahlström, 2008). In addition, most of the forest is privately owned, divided into many small plots managed by owners with different priorities (Bakx et al., 2024). Since the Second World War, some agricultural land has been afforested mainly with Norway spruce, and forest grazing has ceased, making south-central Sweden an important region for timber production. In south-central Sweden, 28 % of the agricultural land in 1951 had been converted to forest by 2020 (https://www.scb.se/), which corresponds to about 13 % of the productive forest land in 2020. In Norrbotten, on the other hand, the corresponding values were 61 % loss of agricultural land and less than 2 % increase in the productive forest land.

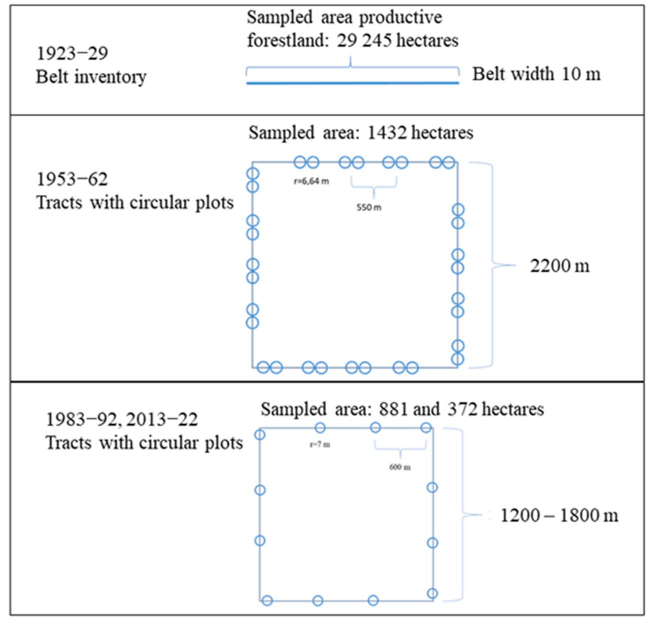

Fig. 1. The systematic sampling design of the Swedish NFI 1923–29 and from 1953 and onwards. Belts and tracts were systematically distributed over the entire country. The sampled area and also the number of callipered trees and sample trees have decreased due to a) increased effectiveness in sampling design, b) establishment of a complementary permanent sample in 1983 and c) reduced proportion of temporary tracts from 2003 (Fridman et al. 2014).

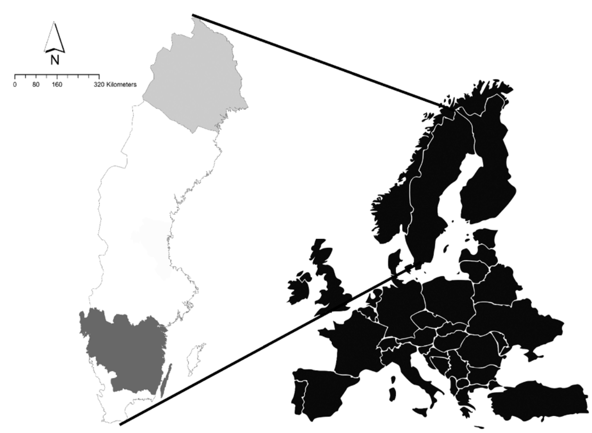

Fig. 2. Europe and Sweden with study case areas Norrbotten (light grey) and south-central Sweden (dark grey) highlighted.

2. Materials and methods

2.1. The Swedish National Forest Inventory

The Swedish National Forest Inventory (NFI), started in 1923, is part of Sweden's official statistics. Its main purpose is to describe the condition and change of Swedish forests (Fridman et al., 2014). The current NFI is based on an annual sample of about 20,000 circular plots, grouped into tracts, of which about 12,000 are surveyed in the field each year, with up to 120,000 trees callipered.

The focus, scope and design of the NFI (Fig. 1) has expanded over its lifetime. Initially focus on the forest as a raw material for the forest industry (Fridman and Östlund, 2024). As data collection has expanded, the use of data from the NFI has become relevant to more areas than just wood resources for the forest industry. These include the development of ground vegetation, biodiversity, and the carbon cycle in relation to climate. The data are used for many different purposes, including as a basis for scenario analysis. (Fridman and Walheim, 2024).

During the first NFI (1923–29), the area sample consisted of 10 m wide transects (called "belts", 5 m on either side of the survey line). These transects were continuously sectioned for land cover classes and forest types and the length of each section was measured with a tape measure. Trees of at least 1.3 m height were callipered within the transects but only the sample trees were assigned to the sections, i.e. site and stand characteristics such as land cover class and stand age, could be assigned to each sample tree (SOU, 1932). Field forms from the first NFI have recently been digitised. From 1953, when circular sample plots were introduced, both calliper trees and sample trees could be assigned attributes from the plot. Data from 1953 –1962 were digitised in the 1960s, transformed and stored in a database in 2010. Data from 1983 onwards were collected using handheld computers, i.e. and have been continuously digitised and stored in a database since then. All NFI data since 1923, except for NFI 1938–52, can now be easily processed as they are digitally stored in harmonised formats.

The first NFI included many sample trees (SOU, 1932), which has been reduced in subsequent inventories (Table 1).

Table 1
Total number of sample trees ≥ 10 cm DBH on productive forestland by period, species group and region.

	1926	1957	1987	2007	2017	Total sum
Sweden						
Pine*	62,456	44,475	26,520	17,845	20,815	172,111
Spruce**	53,377	47,993	29,544	14,765	16,787	162,466
Broadleaved ***	25,516	21,434	20,031	17,869	18,574	40,540
Total	141,349	109,755	67,204	39,588	46,598	404,494
Norrbotten						
Pine	4070	5663	3029	2402	3047	18,211
Spruce	2198	2469	1066	859	966	7558
Broadleaved	971	1052	959	926	929	1369
Sum	7239	9779	4849	3882	4805	30,554
Southcentral Sweden						
Pine	19,240	9894	5819	3405	3653	42,011
Spruce	12,459	11,280	8128	4089	4717	40,673
Broadleaved	7575	6081	6031	5652	5884	11,791
Sum	39,274	24,840	16,809	9435	10,819	101,177

* Mix of Pinus sylvestris (99.1 %), non-native Pinus spp (0.8 %) and Larix spp (0.12 %)

** Mix of Picea abies (99.97 %), non-native Picea spp (0.011 %) and non-native Abies spp (0.0172 %)

*** Mix of Betula spp. (64.5 %), Fagus sylvatica (8.4 %), Alnus spp. (7.8 %), Populus tremula (7.4 %), Quercus spp. (7.25 %), other species (7.8 %)

2.2. Data set

The data used consisted of a list of all individual sample trees, ≥ 10 cm DBH, measured within a ten metre wide transect (called a 'belt'), (1923–1929) or circular sample plots during the 1953–1962, 1983–1992, and 2013–2022 surveys. The 10 cm threshold was used to exclude smaller diameter trees as they were only measured on small parts of sections or plots, i.e. not representing the whole plot. According to the NFI (Skogsdata, 2024) the volume of trees with a diameter < 10 cm represents 8 % of the total volume of trees in Sweden.

For the sake of simplicity, we refer to each inventory period by its middle year: 1926, 1957, 1987 and 2017. We have therefore compared the tree population between four points in time that are up to 90 years apart, even though they are based on data collected over a century.

The inventory periods were chosen because the intermediate periods reflect different phases in the history of forest policy and forest management in Sweden: (i) 1926–1957; selective harvesting, poor regeneration and wartime harvesting for fuelwood; (ii) 1957–1987: large scale felling of old poorly stocked forests and replanting; 1987–2017: Set-aside and retention forestry.

Data from intervening years were excluded because a) they have not yet been digitised (1938–52), b) it was not possible to calculate sample tree probabilities (1963–82), and c) field measurements within formally protected areas, which increased from the 1970s onwards, were not carried out (1993–2002).

In this study, we have focused on forest areas that are outside formally protected areas as defined by the Swedish Environmental Protection Agency's GIS-layer for formally protected areas for the year 2023. This was partly a choice and partly a necessity. Tree stands within established formally protected areas were not included in the NFI field work between 1983 and 2002, i.e. no trees were measured or selected as sample trees. As a result, no estimates can be made of the development of tree populations within reserves over the 30-year periods 1957–1987 or 1987–2017. However, the tree population within reserves is presented as volume per age class for three points in time: 1926, 1957 and 2017.

During the first NFI the sampling intensity was very high resulting in 160,000 sample trees. In later surveys the number of sample trees was lower, but still large enough to present results for population subdivisions, such as oaks in South-central Sweden older than 120 years in 2017 (47 sample trees; Table 1).

The statistics based on sample trees were cross-checked against statistics based on all measured trees for number of trees, tree volume, tree species distribution and diameter distribution (e.g. SOU, 1932, Skogsdata, 2022). The cross-checking confirmed that the sample tree data should also provide a fair representation of the tree population over combinations of these variables and tree age.

2.3. Protocol for selection of sample trees

The method used to select sample trees has varied over time, but basically probability proportional to size (PPS by DBH or basal area [BA]) has been used over all time periods with some changes in the ratio of the number of sample trees by DBH or BA class. Since the probability of inclusion (πij) as a sample tree is known for both for the tree itself (i) and the sample plot (j), the Horwitz-Thompson estimator can be used to estimate the total number of trees ($\widehat{T}$) based on the selected sample trees (n) (Fridman et al. 2014):

$$\widehat{T} = \sum_{i=1}^{n} \frac{1}{\pi ij}.$$

To facilitate the analysis, the tree volume and total number of tree expansion factors were calculated for each sample tree based on its probability of inclusion. This makes it easy to estimate, for example, the total volume for tree age classes or other subpopulations by simply summing the expansion factors for the sample tree characteristics of interest.

2.4. Sample tree data

2.4.1. Age determination of sample trees

Breast height age of sample trees was determined by counting annual rings on cores taken with an increment borer. During the first NFI, ring measurement and counting was carried out in the field using a magnifying glass, but from the 1950s the cores were sent to the laboratory for precise measurements using a microscope. To determine the total age of the tree, the regional, species and site specific number of years to grow from seed to breast height was added to the age in breast height (SLU, 2021, p. 6:26). The same table was used for all trees regardless of sampling year. This is likely to overestimate the time to reach breast height, and therefore the total age of recently established trees, but trees established prior to 1950 have mostly grown from local seed sources and under similar conditions – without soil preparation and clearing of harvested areas.

For bore cores from the first NFI with central rot or where the innermost tree rings were not included in the core, the age of the sample tree was assessed using the stand age class. Cores with incomplete ages from later NFIs were not included in the analysis and the probability of inclusion for the sample trees used was adjusted based on the ratio of the number of sample trees included and the number of calliper trees on the plots. No non-response analysis was performed as the age of these sample trees was unknown.

The standardised method of determining total age does not add any information to the analysis compared to using age at breast height. However, adding the standard number of years to reach breast height makes it easier to interpret the results. However, to analyse tree loss over time in different cohorts, we used the year in which the top shoot exceeded breast height to assign trees to a particular cohort.

2.4.2. Calculation of sample tree volumes

During the first NFI, volume of sample trees was determined by using volume tables (SOU, 1932 p. 121 ff.). However, in order to harmonise the volume estimates for all sample trees used in this study, regardless of the year of selection, volume functions (e.g. Näslund and Hagberg, 1951, 1953) were applied using the geographical location, tree species and detailed measurements on the sample trees, including DBH, height, bark thickness and age.

2.4.3. Annual loss rate

From the data it is possible to estimate the number of live trees larger than 10 cm DBH that belong to cohorts of trees that have passed breast height at certain points in time. The annual reduction over time in the number of trees in such a cohort is the sum of (i) natural tree mortality and (ii) felling but reduced by (iii) the in-growth of trees belonging to the cohort that passed the 10 cm diameter threshold. However, as ingrowth of trees older than 140 years at breast height is extremely rare on productive forest land, the dynamics in older cohorts are almost entirely driven by natural mortality and harvesting. For cohorts with an average age between 80 and 140 years at breast height, ingrowth is still insignificant, but not zero. In estimating the rate of tree loss, it is assumed that trees in a 30-year age class move from one class to the next between observations 30 years apart. This is not entirely true, as trees are surveyed over 10-year periods, but it is reasonable to assume that this does not systematically affect the estimates. In order to obtain a sufficient number of sample trees behind the estimation of the number of trees in very old cohorts at different times, we pooled the results from two adjacent 30-year age classes. The number of sample trees in the oldest cohort analysed (trees 262–322 years old at breast height) is 45–55 depending on the point in time.

The annual loss rate (ALR) was calculated as follows:

$$ALR = 1 - (N2/N1)^{1/y}$$

where N2 and N1 are the number of live trees at the end and beginning of the period, respectively, and y is the number of years between time points (about 30 years in our case).

2.5. Statistical analyses

Although systematic sampling has been used in the NFI since its inception, in this study the precision of the estimates, i.e. the variance, was estimated assuming simple random sampling. This will generally lead to an overestimation of the variance (the variance estimator is described in the appendix to Fridman et al., 2014).

The sampling units are the tracts in the NFIs from 1953 onwards. For the 1923–29 NFI, virtual tracts were created by dividing the transects into 2 km sections.

Using the estimated variance for the estimates, confidence intervals (95 %) were constructed according to Toet et al. (2007). However, CIs were not calculated for the estimates of tree size and loss rate ratios.

3. Results

In total, we analysed data from more than 400,000 sample trees (Table 1). Of these, about 8 % were from Norrbotten and 24 % from south-central Sweden. The main tree species were Scots pine, Norway spruce, birch species and aspen.

3.1. Sweden

3.1.1. Volume per age class

Since the 1920s, the volume of wood in Sweden has more than doubled (Fig. 3a, b). During the period 1926–87, the increase in volume was concentrated in the 60–119 age class (Fig. 3a). Since 1987, however, the volume of this age class has decreased, while both older and younger age classes have increased (Fig. 3a, b). The volume of younger trees has almost doubled in the last 30 years (Fig. 3a).

In 1926 there were 137 million m^3 of trees older than 180 years in Sweden, and by 1987 this had decreased to 52 million m^3 (a decrease of 62 %). Since then, the volume of trees older than 180 years has doubled to 101 million m^3, most of which are between 180 and 240 years old (Fig. 3b).

3.1.2. Tree loss

The loss of older trees at different times (Fig. 4) shows that in the period 1926–57, logging was targeting the oldest trees (>202 years at breast height), and especially the oldest class (>262 years at breast height) whereas the high loss in the period 1957–87 was mainly of trees with a total age of 142–261 years at breast height. In the most recent period (1987–2007; Fig. 4), the harvesting of old trees decreased and the loss rates of trees older than 142 years at breast height approached the expected natural mortality in forests (Eid and Tuhus, 2001).

3.1.3. Volume of individual trees

The volume of individual trees at a given age increased considerably over the study period, with one exception: the oldest trees from 1926 to 1957 where a decrease was observed (Fig. 5).

3.1.4. Volume of trees in reserves by age class

The volume of trees in formally protected areas tripled between 1926 and 2017. Volume increased in all tree age classes except the youngest age class (Fig. 6).

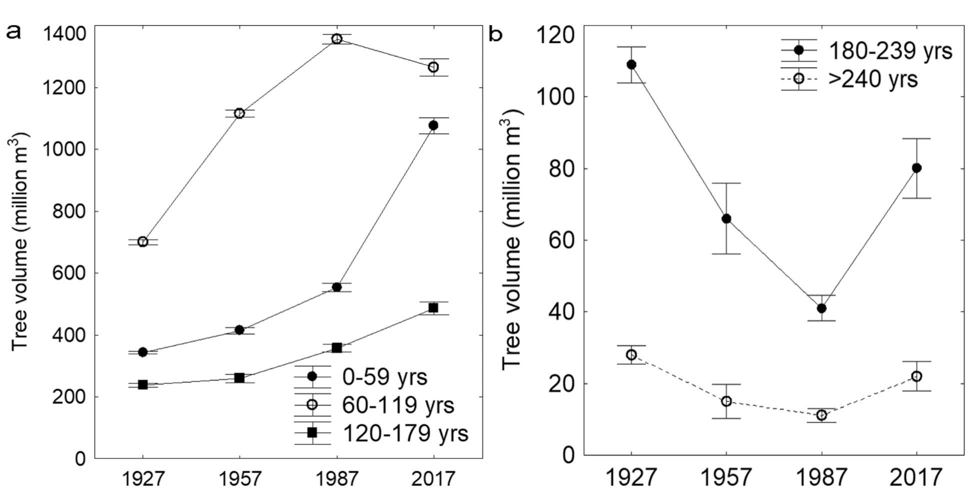

Fig. 3. Volume (million m^3) per tree age class in Sweden. Estimates based on trees ≥ 10 cm DBH outside today's protected areas. a) Younger age classes; b) Older age classes. Error bars represent $CI_{95\ \%}$.

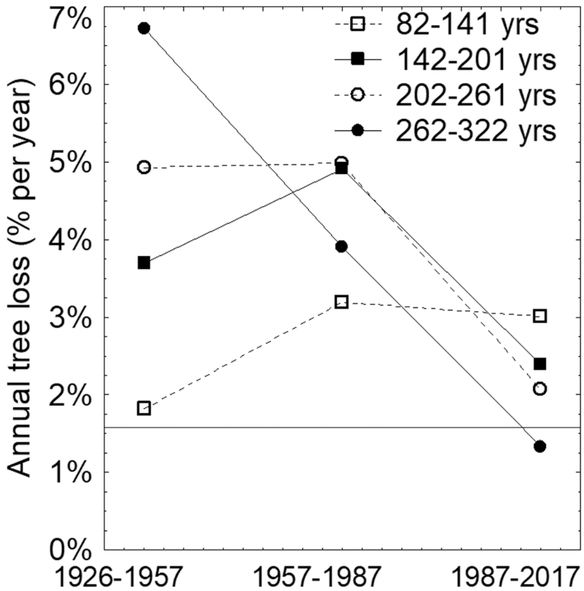

Fig. 4. Annual loss of trees of different age classes during different time periods. Estimates based on trees ≥ 10 cm DBH outside today's formally protected areas. The reference line indicates the annual natural mortality of trees in Norwegian forests (Eid and Tuhus, 2001); the line is the weighted average of spruce and pine, of trees ≥ 30 cm DBH.

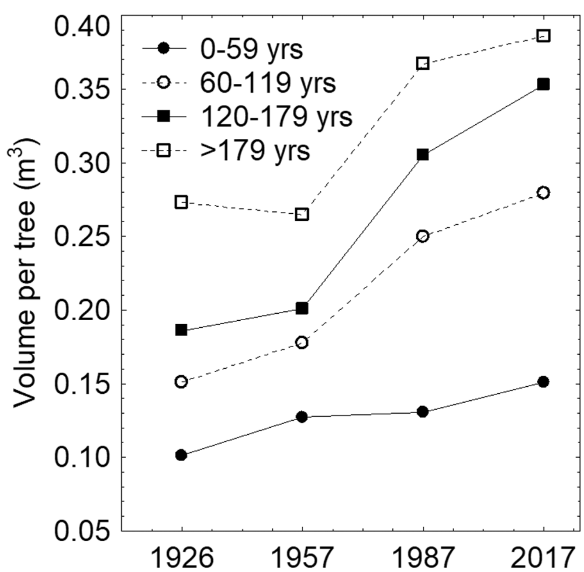

Fig. 5. Mean tree volume per age class over time. Estimates based on trees ≥ 10 cm DBH outside today's formally protected areas.

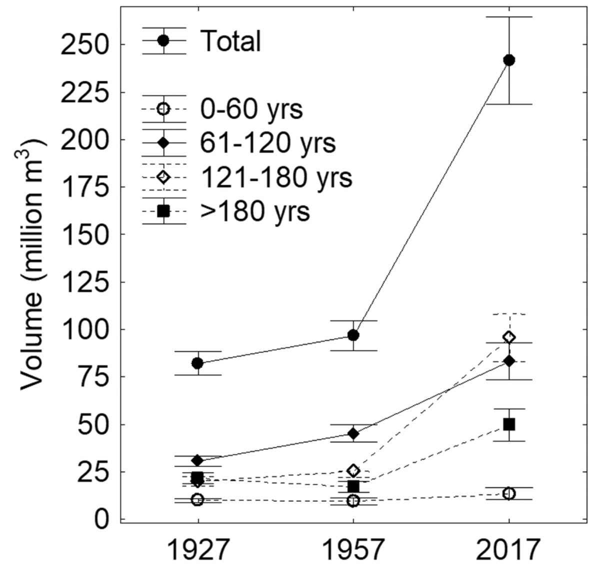

Fig. 6. The volume of trees of different age classes within today's formally protected areas. Only trees with DBH ≥ 10 cm are included. Error bars represent $CI_{95\ \%}$.

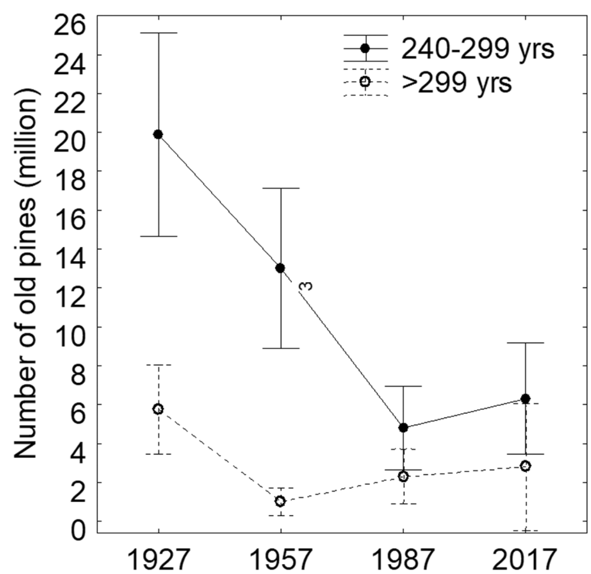

Fig. 7. Number of old Scots pines (*Pinus sylvestris*) in Norrbotten. Estimates based on trees ≥ 10 cm DBH outside today's formally protected areas. Error bars represent $CI_{95\ \%}$.

3.2. Norrbotten

3.2.1. Old Scots pine and Norway spruce

The number of Scots pines over 240 years old is now one third of the number in 1926. The loss up to 1987 was 75 %, but since then the trend has levelled off (Fig. 7).

After 1926, the number of Scots pines over 300 years old fell by more than 85 % to a low in 1957 (Fig. 7). Since then, the number has increased to a level around 50 % of that of 1926 (Fig. 7) (note that the number of sample trees of Scots pine over 300 years old in 1957, 1987 and 2017 was very small).

The number of Norway spruce trees with a diameter of 10–20 cm that were ≥ 160 years old decreased by 85 % from 1926 to 1987. From 1987 to 2017, the number doubled again (Fig. 8). Larger diameter spruces > 30 cm had already disappeared by 1926 due to selective harvesting before 1926, so there was only a small further decrease until 1957 and no increase since then (Fig. 8).

3.3. South-central Sweden

3.3.1. Volume per age-class

The estimated total volume of trees has almost tripled since the 1920s (Fig. 9a). The development of volume in different age classes followed the general trends in Sweden for tree age-classes up to 180 years (Fig. 9a). Until 30 years ago, trees older than 180 years were virtually absent in South-central Sweden (Fig. 9b). It should be noted that part of the increase in volume was due to the conversion of agricultural land into forest.

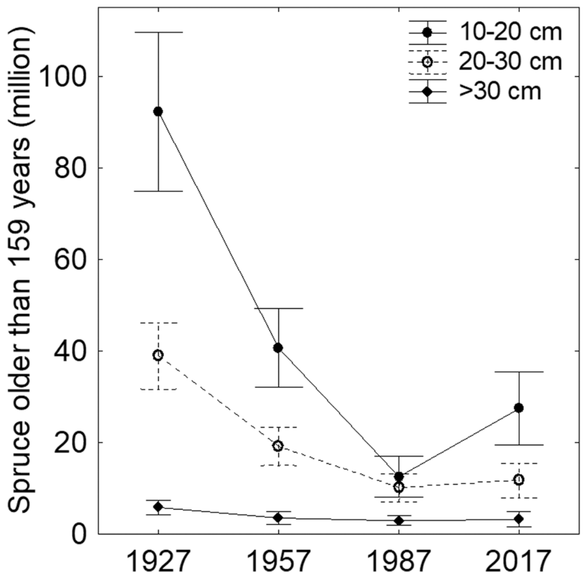

Fig. 8. Number of Norway spruce (Picea abies) in Norrbotten ≥ 160 years by size class. Estimates based on trees ≥ 10 cm DBH outside today's formally protected areas. Error bars represent $CI_{95\ \%}$.

The volume of oak (*Quercus robur, Q. petraea*) has changed dramatically since 1926 (Fig. 9c). Oaks > 120 years old were very rare in the data up to 1987, and since then the volume of such oaks has increased by a factor of 8 (Fig. 9c). Again, it is possible that some of this increase was due to the conversion of agricultural land with scattered trees to forest.

3.3.2. Share of broadleaved trees in total volume

For all three tree age classes, the proportion of volume of broadleaved trees decreased substantially between 1926 and 1957, and for two of the classes also by 1987 (Fig. 10). Since then, the proportion of broadleaved trees has increased substantially and is now well above the 1926 level (Fig. 10).

4. Discussion

4.1. Sweden

The results clearly illustrate the trend of increasing forest stocks in Sweden (Skogsdata, 2023), which also occurred in neighbouring countries since the 1920s, and other boreal and temperate regions (Rautiainen et al., 2011, Henttonen et al., 2020, Breidenbach et al., 2020, Korhonen et al., 2021).

The volume of wood in Sweden has more than doubled since the 1920s, to a large extent due to the implemented policies to promote volume production, a development similar to that in Finland (Henttonen et al., 2020). Although forest management is the main driver, it is possible that increased CO_2 and temperature has also contributed (Collalti et al., 2020, Launiainen et al., 2022).

4.1.1. Volume per age class

Initially, the increase in volume was concentrated in the 75–105-year

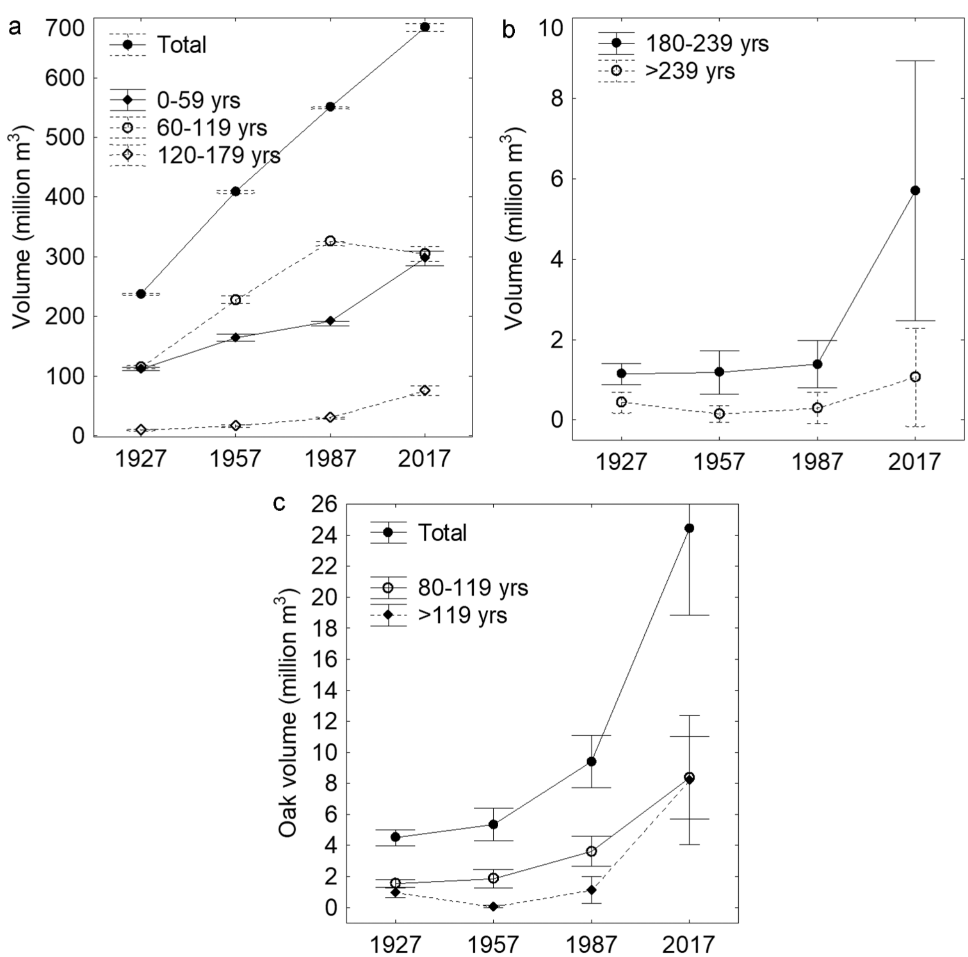

Fig. 9. Tree volume in south-central Sweden over time. a) younger age classes and all trees; b) older age classes; c) oak trees (Quercus sp). Estimates based on trees ≥ 10 cm DBH outside today's formally protected areas. Error bars represent $CI_{95\ \%}$.

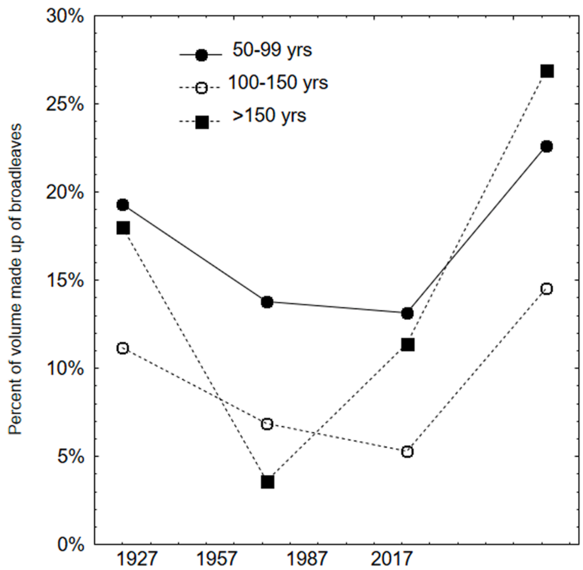

Fig. 10. Proportion of broadleaved trees in total volume over time in south-central Sweden, according to tree age. Estimates based on trees ≥ 10 cm DBH outside today's formally protected areas.

age classes. The widespread use of selective harvesting methods and the reliance on natural regeneration in the first half of the 20th century favoured the harvesting of "over-mature" and large trees while protecting the understorey and middle-aged trees which were considered "developable".

Over the last 30 years, the volume of both older and younger trees has increased rapidly. The volume of trees less than 60 years old has almost doubled over the last 30 years, reflecting the increase in clear-cutting and subsequent investment in forest regeneration during the period 1950–1990. The increase in the volume of older trees reflects reduced harvesting of "over-mature" trees and stands following a shift in forest management around 1990, which emphasised the protection of biodiversity (Kyaschenko et al., 2022). Another cause is the decreasing demand for "oversized" trees as sawmills streamlined their production lines. The recent increase in the total volume of old trees in Sweden contrasts with a recent decline in number of old trees in neighbouring Finland (Henttonen et al., 2019).

4.1.2. Loss rate

The loss of very old trees was high in the first two periods (1926–1957, 1957–1987) due to high-grading targeting large trees in the early 20th century and increased clear-cutting of older stands in the period 1950–1990. In contrast, during the period 1987–2017 loss rates slowed down and approached the natural mortality rate of old trees (Eid and Tuhus, 2001). The latter is a likely effect of voluntarily setting aside of forest stands with old trees as part of an integrated landscape management, as well as the practice of retention forestry at the forest stand level, where older individual trees and groups of trees should be retained (Simonsson et al., 2015, Kyaschenko et al., 2022, Skogsdata, 2023). Limited demand for "oversized" trees may also have contributed.

4.1.3. Volume of individual trees

Trees in Swedish forests today are significantly larger in volume at certain ages than a century ago, and this pattern is consistent across all age classes. When high-grading and continuous cover forestry are applied, the trees left after harvesting are generally smaller trees whether they are old or not. Therefore, high-grading would reduce the average size of trees of a given age, a process that was already underway at the time of the first NFI. The number of old but small trees continued to increase until 1957, but this accumulation stopped when clear-cutting was introduced on a larger scale around 1950, resulting in a significant increase in the average size of trees of a given age. In addition, pre-commercial and commercial thinning of young forests became more common after 1950, with the specific aim of increasing the average size of trees at a given age.

4.1.4. Tree volume in reserves per tree age

The increase in tree volume over time in protected areas was expected (Hedwall et al., 2013, Unar et al., 2022, Fassl et al., 2024) but is nevertheless remarkable. It suggests that a large part of the currently protected forests in Sweden have not been in a steady state regarding volumes, but rather been affected by significant historical disturbances like forest fire, grazing or logging. It also raises questions regarding society's goal with conservation and the potential need for future management of protected forests to preserve more open environments and species restricted to less dark environments and or recurrent large-scale disturbances.

It should be noted that although most forest reserves are in northern Sweden (Skogsdata, 2022), the development is uniform throughout Sweden (data not shown).

4.2. Norrbotten

4.2.1. Scots pine

The 75 % reduction in the number of Scots pines 240–299 years old in non-protected areas in Norrbotten between 1926 and 1987 shows that harvesting practices targeted the most valuable trees. During most of the period 1926–1957, high-grading of primary and old-growth forests was the standard harvesting practice, and later clear-cutting of residual stands with old seed trees became standard. The oldest Scots pines (≥300 years) also showed a similar pattern of decline, and by 1957 their numbers had already reached 15 % of their 1926 levels. After the end of high-grading in the early 1950s, pines just under 300 years old were left to age in stands that were not prioritised for clear-cutting during the period 1957–1987. The decline in the number of very old pines agrees well with a previous study carried out on the same data from this county (Andersson and Östlund, 2004), where an 85 % decline in very old pines was recorded from 1926 to 1996. Using a longer time series, we were able to show more details of the decline, but also that the trend levelled off since 1987.

Norrbotten, Sweden's northernmost county, contained most of Sweden's remaining old-growth forests in 1926, as indicated by the large number of Scots pines older than 300 years (6 million trees outside current formal protected areas). It is worth noting that Andersson and Östlund (2004) recorded a higher number of old pines outside protected areas (8 million) and there are at least two reasons for this. First, there has been an increase in protected areas from 1996 to the present; therefore, the current study excluded more old-growth forest than Andersson and Östlund (2004) did. Second, Andersson and Östlund (2004) calculated total tree age by adding slightly more years to the age at breast height than we did.

4.2.2. Norway spruce

In 1926, there were many old but small spruce trees in the forests of Norrbotten, but this tree type was drastically reduced during the 1900s. This may have been partly due to growth combined with a lack of new recruits, but we believe that this change in stand structure was mainly due to the change from high-grading and selective logging, where such spruce would accumulate, to clear-cutting where such trees would be removed. During the period 1987–2017 new understorey consisting of small old spruce trees developed in stands that had been allowed to grow since the early 1900s.

4.3. South-central Sweden

The most striking feature of the data from South-central Sweden was the threefold increase in wood volume, which was larger than the national estimate. Also noteworthy was the even stronger increase in oak (cf. Petersson et al., 2019). There was also a general shift towards more broadleaved species, despite the management paradigm of promoting conifers and controlling broadleaves (Bärring, 1965, Östlund et al., 2022). The conversion of former agricultural land to forest land would have contributed to the volumes, and possibly also to the relative increase in broadleaved trees.

It is noteworthy that oak volume increased in all age classes (cf. Petersson et al., 2019), despite numerous claims that oaks are rare, declining and sensitive to shade (e.g. Diekmann, 1996, Götmark et al., 2005, Lindbladh and Foster, 2010). It is likely that today's forests in southern Sweden are denser and darker than they have been for a long time, i.e. since agriculture and livestock grazing began several thousand years ago (Lindbladh and Foster, 2010).

Increasing wood volume appears to be a general trend worldwide (Rautiainen et al., 2011). One consequence of increasing volume per hectare is a darkening of the forest interior (Landuyt et al., 2024). It appears that forests today are darker and possibly cooler than a century ago when forest conditions were different and influenced by past or ongoing grazing by domestic animals (Segerström and Emanuelsson, 2002, Cserhalmi and Israelsson, 2004, Dahlström, 2008, Kardell, 2016, 2017, Milberg et al., 2019, Henttonen et al., 2020).

This shading is likely to reduce the biomass of the ground, field and shrub layer (e.g. Bergstedt and Milberg, 2001, Hedwall et al., 2013, Sandström et al., 2016, Jonsson et al., 2021, Skogsdata, 2023, Backéus et al., 2024), and reduce the natural regeneration of trees (e.g. Petersson et al., 2019). Ectotherms, many of which reach their northern distribution limit in Sweden, are sensitive to shaded environments (e.g. Wikars, 2004, Lindhe et al., 2005, Lundell et al., 2015, Milberg et al., 2016, Eriksson, 2022), which also points to a potential, negative driver of some insect assemblages.

As a result of the outbreak of the Second World War, coal and oil imports to Sweden suddenly ceased in 1939 and the authorities quickly implemented several measures to ensure that enough fuelwood was cut (SOU, 1952). Nationally, about 141 million m^3, of mainly thinner dimensions, was harvested in 1939–45 (SOU, 1952). For logistical reasons, much of the harvesting took place in southern Sweden, close to the country's population and industrial centres. It is in this light that we interpret the decline in broadleaved trees from 1926 to 1957 (Fig. 10). However, the fuelwood boom is not clearly visible in the data on the total volume of trees (Fig. 9) probably because the war also meant a reduced demand for conifer-based forest products as exports ceased.

4.4. Implications for the assessment of trends important for biodiversity

Indicators are a preferred method for assessing the state of the environment (Noss, 1990), but the results relevant for Swedish forest biodiversity have sometimes been contradictory. Quantitatively based indicators mostly show positive trends (e.g. area of old forest; volume of dead wood, area of stands with large trees) or no clear trend (area of older broadleaved forest, breeding forest birds (Naturvårdsverket, 2022, Skogsstyrelsen, 2022, Green et al., 2024). In contrast, biodiversity indicators show negative trends (e.g. conservation status of habitat types and number of threatened red-listed species (Naturvårdsverket, 2020, 2022, Skogsstyrelsen, 2022). The current study confirms, on a longer time scale, that several variables related to trees have changed in directions that should be favourable for biodiversity, especially so in the last 30 years (old pines, old oaks, old trees, large trees, proportion of broadleaved trees). However, such positive changes do not automatically translate into improved conditions for biodiversity (cf. Kyaschenko et al., 2022, Mönkkönen et al., 2022, Ram et al., 2017). More detailed studies are welcome to clarify these different trends.

4.5. Conclusions: implications of policy

Looking back over a century, a number of points emerge. First, it seems clear that the first Forestry Act, introduced in 1903 to ensure the regeneration of the forest, contributed to a significant reduction in the number of old trees. Also, the lack of investment in regeneration during the period 1920–1950 resulted in low volumes of trees aged 60–119 years in 2017. However, the depletion of the forest in terms of tree volume reversed into a steady increase in standing volume.

Another conclusion is that it takes many decades for investment in regeneration, or lack of such investments, to have a clear impact on the tree population. Policy makers therefore need to take a very long-time perspective when deciding whether to encourage or discourage action. For example, the effects of more intensive regeneration practices around 1950 became apparent on the total volume of the tree population 30 years later.

Finally, the development of the tree population in Sweden over the last 100 years reflects the persistent policy of restoring forest resources. In the first phase (1926–57), the aim was to protect the growing stock from purely exploitative harvesting by enforcing compulsory, mostly natural, regeneration and protecting young vigorously growing trees. During the second phase (1957–87) policy focused on investment in forest regeneration – clearing understocked forests and concentrating on harvesting overmature stands, while continuing to increase the growing stock. The third phase marks a shift towards restoring structures important for biodiversity in the tree population, resulting in a significant increase in old and large trees – particularly broadleaves. Meanwhile, the impact of earlier policies is reflected in the rapidly increasing volume of young and middle-aged trees.

CRediT authorship contribution statement

Per Milberg: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Anna-Lena Axelsson:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Jonas Fridman:** Writing – review & editing, Software, Resources, Methodology, Data curation, Conceptualization. **Jonas Jacobsson:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors have no known competing interests.

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Data availability

The data set is available at: https://doi.org/10.5878/k65t-qb32.

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