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

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1 Table
10 Figures

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1 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). The changes in tree population structure since 1923 are described and related to policy. During the first part of the study period, policy aimed at restoring the growing stock and productivity of forest land, but with methods that changed over time. In the last 30 years, a new forestry paradigm was launched to include restoration of tree population diversity, presuming this would also promote biodiversity. Over the last century, timber volumes doubled, tree sizes increased, older trees become more frequent and this was even more pronounced for the deciduous species. Volume, and thus light conditions, in today's protected forests nearly tripled, raising questions related to management of protected areas. We also considered two regional cases. The sparsely populated county of Norrbotten, which was the last region exploited for forestry in Sweden in the 1890s, had many old pines as well as many old but small spruce in 1926. These numbers shrunk in the coming decades initially due to selective high-grading and then through extensive clear-cutting. After the policy shift around 1990, the negative trends reversed. In densely populated South-central Sweden, forests had long been subjected to grazing, timber and firewood harvests and charcoal production. During the last century, timber volumes tripled, older trees become more frequent and deciduous trees became more prevalent.

Keywords: Sweden, Picea abies, Pinus sylvestris, Quercus, 20th century, NFI, sample tree, tree age

Introduction

Trees have a limited lifespan. Although the maximum biological age varies among species, a more important factor that determines tree age distribution in production forests is the average size considered suitable for harvest and the time needed for trees to grow to that size. Such considerations varies both in time and space depending on logistics, market factors and societal limitations (i.e. laws, regulations and policy). With the slow growth in boreal forests, detailed long-term forest data are helpful to evaluate the broad patterns of change, and the relative importance of different forest management methods applied, and to what extent changes in policy achieve their aim. Also, when developing forest policy, an analysis of past development of the targeted forest is important, and preferably this should be based on sound and detailed data covering as long a timespan as possible.

In this study, we use a 100-year data set from sample trees within the Swedish National Forest Inventory (NFI) (Fridman et al. 2014). The measurements have been made with comparable methodology and definitions during the entire 100-year period. We focus on i) tree age (assessed by year ring counting), ii) size (diameter at breast height 1.3 m above ground (DBH) measured by caliper) and iii) tree volume (calculated based on models using measured height and DBH). This study exploits recently digitized data of sample trees from the 1920s, and data from 1953 and onwards that were continuously digitized after fieldwork and stored in the NFI database.

Previously, most statistics based on data from the Swedish NFI have used field assessments of stand age to capture the age structure of tree populations. In contrast, using individual tree age enables a deeper understanding of both tree population age structure and tree population age dynamics. We are only aware of three previous studies that have used sample tree data from the first NFI (1923-1929). Andersson & Östlund (2004) analysed density changes of old trees in the county of Norrbotten, between 1926 and 1997. Axelsson (2001) studied changes in tree age for large coniferous trees in the county of Dalarna between 1923 and 1990. Preliminary analyses of sample tree data were conducted by Elgan & Persson (2022) comparing data from the 1920s and today. The current study is the first attempt to analyse the dynamics of the tree populations on larger temporal and spatial scales.

Since the first NFI, sample trees have been selected through well-defined sampling schemes (Ståhl 2024). The probability of inclusion is known for each sample tree, and it is consequently possible to estimate the total number of trees in the tree population, or a subpopulation thereof, using these sample trees. Hence, the estimated population during different time periods can be regarded as a census of the then living tree population. These data allow for analysing the age structure of the tree population over time and drawing conclusions regarding potential drivers behind population changes, drivers such as growth, tree harvesting, and natural mortality.

Historical factors that affect the Swedish tree population

Forest management in Sweden has undergone significant changes both before and during the period under study. During the 1800s, a wave of industrial timber exploitation affected Sweden, starting in the south, and ending in the inland of northern Sweden (Karlsson & Valinger 2023) and was driven by increasingly efficient timber processing and logistics. This exploitation led to fear for the future status of forest resources and resulted in a Forestry Act (1903), and the initiation of a national forest inventory (Fridman and Östlund, 2024).

The 1903 act made regeneration of forests after logging compulsory. Subsequently, there was an increased attention to natural regrowth, planting and seeding. However, following the economic recession in the late 1920s and throughout the second world war, cost considerations prevented long-term investments 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. During the Second World War, Sweden substituted wood for coal, which meant a doubling of harvest of firewood that made up 50 percent of the annual harvested volume (SOS 1948).

Although the consequences of repeated high-grading (selectively cutting only the most merchantable trees, and low or no investments in regeneration) these practices continued until after the Second World War, and affected the development of the tree population 1926-1957 (Tirén 1952).

In the early 1950s, reforestation investments increased considerably – especially in the state-owned forests of northern Sweden (Ebeling 1959) – where earlier high-graded stand, now poorly stocked, were cleared and replanted. High-grading ceased as a common practice, and instead large clear cuttings followed by artificial regeneration become standard management during the period 1957-1987.

During the period 1987-2017, there has been an increasing appreciation of other aspects of forests than only wood fibre production. This shift is reflected in the Forestry Act of 1994 that points out two aims of equal importance in its first paragraph: sustainable harvest and maintenance of biodiversity. The Brundtland report “our common future” (1987), the RIO-conference (1992) and the United Nations Millennium Declaration (2000) further stressed the importance of biodiversity in sustainable forest management. Consequently, forest policy was reassessed, and conservation measures such as retention forestry (Franklin 1989, Simonsson et al. 2015), intentionally leaving individual living and dead trees, groups of living trees (Lindhe et al. 2004, Kyaschenko et al. 2022) and setting aside forests to grow old were introduced and became an integral part of forest management in Sweden. At the same time, there were efforts to formally preserve old-growth forests in reserves of different types (SOU 1997), involving an increase from 1 percent of all productive forests being formally protected in 1990 to 6.1 percent in 2023 (SCB 2024, Table 4.8).

Our hypothesis is that the shifting forest policies outlined above made significant imprints in the tree population. How did the following changes affect the tree population?

- The introduction of the forestry act in 1903 that made forest regeneration after clear-felling compulsory and promoted the use of less intensive high-grading harvesting methods during 1920-1950
- The substantial harvest of firewood during the Second World War.

- The large-scale investments in clearing and regeneration of low-stocked and old forests during 1950-1990.
- The introduction of retention forestry and increased area offset-aside and formally protected old forests after 1990.

There are other drivers of change than those mentioned above, e.g. grazing by domestic and wild animals (Dahlström 2008), climate change (Brecka et al. 2018, Hedwall et al. 2019, Venäläinen et al. 2020, Hedwall et al. 2021) and N-deposition (Binkley & Högberg 2016). but we have deemed the current data less likely to shed light on them.

In addition to analysing the full Swedish tree populations, we also considered data from two regions.

First, the sparsely populated Norrbotten, the northernmost county of Sweden (Figure 2). Here, cutting for local usage and tar and potash production existed since way back in time, but it is unclear to what extent forest were burned to promote grazing for domestic animals (Kempe 1909, Tirén 1937, Zachrisson 1977). Forest exploitation for sawmills started early but their productivity was low (Carlgren 1926). More widespread exploitation began in the late 1800s, mainly driven by a number of administrative and legal changes that facilitated trade, establishment of freedom of trade and land ownership (Karlsson & Valinger 2023). This led to continued effort to improve rivers for rafting of timber (Andersson 1907, Winberg 1944, Törnlund & Östlund 2006) that supplied timber to sawmills established along the coast, subsequently supplemented by pulp industries (that used trees of slimmer dimensions as well as of spruce). At the time of the first National Forest Inventory 1923-1929, almost all Swedish forests had been high-graded once or repeatedly, except for the most remote parts of Norrbotten county. Thus, this is also the only region of Sweden, where significant numbers of trees older than 300 years of age remained at the time of the first national forest survey (Andersson & Östlund 2004).

Second, we selected the densely populated region of South-central Sweden (Figure 2), excluding counties along the coasts with a significant presence of nemoral hardwood forests and a landscape dominated by agriculture. Forests in the mostly hemiboreal south-central Sweden are more diverse in terms of tree species and are more productive than Norrbotten, allowing for shorter forest rotations. Two legislations specifically targeted some deciduous trees southern Sweden (*Fagus sylvatica* SFS 1974:434; *Quercus, Tilia, Acer, Fraxinus* SFS 1984:119), aiming to prevent the conversion from deciduous stands to coniferous. In this area, forests are often mixed with agricultural land, and there is a long history of intensive usage of forests for products (firewood, timber, charcoal, glassworks, fencing) and for grazing by domestic animals (Segerström & Emanuelsson 2002, Dahlström 2008). Furthermore, most forest is privately owned, divided among a large number of relatively small properties managed by owners with differing priorities (Bakxa et al. 2024). Since the Second World War, marginal agricultural land has been afforested mainly with spruce, and forest grazing has ceased, turning South-central Sweden to an important timber production region.

3 Material & methods

3.1 The Swedish National Forest Inventory

The Swedish National Forest Inventory (NFI), started in 1923 and is part of Sweden's official statistics. Its primarily aim is to describe the state and changes of Swedish forests (Fridman et al. 2014). The NFI sample as of today is based on an annual sample of approximately 20,000 circular plots, clustered into tracts, of which around 12,000 are annually surveyed in the field, with up to 120,000 trees calipered. Focus, scope and design (Figure 1) has shifted during the lifespan of the NFI where initially the forest as raw material for the forest industry was prioritized (Fridman & Östlund 2024).

With expanded data collection, the use of data from the Swedish NFI has become relevant for more areas than only the timber resource for the forestry industry, such as the development of ground vegetation, biological diversity, and the carbon cycle in the context of climate. Data are used for many different purposes and also serve as a basis for scenario analyses. (Fridman & Walheim, 2024).

Figure 1.

During the first NFI (1923-29) the belt was continuously sectioned into different landcover classes and forest types (SOU 1932) and the length of each section was measured. Trees at least 1.3 m high were calipered along the 10-meter-wide belt but only the sample trees was assigned to sections, i.e. site and stand characteristics such as landcover class and stand age, could be assigned to each sample tree. From 1953, when circular sample plots were introduced, both calipered trees and sample trees could be assigned attributes from the plot. Data from 1953-1962 was digitized in the 1960s, transformed and stored in a database in 2010. Data from 1983 has been collected using handheld computers, i.e. digitised and stored in a database continuously since then. All NFI data since 1923, except NFI 1938-52, is now easily processed since it is digitally stored in harmonised formats.

The first NFI, 1923–29, involved a huge number of sample trees (SOU 1932), which was reduced in subsequent inventories (Table 1). In 1953, the methodology changed from transects over a region to systematically distributed temporary plots, clustered into tracts, and distributed all over Sweden.

Figure 2.

3.2 Data set

The data used consisted of a list of all individual sample trees, ≥ 10 cm DBH, measured along temporary sample lines in 10-meter-wide belts (first NFI 1923-1929) or circular sample plots during the 1953-1962, 1983-1992, and 2013-2022 surveys. The 10 cm threshold was used to avoid smaller diameter trees since they were measured only on parts of sections or plots, i.e. not representing the whole plot. According to the NFI (Skogsdata 2024) the volume of trees with diameter <10 cm represents 8% of the total volume of trees in Sweden.

For simplicity, we denote each inventory period by its middle year: 1926, 1957, 1987 and 2017. Hence, we considered changes in the tree population between points in time up to ninety years apart, although based on data collected over a century.

The points in time inventory periods were selected because the intermediary periods reflect distinct phases within the history of forest policy and forest management in Sweden: (i) 1926-57; selective harvesting, poor regeneration and wartime harvesting for fuelwood; (ii) 1957-87: large scale clearing of old low-stocked forests and replanting; 1987-2017: Set-aside and retention forestry.

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

In this study, our focus was on forests that are outside formally protected areas defined by the GIS-layer for formally protected areas year 2023 provided by the National Conservation Agency. This was partly a choice and partly a necessity. Tree populations inside established formally protected areas were not included in the NFI field work between 1983 and 2002, meaning no trees were measured or selected as sample trees. Thus, no estimates of the tree population development inside reserves can be made during the 30-year periods 1957-1987 or 1987-2017. However, the tree population inside reserves is presented as volume per age class for the three points in time 1926, 1957 and 2027.

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

The sample tree statistics mirror statistics based on all calipered trees for number of trees, volume of trees, tree species distribution and diameter distribution (e.g. SOU 1932, Skogsdata 2022). This supports that the sample tree data also provides a fair representation of the tree population over combinations of these variables and tree ages.

3.2.1 Protocol for selecting sample trees

The method for selecting 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 number of sample trees by DBH or BA class. Since the probability of inclusion (πij) as a sample tree is known, both for the tree itself (*i*) and the sample plot (*j*), the Horwits-Tompson estimator can be used to estimate the total number of trees ($\hat{T}$) based on the selected sample trees (n) (Fridman et al. 2014):

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

To facilitate analysis, tree volume expansion factors were calculated for each sample tree using the probability of inclusion and the tree volume which make estimates of total volume, for e.g. age-classes by study area, easy-going by just summation of the expansion factors for the sample tree characteristics of interest.

3.2.2 Data collected from sample trees

Table 1.

3.3 Data handling

Age determination of sample trees

The age in breast height of the sample trees have been assessed by counting growth rings on bore cores extracted using an increment borer. During the first NFI (1923–1929) growth ring measurement and ring counting was done in the field using a magnifying glass and then again in the lab, but from the 1950s the cores were sent to lab for precise measurements using microscope. To determine the total age of the tree, regional-, tree species- and site-specific numbers of years to grow from seed to breast height was added to the age in breast height (SLU 2024, p. 6:27). The same table has been used for all trees irrespective of year of sampling.
For bore cores from the first NFI with central rot or where the centre of the tree was not included in the core, the sample tree age at breast height was assessed by using the stand age-class. Cores with incomplete age-counting from later NFI´s were not included in the analysis and did not affect the probability of inclusion for the sample trees used. No non-response analysis were made since the age of these sample trees were unknown.

Calculation of sample tree volumes

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

Annual mortality rate

The data allow for estimating, at different points in time, the number of living trees larger than 10 cm belonging to cohorts of trees passing breast height during a specific period in time. The change over time in the number of trees in such a cohort is the sum of (i) natural tree mortality and (ii) logging as well as (iii) in-growth of trees belonging to the cohort passing the diameter threshold 10 cm. However, since in-growth of trees older than 140 years at breast height is extremely rare on productive forest land, the dynamics in older cohorts is entirely driven by natural mortality and logging. For cohorts averaging ages between 80 and 140 years at breast height, in-growth is still insignificant, however not zero. When estimating tree mortality, it is assumed that trees in a 30-year age class pass from one class to the next between the points in time for the observations, which are 30 years apart. This is not fully true, since trees are surveyed over 10-year periods, but it is reasonable to assume that this does not systematically affect the estimates. In order to reach a sufficient number of sample trees behind estimating the number of trees in very old cohorts at different point of times, we merged the results from two adjacent 30-year age-classes. The number of sample trees in the oldest cohort analysed (trees aging 262-322 years at breast height) is 45-55 depending of point in time.

Annual mortality rate (AMR) was calculated as:

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

where N2 and N1 is the number of living trees at the end and beginning of the time period, respectively, and y the number of years between time points (in our case 60 years).

3.4 Statistical analyses

Although systematic sampling is used in the NFI since the very beginning, the precision of estimates, i.e. the variance, has been estimated assuming simple random sampling in this study. This will generally give 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 NFI´s from 1953 and onwards. Using belt inventory in the 1923–29 NFI, virtual tracts were created by splitting the belts into 2 km sections.

Using the estimated variance for estimates, confidence intervals (95%) was constructed according to Toet et al. (2007). CI has not been calculated for ratio estimates of tree size nor mortality. However, we report number of sample trees behind those estimates.

Results

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

Sweden

Volume per age class

Since the first NFI in the 1920s, the timber volume has more than doubled in Sweden (Figure 3a, 3b). During the period 1926-1987 the increase of volume was concentrated to age-classes 60-119 years (Figure 3a). In contrast, since 1987, volumes of this age class decreased while both older and younger age classes rapidly increased (Figure 3a, 3b). The volume of younger trees almost doubled over the last 30 years (Figure 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 m^3 (62%). Since then, the volume of trees older than 180 years has doubled to 101 million m^3, most of which belong to ages between 180 and 240 years (Figure 3b).

Figure 3.

Mortality

Mortality in older trees at different points in time (Figure 4) bears clear evidence that logging in the period 1926-57 aimed at the oldest trees (>200 years), and especially the oldest class (>280 years) while high mortality in 1957-87 was mainly in trees 220 years old. In the latest period (1987-2007; Figure 4), mortality rates of trees older than 180 years approached the expected natural mortality in production forests (Eid & Tuhus 2001).

Figure 4.

Volumes of individual trees

The volume of individual trees at a given age increased considerably during the study period, with one exception: the oldest trees from 1926 to 1957 where a decline can be observed (Figure 5).

Figure 5.

Volume of trees in reserves per age class

The volume of trees within protected areas tripled from 1926 to 2017. Volume in all tree age classes increased except for the youngest age class (Figure 6).

Figure 6.

Norrbotten

Old pine and spruce

Today, the number of pines 240-299 years old is one third of the numbers in 1926. The loss until 1987 was 75%, but since then the trend reversed (Figure 7).

After 1926, there was a reduction by more than 85% of pines older than 300 years to a low point 1957(Figure 8). Since then, the numbers have increased to a level about 50 percent of the 1926 one (Figure 7) (n.b. that the number of sample trees of pine older than 300 years was very small in 1957, 1987 and 2017).

Figure 7.

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

Figure 8.

South-central Sweden

Volume per age-class

The estimated total volume of trees had almost tripled since the 1920s. The development of volume in different age-classes followed the general trends in Sweden as a whole for tree age-classes up to 180 years. However, trees older than 180 years were practically absent in South-central Sweden until the last 30 years.

Figure 9.

The volume of oaks (*Quercus robur, Q. petraea*) has seen dramatic changes since 1926. Oaks >120 years were very rare in the data up until 1987, and since then the volume of such oaks increased by a factor 8.

Proportion of deciduous trees of total volume

In all three age classes of trees, the proportion of the volume that was made up of deciduous species dropped substantially from 1926 to 1957, and for two of the classes also to 1987 (Figure 10). Since then, the proportion of deciduous trees had increased substantially, now clearly surpassing the 1926 data (Figure 10).

Figure 10.

Discussion

Sweden

The results clearly illustrate the trend of growing stock of forest timber in Sweden (Skogsdata 2023), neighbouring countries and other boreal and temperate regions (Rautiainen et al. 2011, Henttonen et al. 2020, Breidenbach et al. 2020, Korhonen et al. 2021). Since the 1920s, and mainly as a consequence of implemented policies (Henttonen et al. 2020), the timber volume has more than doubled in Sweden. It is unclear to what extent increased growth due to CO_2 and temperature has contributed (Collalti et al. 2020, Launiainen et al. 2022).

Volume per age class

Initially, the increase of volume was concentrated to tree ages 75-105 years. The widespread use of selective harvesting methods and reliance on natural regeneration during the first half of the 20th century favoured harvesting of overmature and large trees while protecting undergrowth and middle-aged trees considered “developable”.

During the latest 30 years, both older and younger tree ages rapidly increased in volume. Volume of trees younger than 60 years almost doubled over the last 30 years, which reflects increased clear-cutting and subsequent investments in forest regeneration during the period 1950-1990. The increase in volume of older-aged trees reflects reduced harvesting of over-mature trees and stands following a shift in forest management around 1990 emphasizing protection of biodiversity (Kyaschenko et al. 2022). The recent increase of old trees is contrary to a recent decrease of old trees in neighbouring Finland (Henttonen et al. 2019).

In 1926, there were 137 million m^3 of trees older than 180 years in Sweden, and by 1987 this had decreased to 52 m^3 (a reduction by 62 percent). Since then, the volume of trees older than 180 years has doubled to 101 million m^3.

Mortality

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

Volumes of individual trees

Today, trees in Swedish forests are considerably larger in volume than a century ago, a pattern consistent over age classes. When applying high-grading and continuous cover forestry, trees left after harvesting are commonly smaller trees whether they are old or not. Thus, the number of small old trees would tend to accumulate under high-grading while at the same time only few new trees are added through regeneration. Hence, high-grading would decrease the mean size of trees of a certain age, an ongoing process at the time of the first NFI. The number of old but small trees continued to grow up to 1957, but this accumulation stopped when clear-cutting was introduced at a larger scale around 1950 resulting in a significant increase of mean tree size at a certain age. In addition, since 1950 precommercial and commercial thinning of young forests became a more common practice specifically aiming at increasing average tree size at a given age.

Volume of trees in reserves per tree age

The increase of tree volume over time within protected areas was expected (Hedwall et al. 2013, Unar et al. 2022, Fassl et al. 2024) but was nevertheless remarkable. It suggests that a large part of currently protected forests in Sweden have been intensively logged and/or been affected by forest fires, or grazing, in the past. It also raises several questions regarding society's aim with preservation, and the potential need for future management of protected forests to preserve more open environments and species confined to less dark environments. The consequence of a darkening of forest is further discussed below.

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

Norrbotten

Pine

The 75% reduction of the number of pines 240-299 years old on non-protected forest land in Norrbotten from 1926 to 1987 shows that harvesting practices targeted the most valuable and less productive trees. Standard harvesting practice during most of the period 1926-1957 was high-grading of primary and old growth forests and later clearcutting of residual stands with old seed trees became standard. Also, the oldest pines (≥300 years) showed a similar pattern of decrease, but the numbers reached a minimum already in 1957 at 15 percent of the 1926 numbers. After the end of high-grading in the early fifties, pines just below age 300 years have been left growing older in stands not prioritized for clearcutting during the period 1957-1987. As a consequence, numbers of really old pines started to increase, and following the introduction of retention forestry and set asides around 1990, the numbers continued to increase. The drop in numbers of very old pines is well in line with a previous study conducted on the same data from this county (Andersson & Östlund 2004), where a 85% reduction of very old pines from 1926 to 1996 was recorded. Based on a longer time series, we were able to show more details of the decline, but also that the trend had reversed to an increase since 1987.

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

Spruce

In 1926, numerous old but small spruces existed in the forests in Norrbotten, but these types of trees were drastically reduced later during the 1900s. This might partly be due to growth combined with a lack of new recruits, but we believe that this shift in population structure mainly represents a change from high-grading forestry, where such spruce trees would accumulate, to clear-cut forestry where such trees would be removed. During the period 1987-2017 new undergrowth consisting of small old spruce trees emerged in stands left growing since the early 19-hundreds.

South-central Sweden

The most striking feature in data from south-central Sweden was the tripling in timber volume, i.e. larger than in the national data. Notable was also the even stronger increase among oaks (cf. Pettersson et al. 2019). There was also a general shift towards more deciduous tree species, despite the management paradigm of promoting conifers and controlling deciduous trees (Bärring 1965, Östund et al. 2022).

It was noteworthy that oak volume increased in all age classes (cf. Pettersson et al. 2019), despite numerous claims that oaks are rare, declining and sensitive to shade (e.g. Diekmann 1996, Götmark et al. 2005, Lindbladh & 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 grazing by domestic animals started several thousand years ago (Lindbladh & Foster 2010).

Increasing timber volumes seems to be a general trend globally (Rautiainen et al. 2011). A consequence of increasing timber volume is a darkening interior of forest (Landuyt et al. 2023) that in turn would reduce biomass in the ground, field and shrub layers, and reduce natural regeneration of trees (e.g. Pettersson et al. 2019). We believe the darkening of forests is the most likely driver for changes recorded in ground and field layer vegetation in production forests and reserves in Sweden (Hedwall et al. 2013, Sandström et al. 2016, Jonsson et al. 2021, Backéus et al. 2024). Also, it is the likely reason that some invertebrate and vascular plants that are confined to sun-exposed or semi-open environments are now rare (e.g. Wikars 2004, Lundell et al. 2015, Eriksson 2022).

As a consequence of the Second World War, coal and oil imports to Sweden suddenly ceased in 1939 and the authorities quickly enforced a number of measures to ensure that fuelwood in sufficient quantities were cut (SOU 1952). Nationally, about 141 million m^3, mainly of slimmer dimensions, were harvested 1939-45 (SOU 1952). For logistics reasons, much harvesting took place in southern Sweden which was close to population and industrial centres of Sweden. It is in this light that we interpret the decrease in deciduous trees from 1926 to 1957 (Figure 10). However, the firewood boom did not clearly show in the data on total volume of trees (Figure 9) probably because the war also meant reduced demand of other forest products as export ceased.

Conclusions

Implications for assessment of trends important for biodiversity

Indicators are a preferred method to evaluate the status of the environment. Sweden has, since 1999, an environmental objectives system (Anonymous 2018), with 16 environmental quality objectives. One of these is ”Sustainable Forests” (Skogsstyrelsen 2022), that is evaluated by five indicators (area of formally forests; Change in area of old forest outside of protected areas; Breeding forest birds; general conservation measures in connection with regeneration felling; structures in the forest landscape). Another objective relevant for forests is “A Rich Diversity of Plant and Animal Life” (Naturvårdsverket 2022), evaluated by three indicators (Preservation status for habitat types; Redlisted species; Protected productive forests). The outcomes have partly been contradictory, with many indicators showing positive trends (Formally protected forests; Increase in area of old-grown forests; general conservation measures in connection with regeneration felling; structures in the forest landscape), while those dealing with biodiversity show negative trends (Breeding forest birds; Preservation status for habitat types, redlisted species). The current study confirms, on a longer time frame, that several forestry variables have changed in directions that should be favourable for biodiversity, especially so during the last 30 years (old pines, old oaks, old trees, proportion of deciduous trees). Such positive changes do not, however, automatically translate into improved conditions for biodiversity (cf. Kyaschenko et al. 2022, Mönkkönen et al. 2022). We see three main reasons why improvements in the forestry indicators might not directly translate into improvements in biodiversity indicators: follow-up times, the indicators used, and other concurrent changes in forests or forestry.

First, it is possible that important parts of biodiversity do not easily re-colonise due small population sizes combined with long distances, or the potentially long time needed for old trees to become suitable (e.g. old hollow oaks, Ranius et al. 2009). The spatial distribution of source populations might also slow down recolonisation Hence, changes are expected to be slow and extended in time. If this is correct, then one simply has to wait longer for the benefits to manifest themselves in terms of biodiversity.

Second, the indicators used might be inappropriate, e.g. do not respond to improved conditions, or only slowly so, or they might respond to some other unknown factor. Sweden uses three biodiversity-related variables: (i) an index based on 13 species of breeding forest birds, (ii) an index based on the change of red-list status of forest species, and (iii) an index of the status of forest habitats. Although indices have many advantages, there is a degree of non-transparency and uncertainty about which contributor(s) to the index that drive a change, or counterbalance trends in other contributors.

Third, something else has happened that might counteract the positive changes. One such change, documented in the current study, is the substantial increase in standing timber volume over time, in both production forests and reserves. Apparently, forests today are darker and cooler than a century ago, when forestry status was poor and influenced by previous or ongoing grazing by domestic animals (Segerström & Emanuelsson 2002, Cserhalmi & Israelsson 2004, Dahlström 2008, Kardell 2016, 2017, Milberg et al. 2019, Henttonen et al. 2020). This darkening likely reduces biomass of the ground, field and shrub layer (e.g. Bergstedt & Milberg 2001, Hedwall et al. 2013, Sandström et al. 2016, Jonsson et al. 2021, skogsdata 2023). Ectothermic animals, many of which reach their northern distribution limit in Sweden, are sensitive to shaded environments (e.g. Wikars 2004, Lindhe et al. 2005, Milberg et al. 2016), also pointing to a potential, negative driver of part of insect assemblages.

In conclusion, a better understanding of both the indicators used, and the effect of denser forests on biodiversity would be welcome.

Implications for policy

In the perspective of a century, a few points emerged. First, it seems apparent that the first forestry act instated to ensure regeneration of forests in 1903, if anything contributed to a significant reduction of old trees, and the lack of investment in regeneration during the period 1920-1950 resulted in small volumes in 2017 of tree ages 60-119 years.

A further conclusion is that it takes many decades for investments in regeneration or lack of such investments to clearly affect the tree population. Thus, policy makers need apply a very long time perspective when deciding on promoting or discouraging actions. The effect on the population of trees with a diameter exceeding 10 cm will be noticed only after 30 years.

Another conclusion is that the policy shift in the early 1990s resulted in a sharp shift in several trends relevant for biodiversity.

Finally, the development of the tree population in Sweden during the last 100 years reflects the persistent intention from policy-makers to restore forest resources. During the first phase 1926-1957 by protecting the growing stock from pure exploitative harvests and compulsory regeneration. During the second phase 1957-1987 policy focused on investments in forest generation – clearing of understocked forests and focusing on harvesting overmature forest stands, while still increasing the growing stock. The third phase marks a clear shift towards restoring structures important for biodiversity in the tre population, which resulted in a significant increase of old and large trees – especially deciduous trees. Meanwhile the impact of earlier policies is reflected in the rapidly growing volume of younger and middle-aged trees.

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Author contributions

- Conceptualization - Ideas; formulation or evolution of overarching research goals and aims: JJ, ALA, JF, PM
- Methodology - Development or design of methodology; creation of models: JJ, JF, PM
- Formal analysis - Application of statistical, mathematical, computational, or other formal techniques to analyze or synthesize study data: JJ, PM
- Investigation - Conducting a research and investigation process, specifically performing the experiments, or data/evidence collection: JJ, PM

- Resources - Provision of study materials, reagents, materials, patients, laboratory samples, animals, instrumentation, computing resources, or other analysis tools: ALA, JF
- Data Curation - Management activities to annotate (produce metadata), scrub data and maintain research data (including software code, where it is necessary for interpreting the data itself) for initial use and later reuse. JF
- Writing - Original Draft - Preparation, creation and/or presentation of the published work, specifically writing the initial draft (including substantive translation): JJ, PM
- Writing - Review & Editing - Preparation, creation and/or presentation of the published work by those from the original research group, specifically critical review, commentary or revision – including pre-or postpublication stages: JJ, ALA, JF, PM

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Figure and Table legends:

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

Figure 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. Sampled area*, and also the number of calipered trees and sample trees *is decreasing 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).*

Figure 2. *Europe and Sweden with study cases areas Norrbotten (light grey) and South-central Sweden (dark grey) highlighted.*

Figure 3. *Volume (million m³) per tree age class in Sweden. Estimates based on tree ≥10 cm DBH on productive forestland outside today's protected areas. 3a) younger age classes; 3b) older age classes.*

Figure 4. *Annual mortality of trees of different age classes during different time periods. Estimates based on trees ≥10 cm DBH on productive forestland outside todays formally protected areas. The reference line indicates annual natural mortality of trees in Norwegian production forests (Eid & Tuhus 2001); the line is the weighted average of spruce and pine, of trees ≥30 cm DBH.*

Figure 5. *Average tree volume per age class over time. Estimates based on trees ≥10 cm DBH on productive forestland outside today's formally protected areas.*

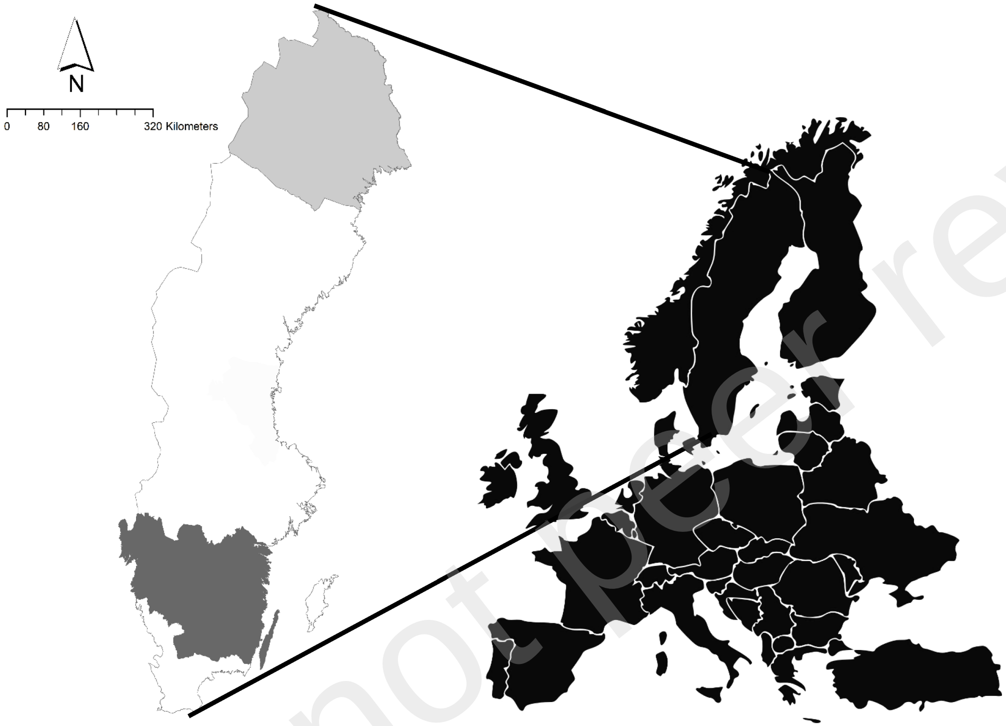
Figure 6. *The volume of trees of different age classes within today's formally protected areas. Only trees with DBH >10 cm are considered.*

Figure 7. *Number of old Scots pine trees (Pinus sylvestris) in Norrbotten. Estimates based on trees ≥10 cm DBH on productive forestland outside today's formally protected areas.*

Figure 8. *Number of Norway spruce (Picea abies) in Norrbotten ≥160 years, according to size class. Estimates based on trees ≥10 cm DBH on productive forestland outside today's formally protected areas.*

Figure 9. *Volume of trees in South-central Sweden over time. 10a) younger age classes and all trees; 10b) older age classes; 10c) oak trees. Estimates based on trees ≥10 cm DBH on productive forestland outside today's formally protected areas.*

Figure 10. *Proportion of deciduous trees of total volume over time in south-central Sweden, according to tree age. Estimates based on trees ≥10 cm DBH on productive forestland outside today's formally protected areas.*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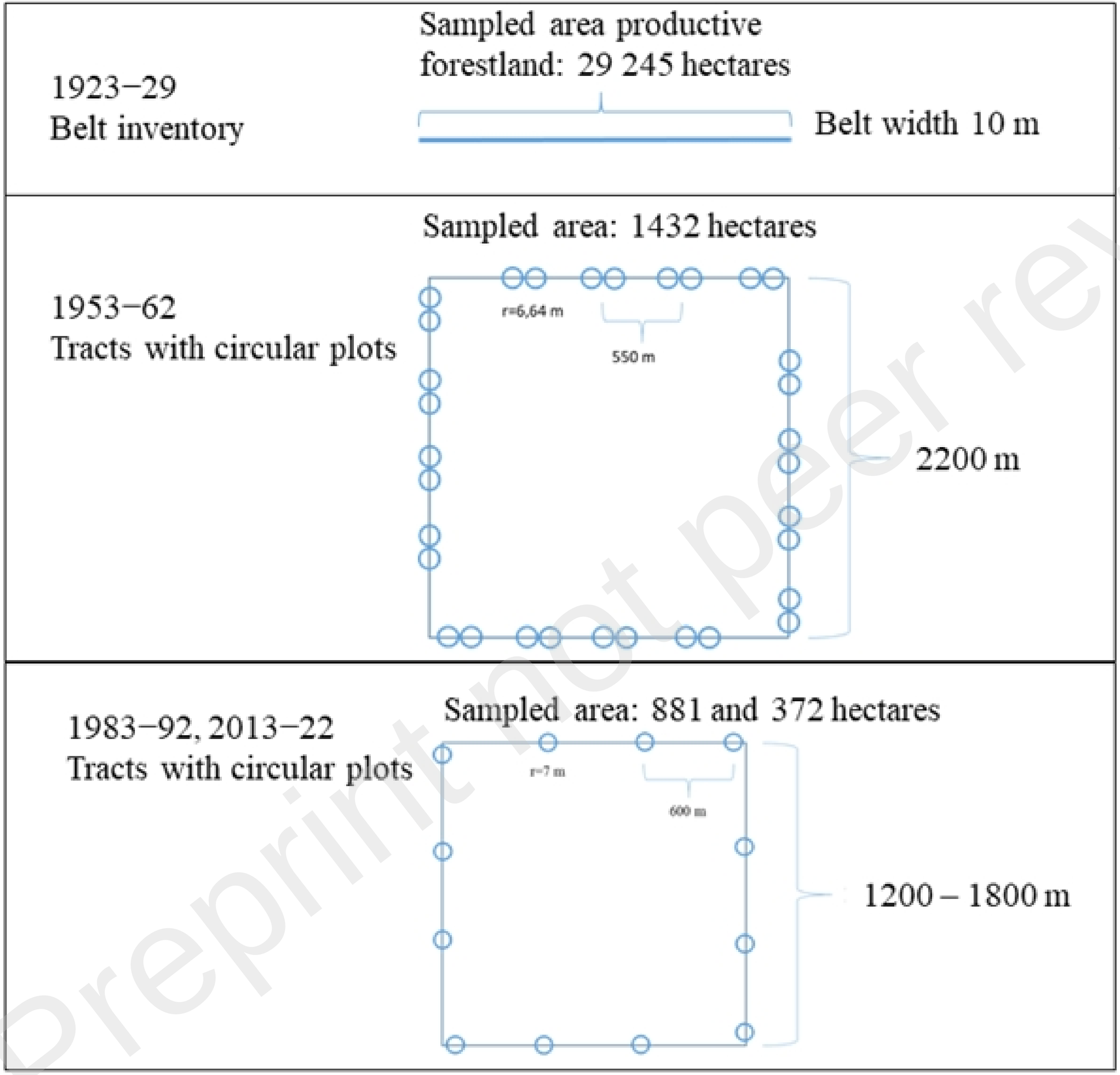
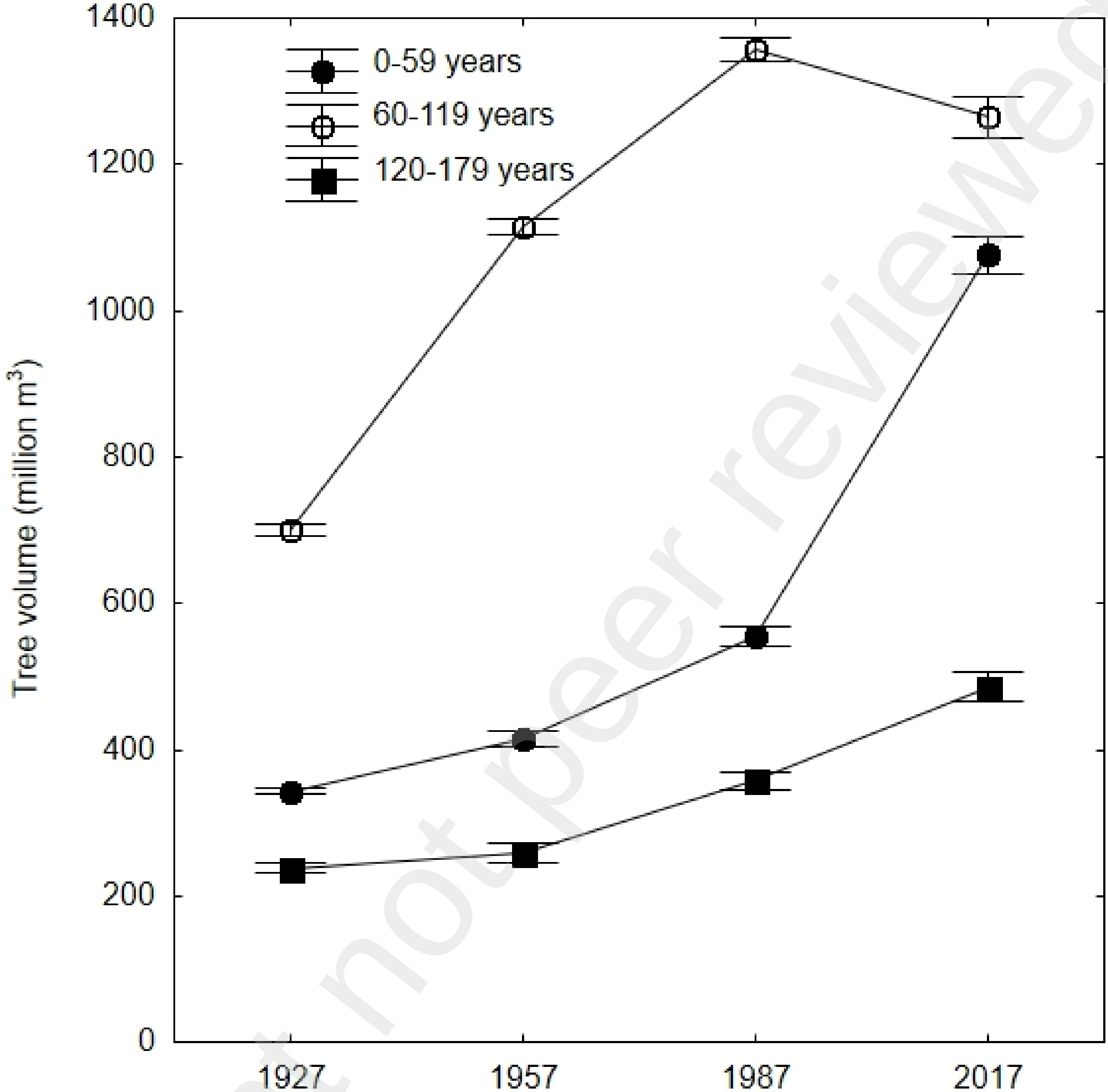
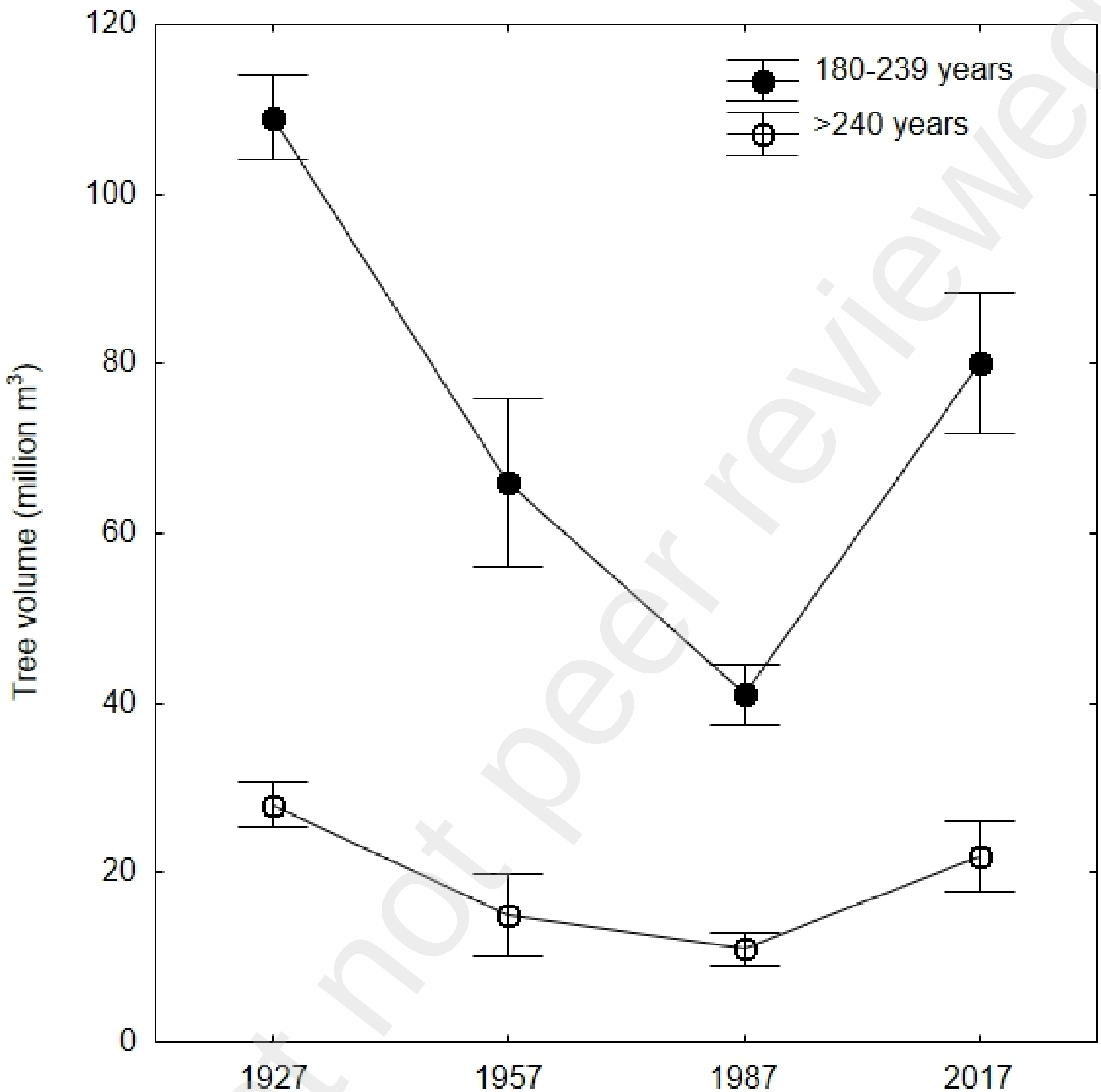
0 80 160 320 Kilometers

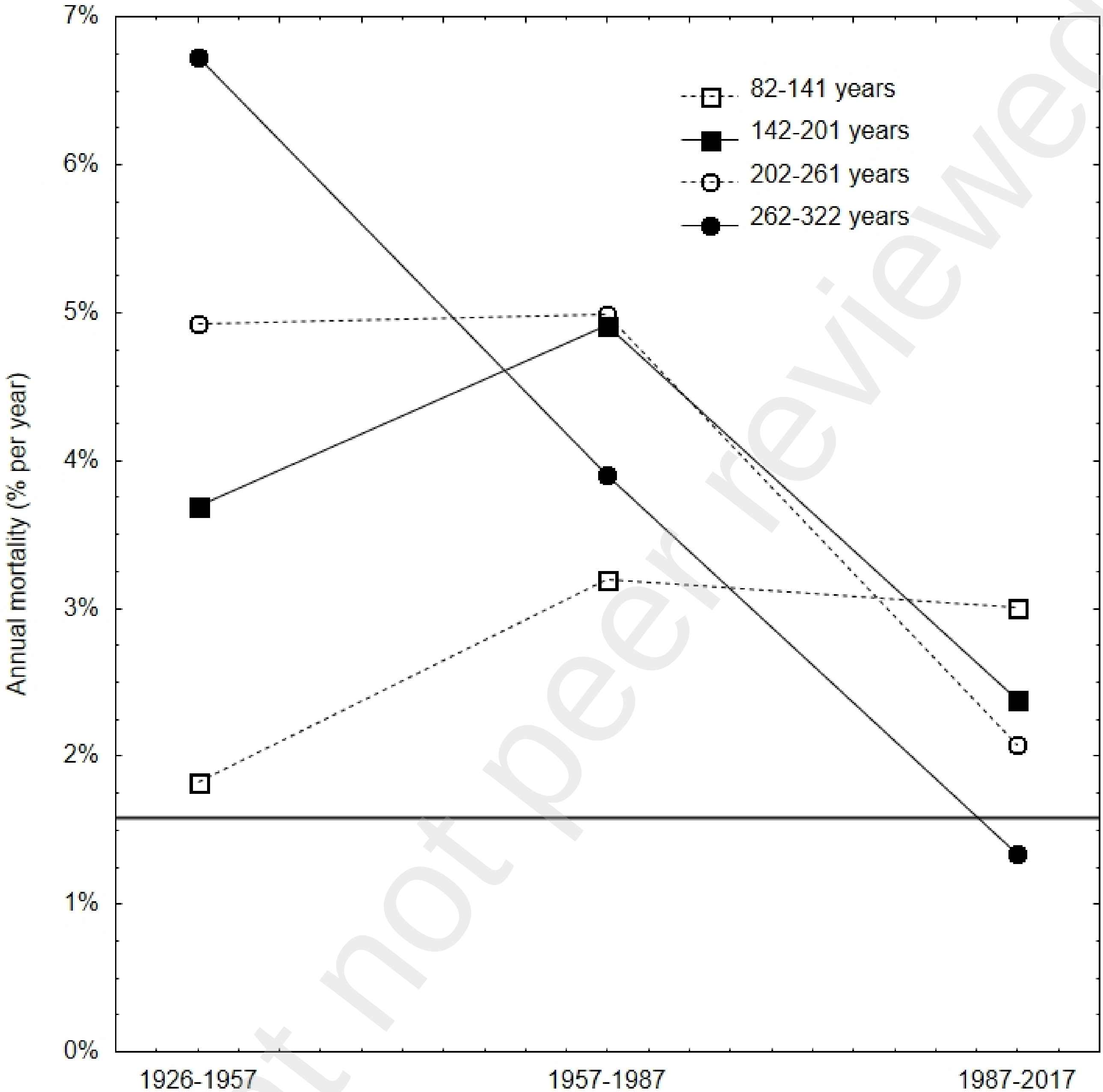

1923−29
Belt inventory
Sampled area productive
forestland: 29 245 hectares
Belt width 10 m
1953−62
Tracts with circular plots
Sampled area: 1432 hectares
r=6,64 m
550 m
2200 m
1983−92, 2013−22
Tracts with circular plots
Sampled area: 881 and 372 hectares
r=7 m
600 m
1200 – 1800 m



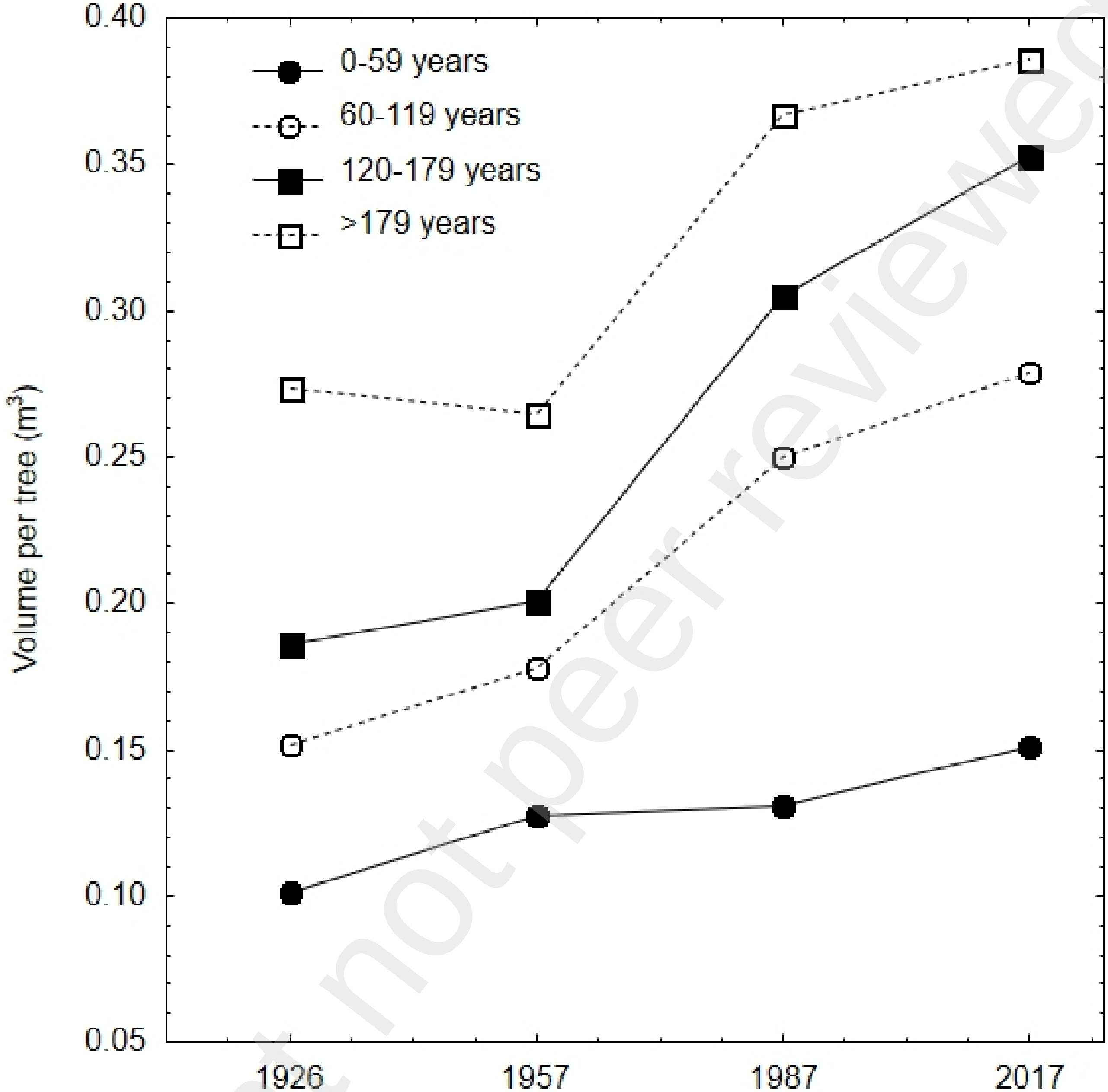
0-59 years
60-119 years
120-179 years
Tree volume (million m3)
1400
1200
1000
800
600
400
200
0
1927
1957
1987
2017



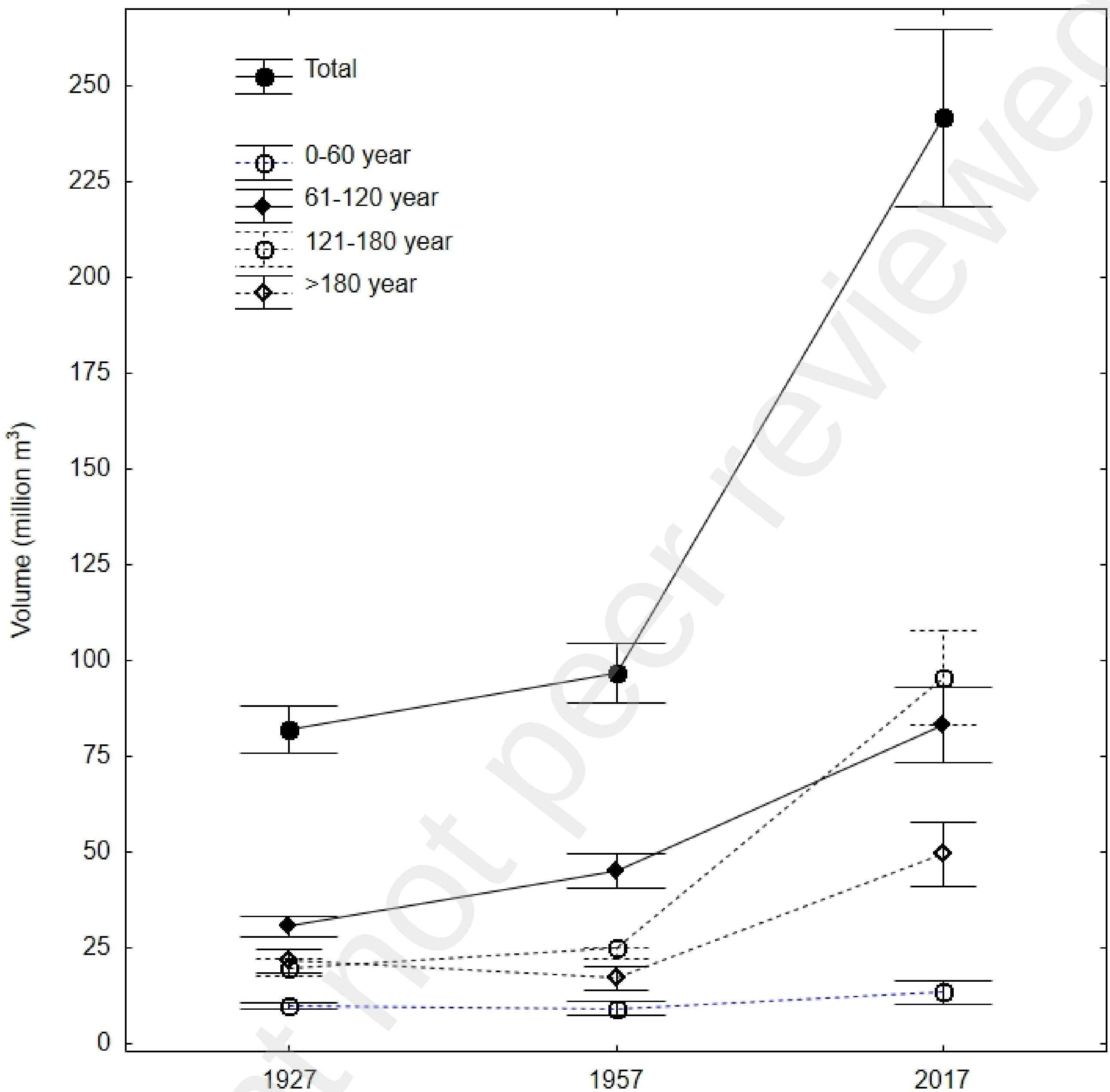
120
100
80
60
40
20
0
Tree volume (million m^3)
1927
1957
1987
2017
180-239 years
>240 years

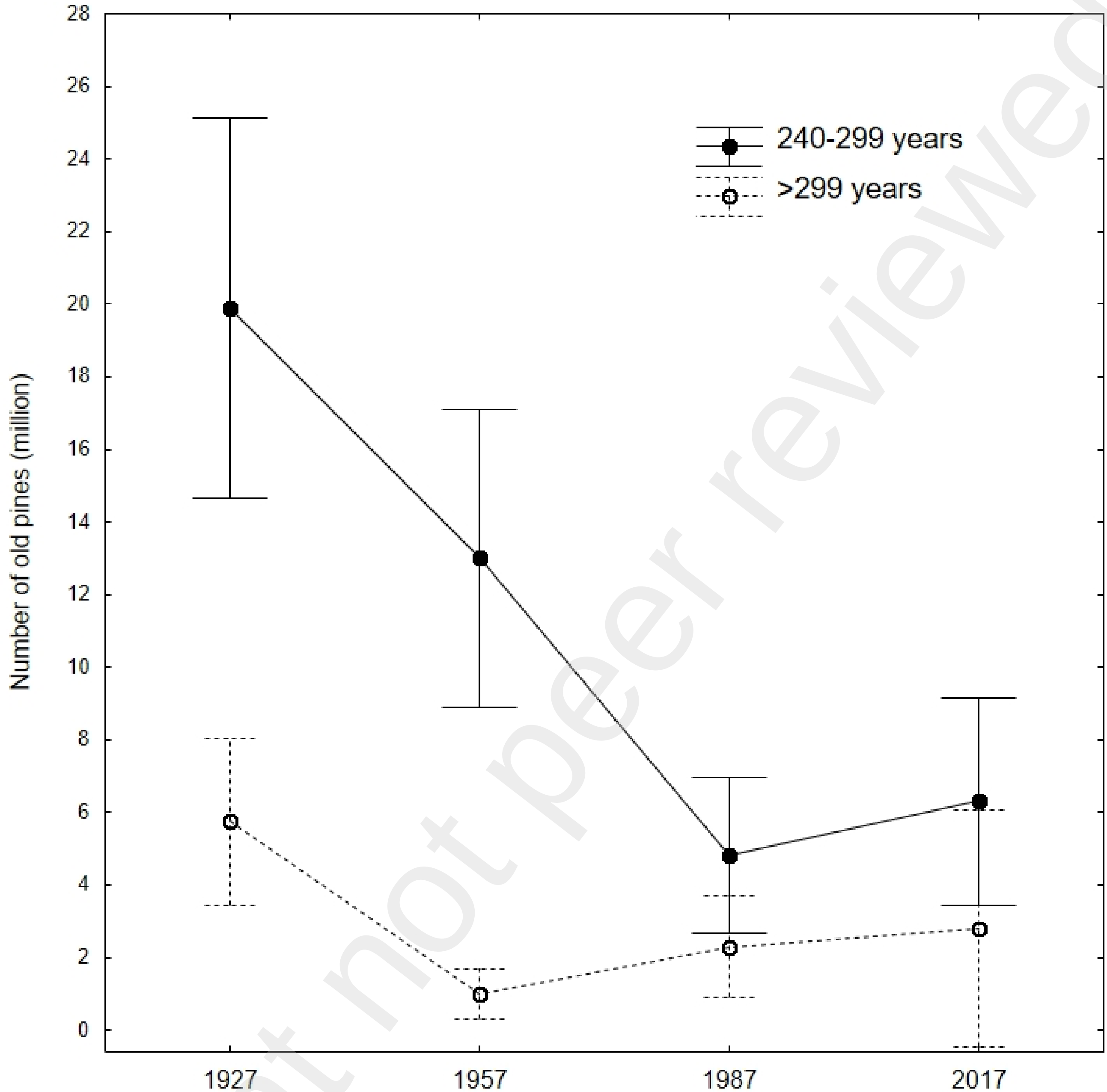


7%
6%
5%
4%
3%
2%
1%
0%
Annual mortality (% per year)
1926-1957
1957-1987
1987-2017
82-141 years
142-201 years
202-261 years
262-322 years

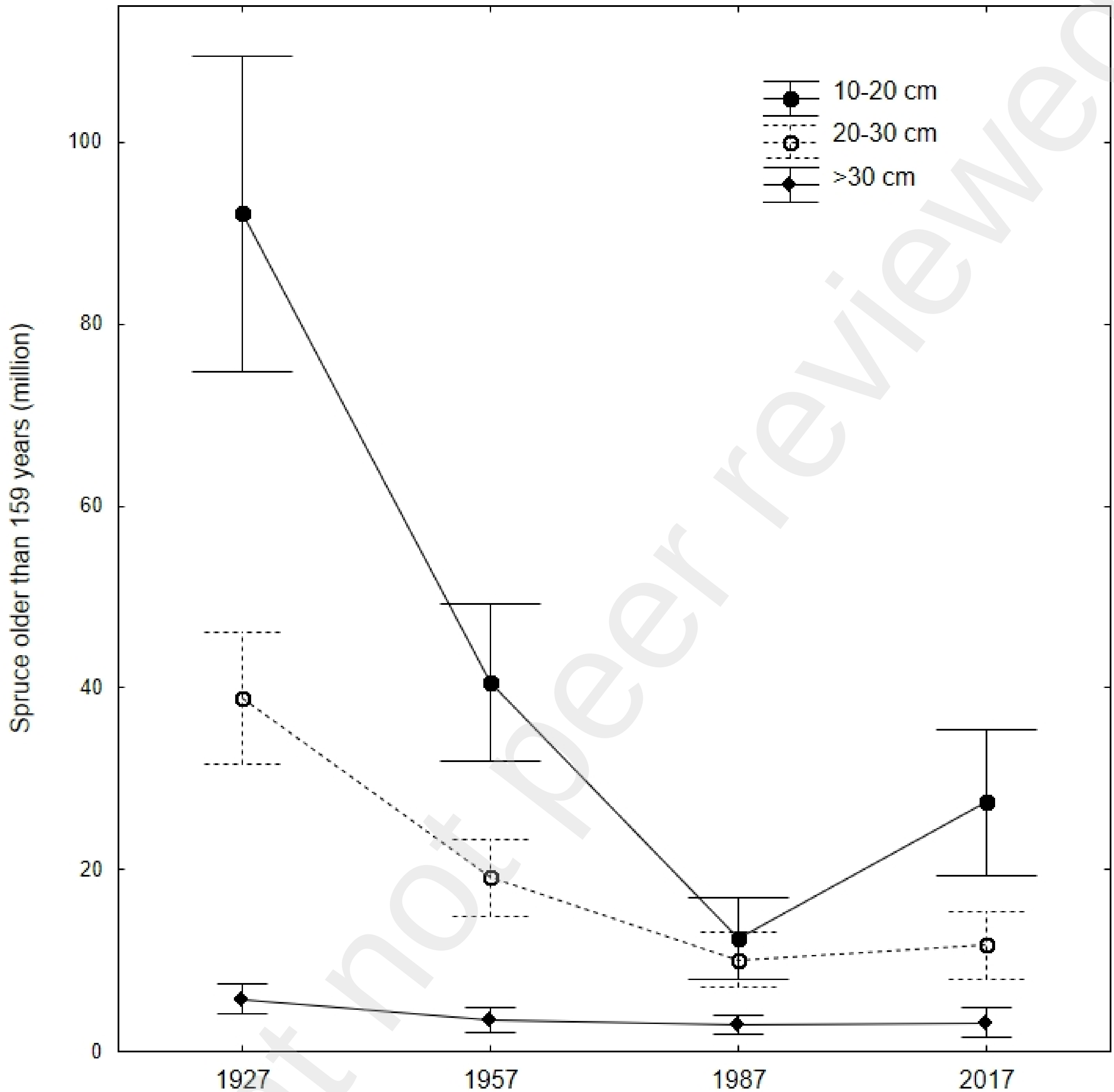


0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
Volume per tree (m3)
1926
1957
1987
2017
0-59 years
60-119 years
120-179 years
>179 years

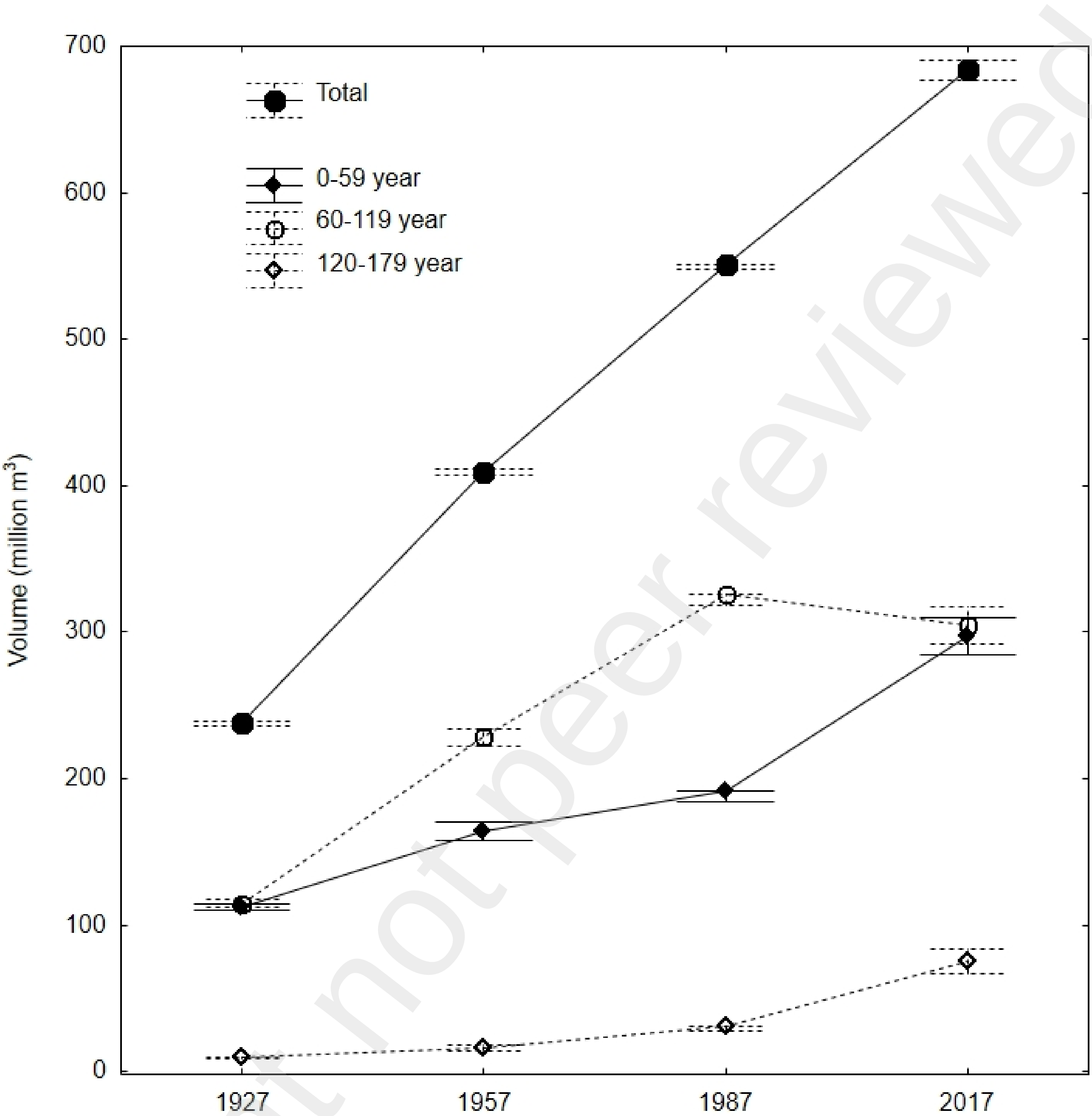

Total
0-60 year
61-120 year
121-180 year
>180 year
Volume (million m3)
0
25
50
75
100
125
150
175
200
225
250
1927
1957
2017

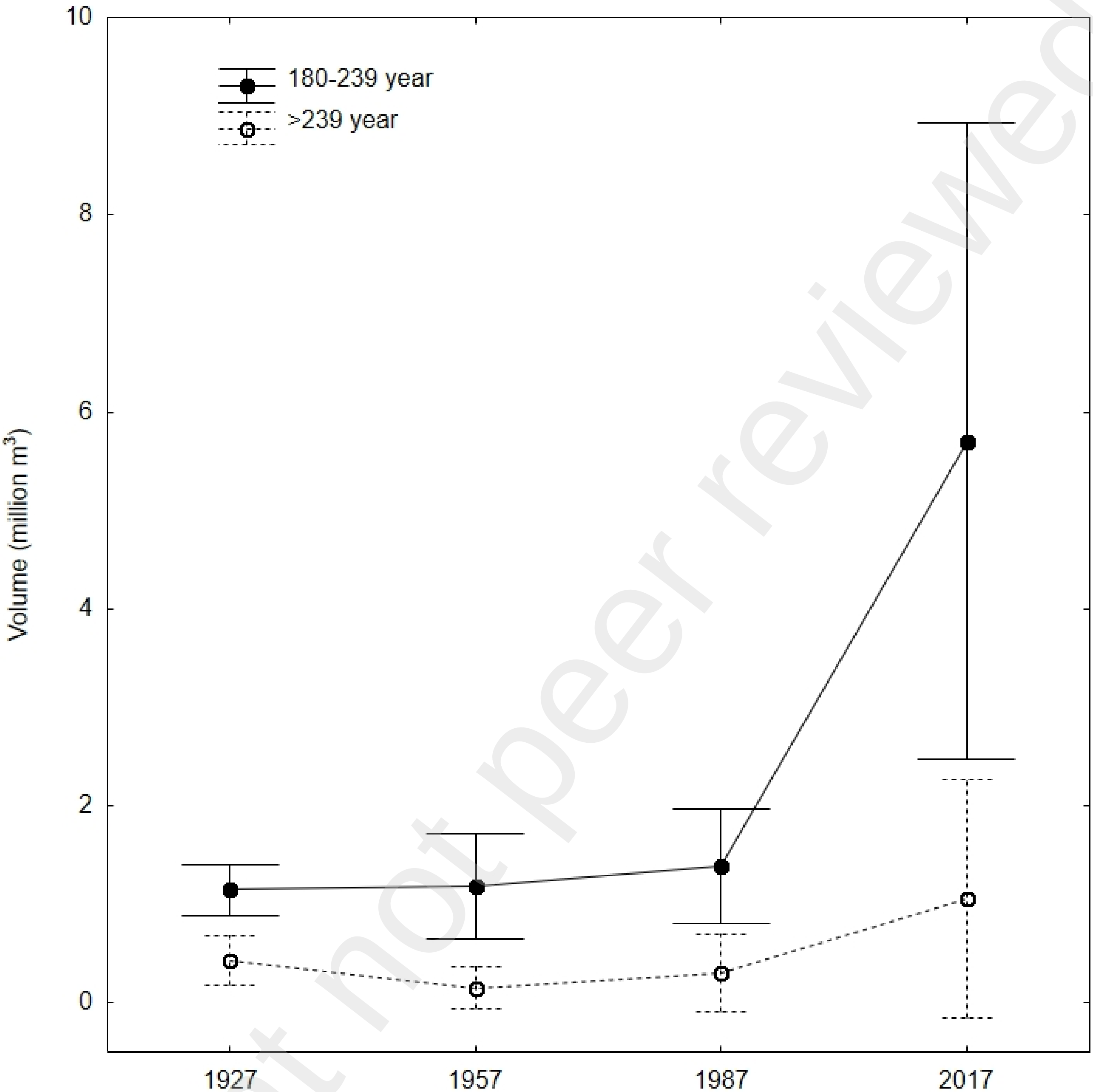


Number of old pines (million)
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
1927
1957
1987
2017
240-299 years
>299 years

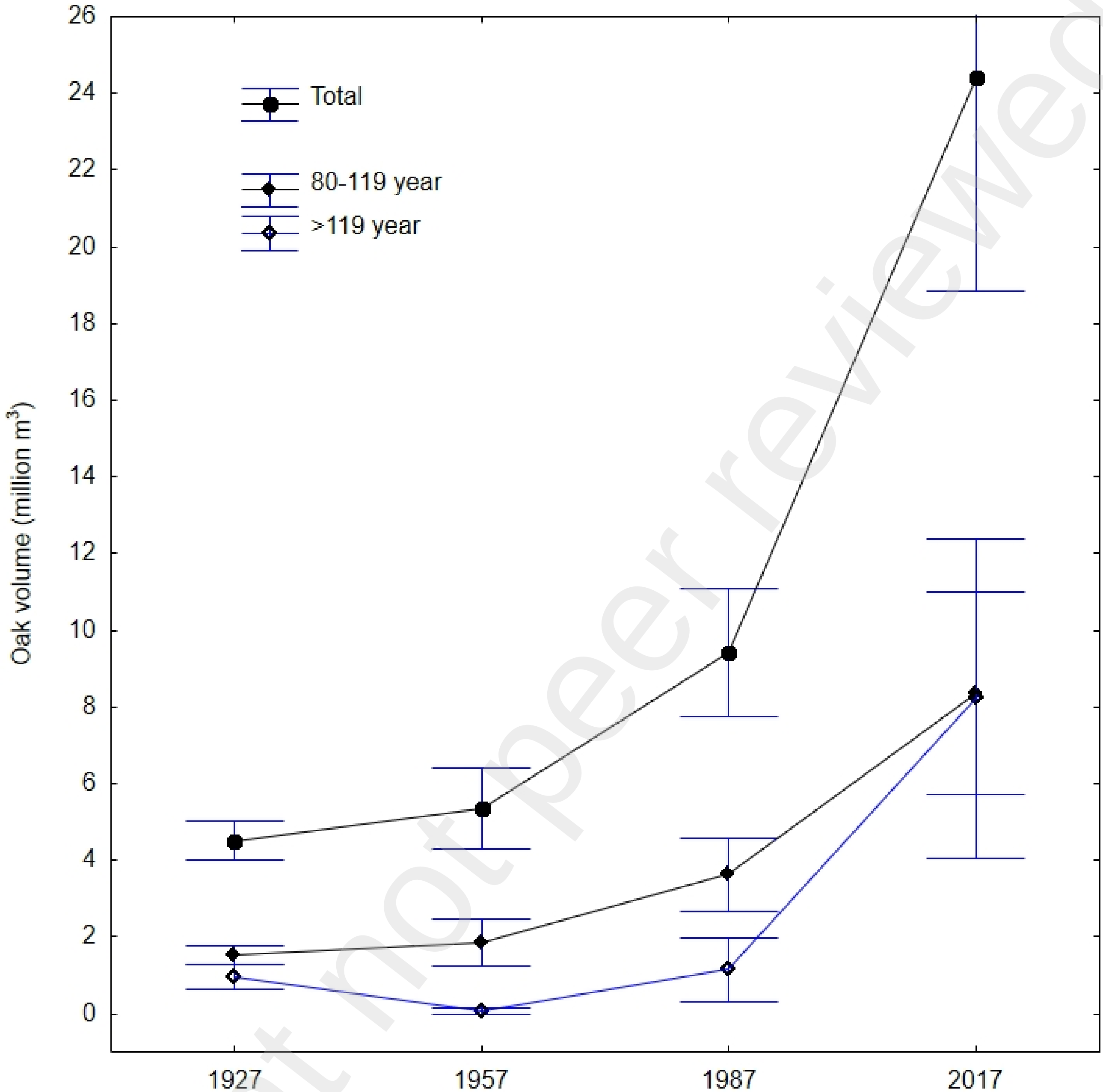


10-20 cm
20-30 cm
>30 cm
Spruce older than 159 years (million)
0
20
40
60
80
100
1927
1957
1987
2017

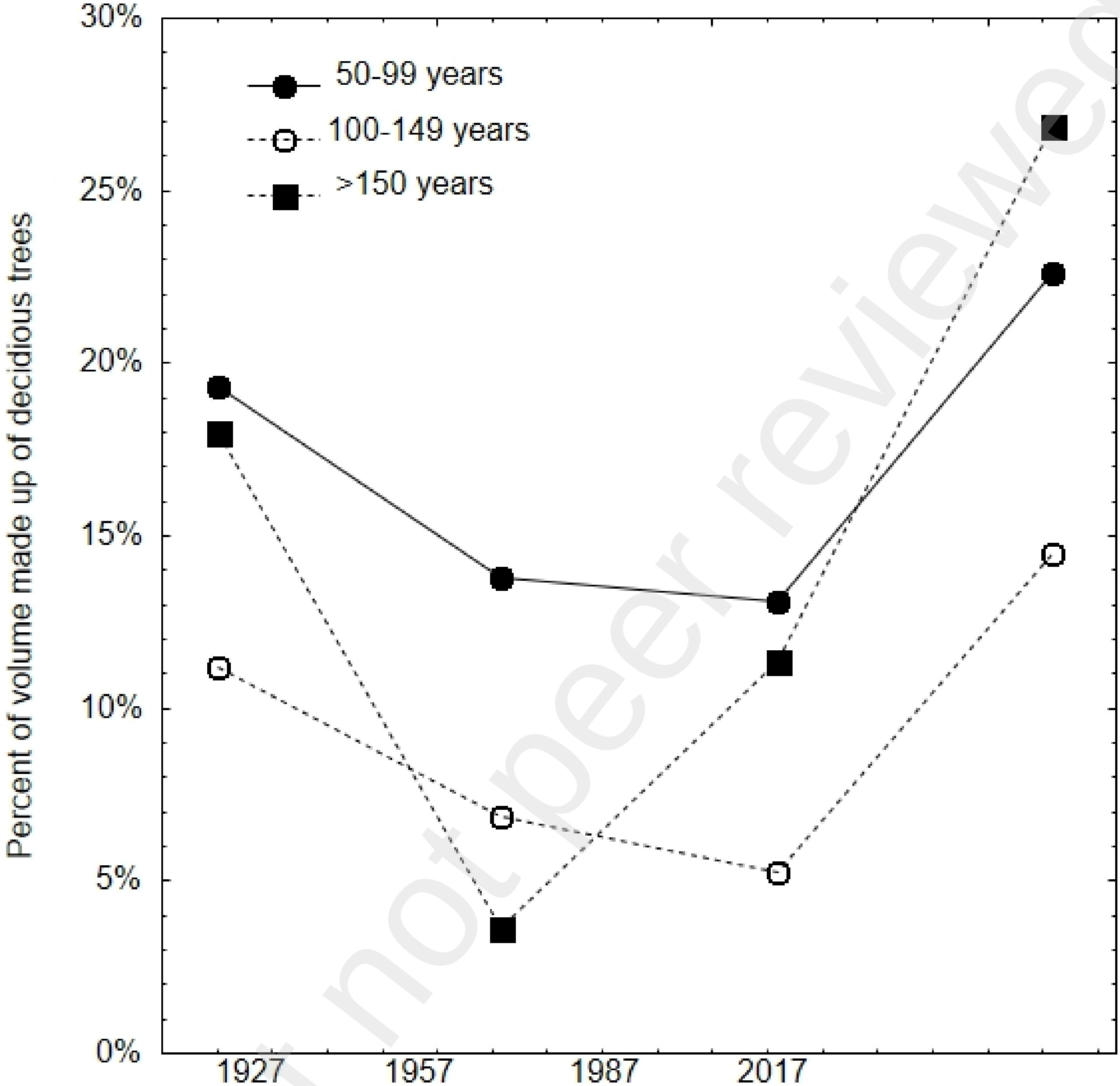

Total
0-59 year
60-119 year
120-179 year
Volume (million m3)
700
600
500
400
300
200
100
0
1927
1957
1987
2017



10
8
6
4
2
0
Volume (million m^3)
180-239 year
>239 year
1927
1957
1987
2017



26
24
22
20
18
16
14
12
10
8
6
4
2
0
Oak volume (million m3)
Total
80-119 year
>119 year
1927
1957
1987
2017



50-99 years
100-149 years
>150 years
Percent of volume made up of decidious trees
30%
25%
20%
15%
10%
5%
0%
1927
1957
1987
2017

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
Deciduos***	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	4,070	5,663	3,029	2,402	3,047	18,211
Spruce	2,198	2,469	1,066	859	966	7,558
Deciduos	971	1,052	959	926	929	1,369
Sum	7,239	9,779	4,849	3,882	4,805	30,554
Southcentral Sweden						
Pine	19,240	9,894	5,819	3,405	3,653	42,011
Spruce	12,459	11,280	8,128	4,089	4,717	40,673
Deciduos	7,575	6,081	6,031	5,652	5,884	11,791
Sum	39,274	24,840	16,809	9,435	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%), Fogus sylvatica (8.4%), Alnus spp. (7.8%), Populus tremula (7.4
Quercus spp. (7.25%), other species (7.8%)