Large trees have increased greatly in Finland during 1921-2013, but old trees tell a different story

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Abstract

Large and old trees have a vital role in preserving biodiversity in forest ecosystems. We used National Forest Inventory data from 1921 to2013 for studying changes in densities (stems per ha) of large trees (diameter ≥40 cm) in Finland. In addition, densities of old trees (age ≥150 years) are reported from 1971 to 2013. We present results separately for the three subzones of the boreal biogeographical zone. Large trees have increased as much as 325%. The change has occurred mainly since the 1970s. On country level, old trees have become slightly less common (-4%) since the 1970s, although a decrease was actually observed only in the northern boreal subzone. The large majority of old trees in Finland are quite small in diameter, however. Trees that are both large and old show a notable increase from 1971 to 2013. During the 2010s, densities of large trees were higher in the southern boreal subzone than in the northern boreal subzone, but in the 1920s the opposite was true. Densities of old trees have been much higher in the northern boreal subzone. The observed densities of large trees are still considerably smaller than those observed in unmanaged old-growth forests in Scandinavia. High densities of large and/or old trees were observed in areas with restrictions on wood production emphasizing their role in maintaining biodiversity. The results reflect the destructive effects of former land use and the transition from dimensional cuttings to clear cuts and thinning from below after the 1940s. Proportionally larger changes were observed for southern Finland, where a higher human population density and the resulting more intensive land use had more severe detrimental effects on forests. As the densities of large trees and old trees have developed in a completely different manner in Finland, our results suggest that monitoring only the size distribution of trees will not sufficiently describe the role of old trees as constituents of biodiversity. Thereagainst, densities of large trees and large old trees developed in a similar manner.

Introduction

The world's forests have developed in a diverse manner during the past century. Developing countries with large forest resources have in many cases reported reductions of forest areas (Keenan *et al.*, 2015) and growing stock volumes (Köhl *et al.*, 2015). In industrial countries, forest areas have generally been stable (Keenan *et al*., 2015) and growing stock volumes have shown an upward trend (Kauppi *et al.*, 1993, Köhl *et al.*, 2015). Notable exceptions are Russia and Canada, the two countries with very large forest resources, but with less intensive land use and, consequently, more gradual changes of growing stock (Kauppi *et al.*, 2018).

Large old trees have been in focus because of their role as a versatile provider of ecosystem services. Lindenmayer *et al.* (2012) summarized these ecological roles and stressed that smaller and younger trees cannot provide many of them. The review by Lindenmayer *et al.* (2012), suggested that large old trees have become much less common than they were during the pre-industrial era in many parts of the world. Faison (2013) commented that data from national and continent-wide forest inventories suggest a more complicated story of large old tree dynamics at broad scales than suggested by Lindenmayer *et al.* (2012). Cecile *et al.* (2013) also pointed out that "large" and "old" are not synonymous and emphasized the value of small but old trees. Analyzing data from undisturbed primary forests and older secondary forests in cold, temperate and tropical zones, Lutz *et al.* (2018) observed that the largest 1% of trees ≥ 1 cm at breast height comprised 50 % of aboveground live biomass, which emphasizes their role in global forest carbon cycling.

Reductions of forest area and growing stock are obvious threats to large old trees. Selective dimensional cuttings may reduce large tree individuals of species with high commercial value even in regions where annual increment exceeds drain (e.g., Bawa & Seidler, 1998, Bowles *et al.*, 1998). On the other hand, the trend-like increase of growing stock, observed in many developed countries, could indicate an increasing trend also in the frequency of large trees. This type of development was observed by Kauppi *et al.* (2015), who analyzed forest inventory data from the USA and Finland, covering an area equivalent to 3% of forested area of the world. In addition to inventories in developed countries, Faison (2013) also cited long-term studies in tropical forests, which reported recent increases in large trees or forest biomass.

Today's silviculture tends to regenerate old stands and replace them with fast-growing monocultures. Efficient soil preparation and planting methods lead to a fast early development of stands. Timely thinnings provide ample growing space for the remaining trees. As a result, trees can reach a large size at a younger age than the large trees of previous tree generations. There are also indications that the climatic warming has already enhanced forest growth in some regions (Pretzch *et al.,* 2014, Henttonen *et al.,* 2017). Large but relatively young trees produce some of the ecosystem services provided by large old trees, but definitely not all of them. Lindenmayer *et al.* (2014) further stressed the distinction between large old trees and large young trees, and pointed out that in some forests a rapid growth of large young trees is not a positive outcome but a major ecological problem endangering slow growing, ecologically valuable tree species.

Forest inventories have traditionally aimed at assessing forest resources available for various forms of wood use, but today the goals are more versatile, including biodiversity, carbon balance and cultural and aesthetic values of forests (Tomppo *et al.*, 2010, Blicharska & Mikusinski, 2013) Forest inventories provide detailed information about size distribution of trees (e.g., Chirici *et al.,* 2011, Tomppo *et al.,* 2011). While tree and stand age are highly useful indicators of biodiversity, long time series on the age distribution of individual trees are rarely available (Chirici *et al.,* 2011). Accurate assessment of tree age requires knowledge about stand history or a count of tree rings (or, for relative young trees of certain species, a count of tree whorls). Trees have often not been cored in large-scale inventories, as coring is laborious and may damage some species (e.g., Mäkinen *et al.*, 2007), and stand history records with ample coverage are rarely available. Chirici *et al.* (2011) discussed the possibilities of using models based on tree size for predicting the missing tree age.

An exception is available from Finland, where systematic nation-wide forest inventories (NFI) were started – among the first in the world – in 1921, and have been repeated regularly thereafter. The development in Finland has followed the pattern typical for developed countries with a stable forest area, a growing stock increase of 65% and a roughly doubled annual growth during the monitoring period. All subzones of the boreal zone are represented in Finland from the southern boreal to the northern boreal zone. According to a recent estimate (Crowther *et al.,* 2015) about one fourth of the trees (diameter ≥10 cm) of the world are in the boreal zone. Since the 1930s, the Finnish NFIs have included coring a sub-sample of trees. However, these old data on tree age are not currently available in digital form. Kauppi *et al.* (2015) showed that large trees (*dbh* ≥30 cm) have become more common in Finland since the 1950s. As the field data of NFI1 (1921-1924) have been recently digitized, it is possible to extend the study period considerably. Also, combining tree size data with age information provides deeper insight on the ecological role of today's large trees.

We studied, whether the increase of large trees, observed by Kauppi *et al.* (2015), also applies when large trees are defined using thresholds larger than 30 cm. Are today's large trees younger than similar-sized trees of former tree generations? What is the size-distribution of old trees? How common are trees that are both large *and* old? Have the densities of large and/or old trees developed in a similar fashion over time in the climatically different subzones of the boreal biogeographical zone? Are there differences between tree species groups? The underlying question is: If large trees possess features valuable for biodiversity at some time point, can we trust that the relationship between tree size and those features will remain unchanged over time, and tree size can be used as a proxy for those features?

Materials and methods

We estimated tree densities (stems per hectare) and the total numbers of trees by tree diameter (*dbh*) class, tree age class and tree species group. In addition, we present results on the frequency of large trees in individual sample plots (approximately 500 m^2). Also estimates of mean tree age by *dbh* class are presented. Only living trees are reported, as dead trees, which are vital for many endangered species, have not been monitored in a consistent fashion throughout the study period. We applied the same definition for "large" (≥40 cm) and "old" (≥150 years) trees in each subzone of the boreal biogeographical zone, but also provide densities of large trees using different thresholds.

Sampling design and measurements in the Finnish NFI

We used the NFI data from the 1920s (the 1st NFI, NFI1) and from the 1970s to 2010s (NFI6-NFI11). The development of the Finnish NFI from the 1920s to the early 2000s is described in Tomppo *et al.* (2011). Only the most important details and changes related to the assessment of forest area and the tree *dbh* and age distributions are summarized here.

From the 1930s to 1960s (NFI2-NFI5) tree *dbh* was measured at 1.3 m above the highest root collar instead of measuring at 1.3 m from the origin point of the tree as in NFI1 and NFI6-NFI11. In addition, data from NFI2 (1936-1938), NFI3 (1951-1953) and NFI4 (1960-1963) are not available in digital form. Sample tree ages are available only in field forms of NFI5 (1964-1970). Therefore, the data from NFI2-NFI5 were not employed here.

NFI1 (1921-1924)

The sample of NFI1 (1921-1924) consisted of inventory lines oriented from southwest to northeast with a 26 km distance between subsequent lines in most parts of the country. The combined length of the inventory lines was 13 348 km, excluding water areas. Land use and site characteristics were assessed for each land figure and forest stand intersected by an inventory line. Stand volumes (per ha) were estimated visually. The assessments were calibrated using sample plot measurements. The sample plots were 10 m × 50 m line strips located at the end of each 2000 m of the inventory line. If the plot was not entirely within a single forest stand, it was shifted so that it fit into a single stand. For small stands, it was also possible to measure plots shorter than 50 m. On the sample plots, the *dbh* of each tree was measured and registered in 2 cm classes (0-2 cm, 2-4 cm, …). For trees forked (split into several stems) below 1.3 m, *dbh* was measured separately for each stem. Some of the field crews of NFI1 had not registered stems with a *dbh* below 4 cm.

The definition of forest land was based on a visual classification describing site productivity (Ilvessalo 1927). Forest land was divided into productive forest land and forest land of poor growth potential.

NFI6 (1971-1976)-NFI11 (2009-2013)

In the 1970s and 1980s, the estimation of tree densities was based on measurements on temporary sample plots. Sample trees were selected using angle count sampling, i.e., a tree was included into an angle count plot (Bitterlich 1948), if its distance from the sample plot centre was at most $r = 50 \times dbh/\sqrt{\text{BAF}}$, where BAF is the basal area factor (BAFs in Table 1). From 1971 to 1994 *dbh*s were registered in 1 cm classes (2.5-3.5 cm, 3.5-4.5 cm, …). Since then the accuracy has been 1 mm. Trees with a *dbh* below 2.5 cm were not measured in NFI6. Since 1977, all trees taller than 1.35 m have been measured. Since 1992, the angle count plots have been restricted to a maximum radius of 12.52 m in southern Finland and to 12.45 m in northern Finland, corresponding to a *dbh* of 35.4 and 30.5 cm, respectively (Table 1). Trees with a *dbh* exceeding these limits were thus measured from fixed area circular plots of 492.4 and 487.0 m^2 in southern and northern Finland, respectively. Since 1992, *dbh* has been measured separately for each stem, if a tree was forked (split into several stems) below the height of 1.3 m. From the 1960s to 1991, the *dbh* for forked trees was calculated as a square root of the sum of dbh^2s of the stems. Due to forked trees, the terms “number of stems” and “stem density” would be more precise, but for simplicity we will use “number of trees” and “tree density”.

In the 1970s and 1980s, tree age was measured from a sub-sample of plots (southern Finland) or trees (northern Finland). Tree cores bored to the pith were taken at 1.3 m height. The number of annual rings was primarily counted in the field from a core, but it was possible to send cores with thin unclear annual rings to be measured in the laboratory. The number of years needed to reach the height of 1.3 m was assessed either by counting tree whorls or by using models which predict the time to reach 1.3 m height as a function of tree species, site fertility class and effective temperature sum. Since 1990, tree age at 1.3 m has been measured in the laboratory from cores collected from a subsample of trees (every 7th tree) on temporary plots. On permanent plots established since 1992, tree ages have been assessed without boring cores by counting whorls or by coring a similar tree outside the plot. In northern Finland, the first permanent plots were established already in the 1970s, but the first measurement on those plots did include coring a sub-sample of trees.

Biogeographical zones and subzones

We calculated results separately for the three subzones of the boreal biogeographic zone: southern boreal, middle boreal and northern boreal (Figure 1) (Ahti *et al.,* 1968), where the average lengths of growing season are 160-175, 140-160, and <140 days, respectively (Tuhkanen 1980). Small parts of southernmost Finland actually belong to the hemiboreal subzone, which is part of the temperate zone. These parts were merged into the southern boreal subzone. The amounts of sample plots and trees in boreal subzones in NFI1, NFI6 and NFI11 are given in Table 1.

The borders of biogeographical zones and subzones were downloaded from the service LAPIO of the Finnish Environment Institute (SYKE). The NFI plots were located to these subzones using the function pnt.in.poly of R package SDMTools (VanDerWal *et al.,* 2014).

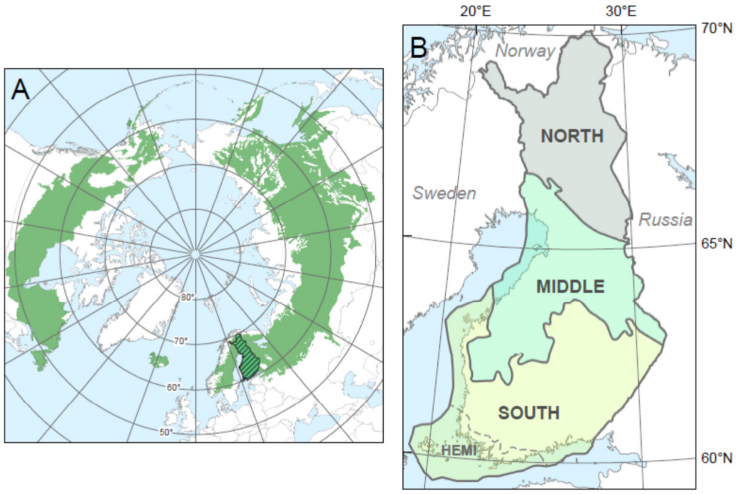

Figure 1. The three subzones of the boreal biogeographical zone in Finland. SOUTH=southern boreal (incl. HEMI=hemiboreal zone), MIDDLE=middle boreal, NORTH=northern boreal.

Table 1. Sample plot type and size, the number of sample plots in forest and the number of sample trees in boreal subzones in NFI1 (1921-1924), NFI6 (1971-1976) and NFI11 (2009-2013). n_{dbh} and n_{age} are the number of trees with diameter and tree age measured, respectively. In NFI11, only trees from temporary plots are included in n_{age}. BAF is the basal area factor in angle count sampling and *rmax* is the maximum plot radius.

Inventory	Sample plot type and size	Sample plots	Sample trees *dbh* ≥ 4 cm		Sample trees *dbh* ≥ 40 cm	
			n_{dbh}	n_{age}	n_{dbh}	n_{age}
SOUTH (Hemiboreal + southern boreal subzone)						
NFI1	Fixed area 10 m × 50 m	1663	101922		54	
NFI6	Angle count BAF=2	26537	173133	18921	2445	254
NFI11	Angle count BAF= 1 and *rmax* = 9 m[a] BAF= 2 and *rmax* = 12.52 m[b]	25377	229504	25362	7112	815
MIDDLE (Middle boreal subzone)						
NFI1	Fixed area 10 m × 50 m	1423	80347		33	
NFI6	Angle count BAF=2	24738	106976	12526	873	94
NFI11	Angle count BAF= 1.5 and *rmax* = 12.45 m[c] BAF= 2 and *rmax* = 12.52 m[b]	20724	175544	19144	1242	124
NORTH (Northern boreal subzone)						
NFI1	Fixed area 10 m × 50 m	1282	41663		77	
NFI6	Angle count BAF=2 or 1[d]	6139	24560	4307	903	160
NFI11	Angle count BAF= 1.5 and *rmax* = 12.45 m	7500	51873	5895	789	93

a) County of Åland
b) Southern Finland
c) Northern Finland
d) Northernmost Finland (Enontekiö, Inari and Utsjoki), data from NFI7 in 1978

Estimation

Calculation of tree densities,the total number of trees and mean ages

We estimated tree densities (trees per hectare) and the total numbers of trees (millions of stems) for the biogeographical subzones. The estimates were derived for living trees by tree species groups, *dbh* classes (NFI1-NFI11) and *dbh* × tree age (NFI6-NFI11) classes. The mean ages of trees by *dbh* classes were calculated for NFI6 and NFI11. The 2 cm odd *dbh* classes employed in NFI1 were used. The minimum *dbh* in all calculations was 4 cm. For the high *dbh* classes we combined the *dbh*s ≥40 cm ("large trees"). We also provide the densities of trees ≥30 cm, ≥35 cm, ≥45 cm, ≥50 cm and ≥60 cm. To characterize old trees, tree densities and the total numbers of trees were estimated for trees ≥150 years. Some results are presented also for trees ≥100 years.

Sampling errors were derived for the estimates in each tree species group and *dbh* class in NFI1 and NFI11 using the estimation methods of the Finnish NFIs (detailed description in Supporting material 1). These methods are presented in Lindeberg (1924) (NFI1, line survey sampling errors), Ilvessalo (1927) (NFI1, line survey) and Tomppo *et al.* (2011) (angle count plot inventory). The sampling errors in NFI6–NFI11 presented in Figures 3-6 were estimated for different sampling designs using the SURVEYMEANS procedure in SAS/STAT 14.1 software (SAS Institute Inc., 2015). The comparison of sampling variance estimates for NFI11 showed that the estimates using SURVEYMEANS were slightly higher than the estimates derived using the method presented in Tomppo *et al.* (2011).

Three tree species groups were employed in the estimation: Scots pine (50% of growing stock in Finland, includes also the other conifers except for Norway spruce), Norway spruce (30%) and broadleaved tree species (Korhonen *et al.*, 2017). In Finland, broadleaves consist mainly of two birch species, aspen and two alder species, with a combined share of 20 % of the growing stock (Korhonen *et al.,* 2017): *Betula pubescens* Ehrh. (12%), *Betula pendula* Roth (5%), *Populus tremula* L. (2%) and *Alnus incana* (L.) Moench and *Alnus glutinosa* (L.) Gaertn. (1%).

Retention trees are left to regeneration areas to maintain biodiversity of forests. The status of a tree being a retention tree has been registered for all trees measured on sample plots in NFI11 (2009-2013). We estimated the numbers of large and old retention trees separately in NFI11. All trees left in clear cut areas were considered retention trees in the estimation.

We estimated the densities of large and old trees separately for protected areas. These include areas, where forest use is restricted by the Nature Conservation Act, areas which belong to EU's Natura 2000 network (http://ec.europa.eu/environment/nature/natura2000/index_en.htm) and areas which have been reserved for nature conservation programmes by the Ministry of Environment (http://www.ym.fi/en-US/Nature/Biodiversity/Protection_of_habitats).

A special feature of the forests in Finland is the abundance of peatlands, particularly in the middle and northern parts of the country, totaling as much as 29% of the area of forest land and poorly productive forest land (Korhonen *et al.*, 2017). To study how peatland forests differ from those on mineral soils, we calculated densities of old trees per *dbh* classes also for peatland forests.

For 1971-2013, we used data from two land use categories: forest land and poorly productive forest land (Tomppo *et al.*, 2011). For forest land, the potential productivity over a rotation is over 1 $m^3ha^{-1}year^{-1}$, and for poorly productive forest land between 0.1 and 1.0 $m^3ha^{-1}year^{-1}$. Forest sites not included in these two categories are unlikely to produce trees larger than 40 cm, although trees older than 150 years can be found on them.

In the 1920s, the terms productive forest land and forest land of poor growth were in use, and the definitions for both categories were different from the current definitions (Ilvessalo, 1927, Tiihonen, 1968). However, despite of the changes in definitions, the combined area of the two categories has remained highly similar in each biogeographical subzone (Figure 2). We therefore conclude that it is reasonable to compare these two former land use categories with the present ones.

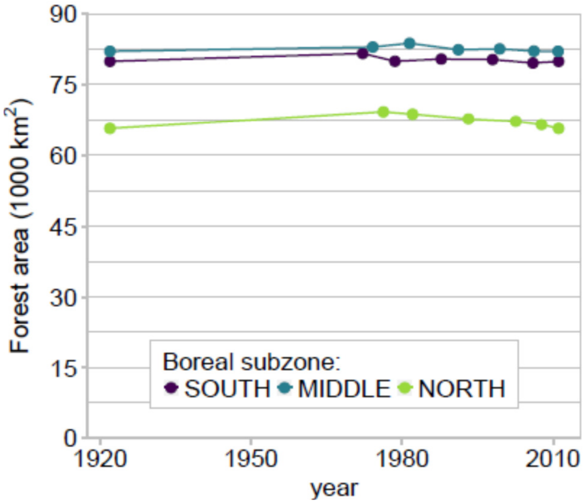

Figure 2. Forest area in the boreal subzones from the 1920s to the 2010s. SOUTH=southern boreal (incl. hemiboreal zone), MIDDLE=middle boreal, NORTH=northern boreal.

Harmonizing diameter classification

We used 2 cm *dbh* classes applied in NFI1 and harmonized the data from later inventories accordingly. For that part of data, where *dbh* was registered in 1 cm classes (1971-1994), the number of trees and their cumulative sum was first estimated for each 1 cm *dbh* class. The number of trees in even 1 cm *dbh* classes (e.g., 6 cm = 5.5 -6.5 cm) was then divided between the adjacent odd *dbh* classes. The monotone spline regression functions for the cumulative sums of the numbers of trees were fitted using the TRANSREG procedure in SAS/STAT

14.1 software (SAS Institute Inc., 2015) and the values predicted with 0.5 cm intervals were summed to define the proportions for each *dbh* class.

For the data measured since 1996, where *dbh* was registered in 1 mm classes, the trees with *dbh*s at the borders of the 2 cm classes (e.g., *dbh* 60 mm = 59.5-60.5 mm) and with an odd sample tree number were classified to the upper *dbh* class.

Plot-level frequencies of large trees

In order to describe how evenly large trees are distributed, we calculated plot-level frequencies of trees with a *dbh*≥40 cm for the 1920s (NFI1), 1990s (NFI9) and 2010s (NFI11). In NFI1, the plots were mainly 10 m × 50 m (500 m^2) rectangles. In NFI9 and NFI11, trees with a *dbh* >35.4 (southern Finland) and >30.5 cm (northern Finland) were measured from fixed area circular plots of 492.4 and 487.0 m^2 in southern and northern Finland, respectively.

In estimating the plot-level frequencies, only plots which were entirely within one forest stand were included from the NFI9 and NFI11 data. Plots smaller than 500 m^2 were excluded from the NFI1 data, because we aimed at comparing plots of similar size between inventories in calculating plot-level frequencies of large trees.

Results

Large trees

The densities of large trees have changed in similar fashion regardless of the threshold applied in defining "large", if the threshold is at least 40 cm (Figure 3 a-f). There are roughly ten times as many large trees in the southern boreal subzone as in the 1920s (Figure 3 c-f). The increase has been less intense for the middle and northern boreal subzones, but nevertheless very clear. Unlike today, in the 1920s the density of large trees was higher in the northern boreal subzone than in the other subzones. Today their density is more than two times higher in the south. Increasing the threshold to ≥45 cm reduces the densities of large trees by roughly two thirds in all subzones (Figure 3 c,d), and further increasing it to ≥50 cm has a similar effect (Figure 3c,e). Applying the threshold of ≥60 cm results in a large random variation between the successive inventories due to the low number of such trees (Figure 3f).

From here on, we will apply the threshold *dbh* ≥40 cm for large trees in each subzone. These trees increased from 16.6 million (1921-1924) to 26.6 million (1971-1976) and to today's (2009-2013) 70.6 million (Table 2). This equals a 325% increase in 90 years, calculated as (N2-N1)/N1.

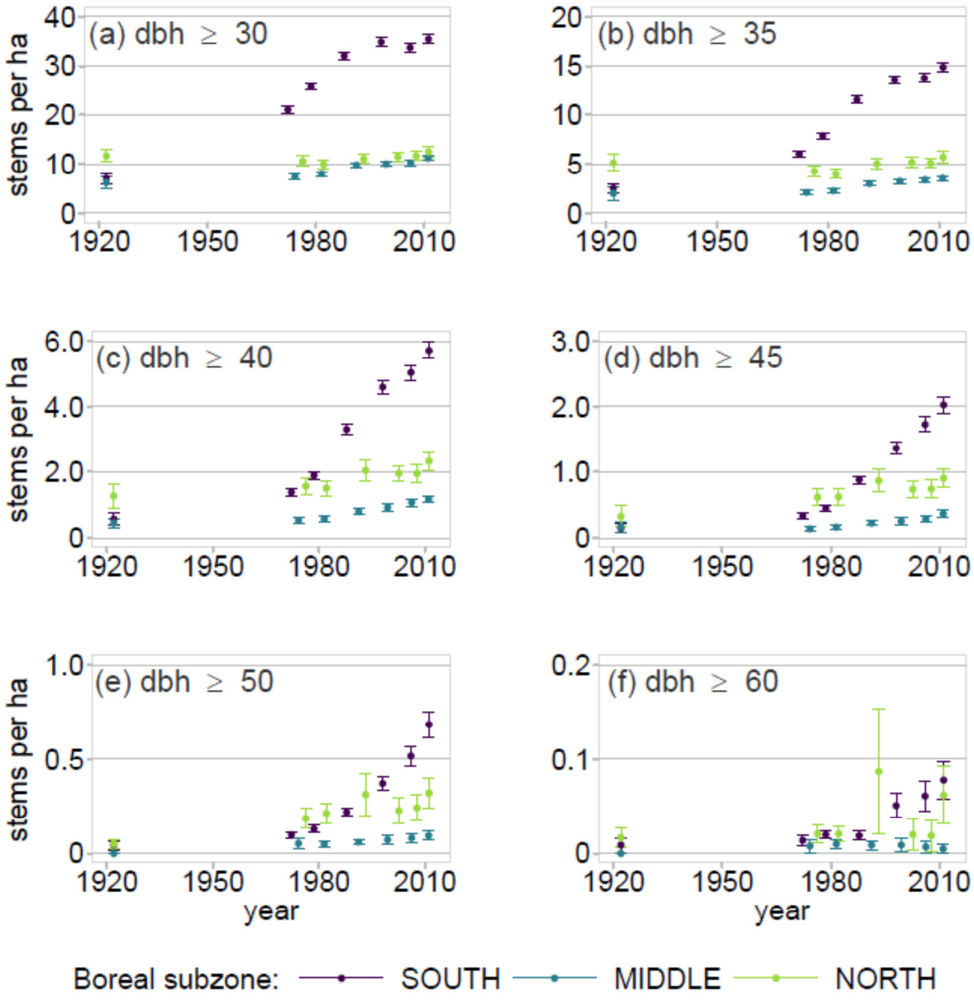

Figure 3. Tree densities (stems per ha) using different *dbh* thresholds. SOUTH=southern boreal (incl. hemiboreal zone), MIDDLE=middle boreal, NORTH=northern boreal. Error bars indicate 2×sampling errors.

Table 2. Total number of trees (million stems) with a *dbh* ≥40 cm and the changes from the 1920s, 1970s and 2010s in the boreal subzones. Sampling errors in parenthesis.

Tree species group	Inventory years			Change from 1921-1924 to 2009-2013
	1921-1924	1971 -1976, 1978	2009-2013	
	million stems			
	SOUTH (Hemiboreal + Southern boreal subzone)			
Scots pine	2.2 (0.79)	4.5	18.5 (0.56)	16.3 (0.97)
Norway spruce	1.0 (0.31)	5.2	20.2 (0.64)	19.2 (0.71)
Broadleaved sp.	1.3 (0.47)	1.5	7.0 (0.29)	5.7 (0.55)
All species	4.6 (1.03)	11.3	45.7 (1.03)	41.1 (1.46)
	MIDDLE (Middle boreal subzone)			
Scots pine	2.8 (0.85)	2.8	4.1 (0.26)	1.3 (0.89)
Norway spruce	0.3 (0.28)	1.2	4.5 (0.31)	4.2 (0.41)
Broadleaved sp.	0.3 (0.16)	0.5	1.0 (0.11)	0.7 (0.19)
All species	3.4 (0.90)	4.5	9.6 (0.45)	6.2 (1.00)
	NORTH (Northern boreal subzone)			
Scots pine	6.1 (0.87)	8.9	11.6 (0.74)	5.5 (1.14)
Norway spruce	2.2 (0.64)	1.7	3.3 (0.38)	1.1 (0.74)
Broadleaved sp.	0.3 (0.42)	0.2	0.3 (0.08)	0.0 (0.43)
All species	8.6 (1.19)	10.9	15.3 (0.85)	6.7 (1.46)
	Total			
Scots pine	11.1 (1.45)	16.2	34.2 (0.96)	23.1 (1.74)
Norway spruce	3.5 (0.76)	8.1	28.0 (0.80)	24.5 (1.11)
Broadleaved sp.	2.0 (0.65)	2.2	8.3 (0.32)	6.4 (0.73)
All species	16.6 (1.81)	26.6	70.6 (1.40)	54.0 (2.29)

Large trees are less useful for biodiversity, if they are concentrated on a small number of sites, as the gaps between these sites limit movement and gene exchange of species. Forest sites with large trees are scattered in Finland, but less so than in the 1920s. During 1921-1924, 98% of the sample plots in southern boreal subzone did not contain a tree with a *dbh* ≥40 cm (Table 3). In 2009-2013, the percentage had dropped to 87% in the south. In the northern boreal subzone, a smaller share (95%) of the plots did not include trees ≥40 cm in the 1920s, but in 2009-2013 the reverse was true as 90% of sample plot did not include a tree ≥40 cm). In the middle boreal subzone the change has been smaller still (98% to 97%). In the 1920s, less than 0.5% of the plots in the southern boreal zone contained more than three trees ≥40 cm, today about 2% do.

Table 3. The proportion of plots with n = 0, 1, 2, 3, and >3 trees of *dbh* ≥40 cm. Only plots in forest and within one forest stand are included. Plot size was 500 m^2 in 1921-1924, and since 1992 492 m^2 and 487 m^2 in southern and northern Finland, respectively.

Inventory years	Proportion of plots with n trees of *dbh* ≥40 cm				
	n=0	n=1	n=2	n=3	n >3
	SOUTH (Hemiboreal + Southern boreal)				
1921-1924	0.976	0.019	<0.005	<0.005	<0.005
1996-2000	0.879	0.070	0.028	0.011	0.012
2009-2013	0.872	0.069	0.028	0.015	0.017
	MIDDLE (Middle boreal)				
1921-1924	0.978	0.017	<0.005	<0.005	<0.005
1996-2002	0.969	0.022	0.006	<0.005	<0.005
2009-2013	0.968	0.022	0.007	<0.005	<0.005
	NORTH (Northern boreal)				
1921-1924	0.949	0.043	0.009	<0.005	<0.005
2001-2003	0.919	0.061	0.016	<0.005	<0.005
2009-2013	0.901	0.075	0.018	<0.005	<0.005

Old trees

Using large trees as a proxy for old trees assumes that large trees represent a similar range of tree ages over time. This has not been the case in Finland. Small and medium-sized trees up to 25 cm were on average much older in the 1970s than they were during 2009-2013 (Figure 4). The pattern is similar for all three subzones. For example, trees of *dbh* 15 cm were on average 25-39% (12.5-35 years) older in the early 1970s than today and both absolute and relative differences of mean age were largest in the northern boreal subzone. For trees larger than 35 cm, the reverse has been true in most cases, but the results are less consistent. Trees ≥40 cm were older during 2009-2013 than in the 1970s in the southern and northern boreal subzones. In the middle boreal subzone, the mean age of trees ≥40 cm was roughly the same during 1971-1976 and 2009-2013. Figure S1 in Supporting material 2 provides boxplots for tree age in 2 cm *dbh* classes during 1971-1976 and 2009-2013.

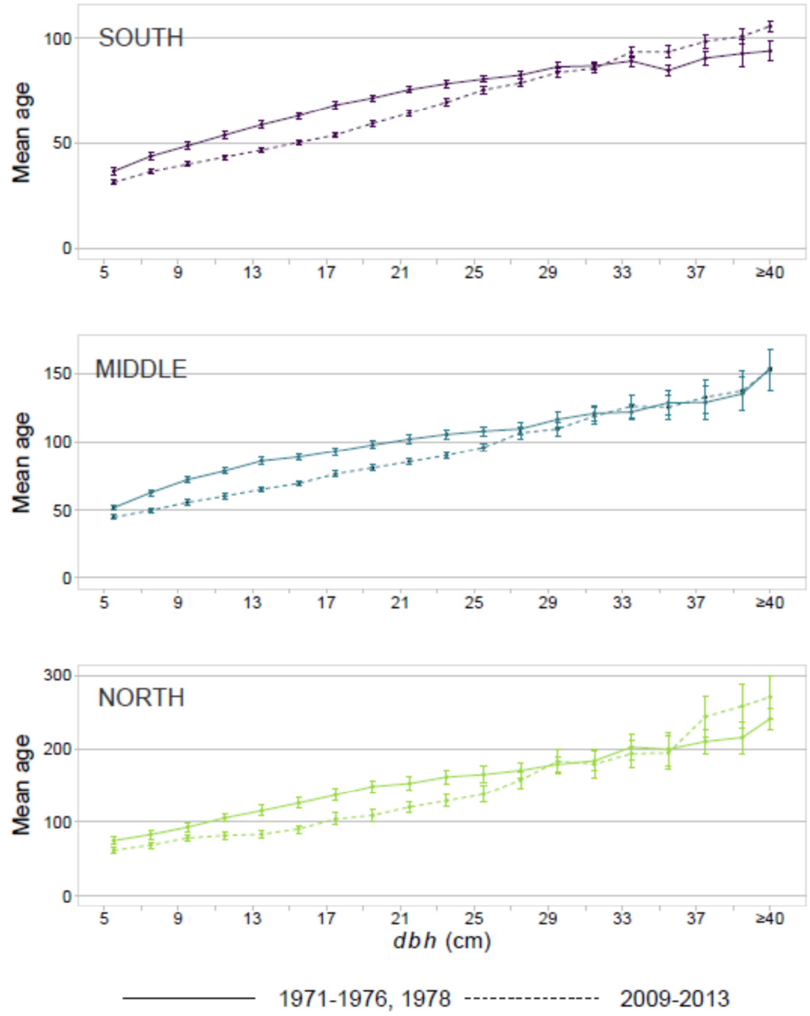

Figure 4. The mean age of trees in 2 cm *dbh* classes. SOUTH=southern boreal (incl. hemiboreal zone), MIDDLE=middle boreal, NORTH=northern boreal. Error bars indicate 2×standard errors of the means.

Large trees of all species groups showed a sizable increase from the 1970s to present (Table 2), but, contrary to that, old trees did not increase at the country level during the same period. Trees ≥150 years showed a small reduction from 829 million to 800 million trees (-3%) (Table 4). Compared to the sampling errors (Figure 5b), this change is, however, small. Trees ≥100 years decreased more, from 3330 million to 2924 million (-12 %, results not shown).

Unlike to the other subzones, old trees in each tree species group have increased in the southern boreal subzone.

Table 4. Total number of trees age ≥150 years (million stems) in NFI6[a)] (1971-1976, 1978) and NFI11 (2009-2013) in the boreal subzones. Minimum *dbh* of a tree was 4 cm.

Tree species group	Inventory years		Change
	1971-1978	2009-2013	
	million stems		
	SOUTH (Hemiboreal + southern boreal)		
Scots pine	15.4	37.8	22.5
Norway spruce	4.5	10.7	6.3
Broadleaved sp.	1.9	4.6	2.7
All species	21.7	53.2	31.4
	MIDDLE (Middle boreal subzone)		
Scots pine	81.2	97.3	16.2
Norway spruce	91.0	104.0	13.0
Broadleaved sp.	24.5	17.6	-6.8
All species	196.6	218.9	22.3
	NORTH (Northern boreal subzone)		
Scots pine	293.4	231.9	-61.6
Norway spruce	185.3	216.2	30.9
Broadleaved sp.	131.6	80.1	-51.5
All species	610.4	528.2	-82.2
	Total		
Scots pine	390.0	367.0	-22.9
Norway spruce	280.8	330.9	50.1
Broadleaved sp.	157.9	102.3	-55.6
All species	828.7	800.3	-28.4

[a)] Data for northernmost Finland from NFI7 (1978)

Old trees (≥150 years) are distributed in a very unbalanced manner between the three biogeographical subzones (Figure 5b): 7% of old trees were in the southern, 27% in the middle and 66% in the northern boreal subzone (Table 4). Contrary to that, densities of large trees were clearly higher in the southern boreal subzone.

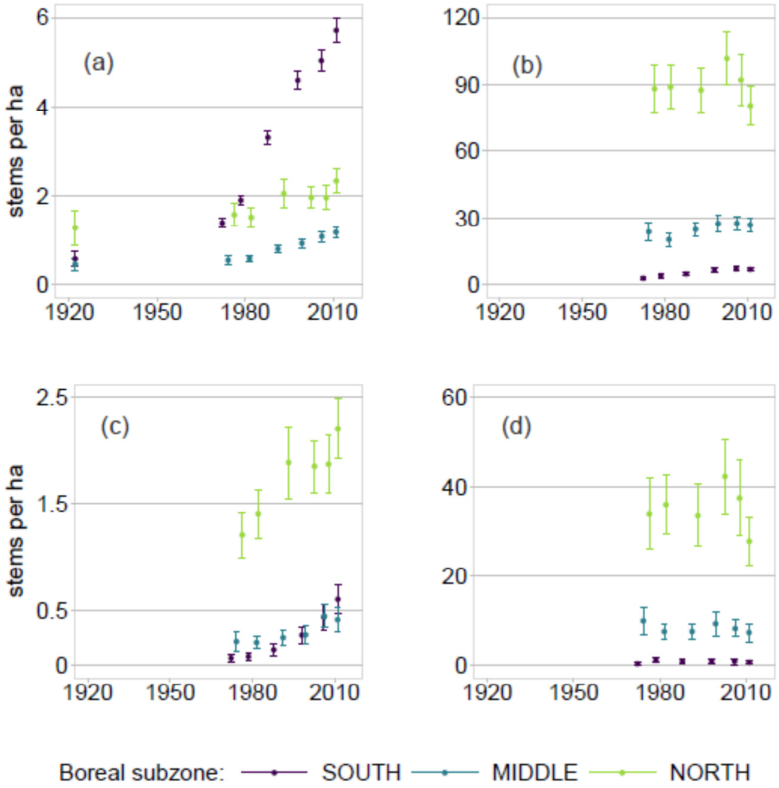

Figure 5. Tree densities (stems per ha) of (a) large trees (*dbh* ≥40 cm), (b) old trees (*tree age* ≥150 years), (c) trees that are both large and old and (d) trees small (*dbh* ≤14 cm) but old in the boreal subzones. SOUTH=southern boreal (incl. hemiboreal zone), MIDDLE=middle boreal, NORTH=northern boreal. Error bars indicate 2×sampling errors.

The number of old trees was very low in the southern boreal subzone during the 1970s (Figure 5b, Table 4). Since then, the number of old pines has increased 146%, spruces 140% and broadleaves 142%. Respective percentages for the same taxa in the middle boreal (20%, 14% and -28%) and the northern boreal subzones (-21%, 17% and -39%) show that the development has not been uniform between species groups and biogeographical subzones. Broadleaves ≥150 years are common in the north, but their estimated densities show especially large variation over time (results not shown). The most recent estimate is well below all prior ones.

Large *and* old trees

Trees that are both large (≥40 cm) and old (≥150 years) form 32% of all large trees, but only 2.8% of all old trees (Figure 6). The density of large trees is currently 3.1 trees per ha, for old trees 35.2 trees per ha, but for large and old trees only 1.0 tree per ha.

Large old trees have been much more common in the northern boreal subzone than in the other two subzones (Figure 5c). In fact, in the 2010s nearly all (95%) large trees of the northern boreal subzone (Figure 5a) were also old (Figure 5c). In the middle boreal subzone, less than half (36%) of the large trees were ≥150 years old, and in the south only 11%.

The density of large old trees increased from the 1970s to present in each subzone (Figure 5c). In the south the relative increase was particularly large, from 0.06 to 0.61 trees per ha, which is more than relative increase of large trees in the same subzone and the same time period (from 1.38 to 5.71 trees per ha). In the middle and northern boreal subzones, the change in densities of large old trees has followed a pattern more similar to the change in the densities of large (*dbh* ≥40 cm) trees (Figure 5a).

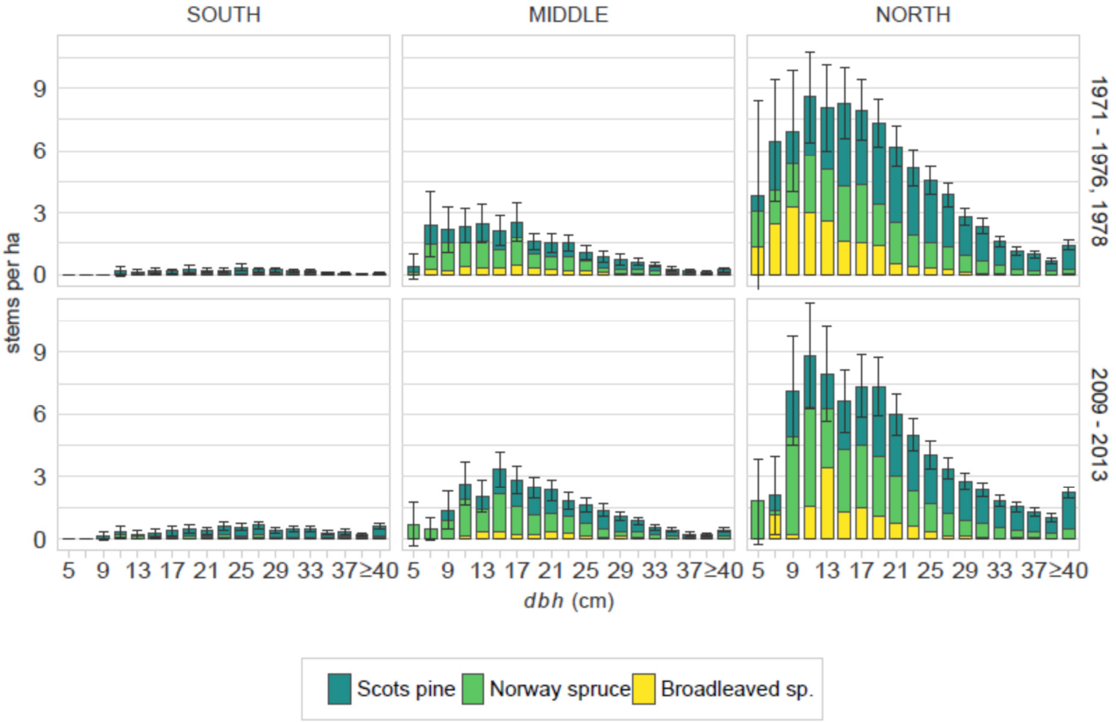

Figure 6 Tree densities (stems per ha) of old trees (≥150 years) in the boreal subzones by *dbh* classes and tree species groups in 1971-1978 and 2009-2013. SOUTH=southern boreal (incl. hemiboreal zone), MIDDLE=middle boreal, NORTH=northern boreal.

Small *and* old trees

The differences between biogeographical subzones are even more pronounced for trees that are small (*dbh* 4–14 cm) but old (age ≥150 years). They are very uncommon in the south, but in the northern boreal subzone their densities ranged between 27-42 trees per hectare during 1971-2013 (Figure 5d). Trees ≥150 years in any individual 2 cm *dbh* class below 30 cm were actually much more common than large old trees in the northern and middle boreal subzones (Figure 6).

The density estimates of small old trees today are lower than they were in the 1970s (Figure 5d), but their sampling errors are large compared to the change. The change in densities shows no consistent pattern, when estimates from the 1980s and 1990s are also considered. These small old trees are mostly spruces and broadleaves (Figure 6). The share of pines increases towards the larger *dbh* classes. For comparison, we present results similar to those in Figure 6, but applying the age threshold of 100 years in Supporting material 3.

Peatlands

The mean density of old trees (≥150 years) on peatlands is 41 trees per ha, somewhat more than the 33 trees per ha observed for mineral soils. However, small (*dbh* 4-14 cm) old trees are much more common and large old trees much less common on peatlands than on minerals soils (Figure S3 in Supporting material 4). Only 0.8 million (3.6%) of the 22.8 million large (≥40 cm) and old (≥150 years) trees are on peatlands.

Protected areas

Protected areas as defined in “Materials and methods” cover 10% of the area of productive and poorly productive forest land in Finland, but account for a much larger share of large trees (17%), old trees (34%) and of trees both large and old (43%) (Table 5). These areas are more common in the north, and, consequently, they account for a larger share of large and/or old trees in the northern boreal subzone. In the southern boreal subzone, however, large trees are equally common in protected and other types of forests.

Table 5. The total number of trees with a *dbh* ≥40 cm and a *tree age* ≥150 years in protected areas and their share (%) of the total number of trees with a *dbh* ≥40 cm and a *tree age* ≥150 years. SOUTH=southern boreal (incl. hemiboreal zone), MIDDLE=middle boreal, NORTH=northern boreal.

Subzone	Trees (*dbh* ≥40 cm)		Trees (*age* ≥150 years[a)])		Trees (*dbh* ≥40 cm) and (*age* ≥150 years)	
	million stems	%	million stems	%	million stems	%
SOUTH	2.5	5	6.4	12	0.6	12
MIDDLE	1.3	14	54.2	25	1.1	33
NORTH	8.2	53	209.4	40	8.2	56
Total	11.9	17	270.0	34	9.9	43

a) Minimum *dbh* of a tree 4 cm.

Retention trees

Another form of nature conservation affecting the amount of large and old trees are the retention trees left on regeneration areas. Today 6% of large trees belong to this group (Table 6). Their share of old trees is only 1.4 %, but 1.5 (6 %) million of the 22.8 million trees in Finland that are both large and old are retention trees.

Table 6. The total number of retention trees with a *dbh* ≥40 cm and a *tree age* ≥150 years and the share (%) of retention trees of the total number of trees with a *dbh* ≥40 cm and a *tree age* ≥150 years. SOUTH=southern boreal (incl. hemiboreal zone), MIDDLE=middle boreal, NORTH=northern boreal.

Subzone	Trees (*dbh* ≥40 cm)		Trees (*age* ≥150 years[a)])		Trees (*dbh* ≥40 cm) and (*age* ≥150 years)	
	million stems	%	million stems	%	million stems	%
SOUTH	2.2	5	1.9	4	0.1	2
MIDDLE	0.5	5	1.9	1	0.3	9
NORTH	1.4	9	7.5	1	1.0	7
Total	4.2	6	11.4	1	1.5	6

a) Minimum *dbh* of a tree 4 cm.

Discussion

In Finland, there are today 70.6 million large trees with a *dbh* ≥40 cm, 800.3 million trees with an age of ≥150 years and 22.8 million trees that are both large (≥40 cm) and old (≥150 years). These numbers demonstrate that one should be specific about which group is being discussed, when addressing large and/or old trees. The fact that large and old trees are far from synonymous (Cecile *et al.,* 2013) is further emphasized by the finding that in Finland small (*dbh* ≤14 cm) old trees are far more common than large old trees.

We observed heavily increased densities of large trees (≥40 cm) during 1921-2013, while old trees (≥150 years) showed no change during 1971-2013, considering the sampling error. The first finding is in line with the general trend of increasing forest resources, in particular growing stock volumes, in countries with a high income level (Kauppi *et al*., 2015, Kauppi *et al.,* 2018), but the second one suggests that many of these new large trees may not provide suitable microhabitats for species dependent on large old trees. On the other hand, trees that are both large and old increased heavily, particularly in southern Finland.

Different criteria for large trees have been applied in scientific literature depending on the studied climatic zone. Kauppi *et al.* (2015) used the threshold of 30 cm for Finland. Our focus is on the value of large trees for biodiversity, and as 30 cm is well below the typical size of dominant trees is old-growth forests, it would probably be too small for the purpose. Clearly, the selection of thresholds for “large” and “old” will affect the numbers. Roughly two thirds of trees with a *dbh* ≥40 cm have a *dbh* ≤45 cm. Selecting a very high threshold for “large” will lead to situation, where large trees and large old trees consist of virtually the same group of trees. This, in fact, is the case for northern boreal subzone in Finland, using the thresholds 40 cm for “large” and 150 years for “old”.

We applied the same definition for “large” (40 cm) and “old” (150 years) trees in each subzone of the boreal biogeographical zone. One might argue that different thresholds for large trees would be appropriate in each subzone, as they represent different climatic conditions and these differences are reflected in the growth rate of trees and forests. On the other hand, many species are dependent on large old trees, but the precise requirements of each species differ. It is difficult to determine a compromise that would optimally meet these requirements in each zone. Also, thresholds much higher than 40 cm would lead to large sampling errors.

A total of 332 species were classified as regionally extinct in the Red list of species for Finland, most of these having become extinct a long time ago (Rassi *et al.,* 2010). Of these, 108 species lived primarily in forests. Organism groups with many with endangered or regionally extinct species depending on forest environment include lichens, bryophytes, butterflies, sawflies, parasitoid wasps, true flies and beetles (Rassi *et al.*, 2010). Changes in forest environment were estimated to be the primary cause of extinction for 17.8% of the species regionally extinct in Finland (Rassi *et al.,* 2010). Several types of changes were included under the term, the first of the list being a reduction of old-growth forests and the decreasing number of large trees. While the former are bound to include old trees, the relative usefulness of large and old trees, or trees that qualify for both categories, was not elaborated.

The relative importance of tree size and age for conserving biodiversity is not trivial to analyze, as they are often correlated with each other. Bryant *et al.* (1983) discussed the age-related browsing resistance of boreal trees. They observed that juvenile birch twigs contain more resin than twigs of mature birches, indicating a higher defense level against browsing herbivores. The better nutritive quality makes old birches a more useful resource for many herbivores. Niemelä *et al.* (1980) discovered an age-specific degree of defoliation of larch (*Larix laricina* (Du Roi) K. Koch) during an outbreak of the larch bud moth (*Zeiraphera improbana* Walker) in northern Quebec. Danell *et al.* (1991) observed that Scots pines from a site with low growth potential in Sweden were more heavily affected by moose browsing than ones from a fast-growing site. They did, however, find evidence for a better nutritional value of pine twigs from the fast-growing site, and concluded that the more severe damage observed in pines from the low-growth site was probably explained by their slow early development and longer exposure to moose feeding. Old trees also are more likely to develop decay and hollows, vital for many species. On the other hand, large stem surface and a large number of branches increase the likelihood of colonization by species such as epiphytic lichens. Lie *et al.* (2009) analyzed two old-growth Norway spruce forests from Norway, in which tree diameter and tree age were not correlated. Both variables showed a weak positive correlation with species diversity of epiphytic lichens.

Our results provide time perspective on the purported reduction of large trees, emphasized in the Red list of species for Finland (Rassi *et al.,* 2010). Studies assessing old-growth forests in the Scandinavian region indicate that large trees were much more common before the era of intensive utilization of forests. Nilsson *et al.* (2002) and Jönsson *et al.* (2009) both suggested historical densities around 20 trees per hectare for trees ≥40cm in Scandinavia. We observed current tree densities of 5.7 such trees per hectare for the southern boreal subzone, and considerably smaller values for the other two subzones (1.2 and 2.3 trees per ha). On the other hand, our results show that large trees are much more common today than they were a century ago. It is probably impossible to determine the previous time period when large trees were more common than today. As the total number of large trees increased by 325% between 1921-2013, it is safe to conclude, that the situation existed quite some time further back in history than the beginning of our study period. If a large majority of trees ≥40 cm would have been harvested in a couple of decades prior to NFI1 (1921-1924), such harvesting rate would have led to an exhaustion of large trees in Finland during the decades that followed NFI1. It is also worth noting, that he use of industrial roundwood roughly doubled in the 1920s (Myllyntaus & Mattila 2002).

From the perspective of preserving biodiversity, the development of old trees has not been equally positive since the 1970s. They have shown no measurable change. The differences between tree species groups and subzones are large, however, as old trees in fact show an increase both in the southern boreal zone.

Large *and* old trees have become more common in each subzone since the 1970s. In the south, there were ten times as many large old trees during 2009-2013 as in 1971-1976. A change of this magnitude should definitely be vital for species dependent on them.

Small *and* old trees have reduced, partially because today's forest regeneration removes even those small trees with no commercial value. Limited quantitative information exists about the ecological role of small old trees. As small old trees are presently common in the northern and middle boreal zones in Finland, but becoming rarer, perhaps more research on their ecological role is called for. Lindenmayer *et al.* (2013) argued that large old trees play a range of key roles (e.g., as wildlife habitat and carbon storage) that are not played by small old trees. On the other hand, the finding by Bryant *et al.* (1983) that old birches have better nutritional value for many herbivores suggests that some species may benefit specifically from small old trees, either because they are quite common or because small size makes them accessible. Small old trees growing near the edge of their ranges could also have value in preserving genetic structures within species (*see,* Hewitt, 2000, McLachlan *et al.,* 2005, Cecile *et al.,* 2013). A special feature of Finland is the abundance of peatland forests and the small old trees are especially common on peatlands, where tree growth is often slow due to excessive moisture.

A disproportionate share of large (17% of trees ≥40 cm) and old (34% of trees ≥150 years) trees are located on protected areas. Their share of large old trees is as much as 43%. Protected areas have slowly expanded in Finland during recent decades, but their area is still low in the southern boreal subzone (where protected areas – as defined in "Materials and methods" – cover 3% of forest land and poorly productive forest land). As many protected areas in Finland have been established during the past 50 years, and did not entirely consist of old-growth forests at the time of establishment, the frequency of large and old trees on them will increase in time. However, their small areal coverage threatens the gene exchange of some species. As noted by Kouki *et al.* (2004), maturation of forests on conservation areas may also reduce light demanding tree species like aspen, which are vital for many endangered species.

As much as 6% of trees that are both large (≥40 cm) and old (≥150 years) consist of retention trees left on regeneration areas, suggesting that the practice has proved effective. As the practice was initiated in the 1990s (Metsätalouden …, 1994), many current retention trees will continue to develop for a long time and as new regeneration areas are added every year, retention trees will further increase. Their ecological value is emphasized by the fact that regeneration areas are distributed over the country, reducing the risk of isolated populations.

The changes in the forests of Finland since the 1920s, illustrated by the development of size distributions of trees can be traced back to two factors. The first is the low initial growing stock due to former land use practices and the second one is the intensified forest management. Historical forms of land use, such as slash and burn cultivation and cattle grazing in forests had a stronger influence on the state of forests in the southern and middle boreal zones due to higher human population densities (Ilvessalo 1927). Both growing stock and annual growth of the forests of Finland began to increase rapidly during the early 1970s (Ihalainen *et al.*, 2017). Our results show that the development of young trees has been faster in recent decades than before the 1970s. The change can be mainly attributed to intensified silviculture initiated during the 1950s and 1960s (Kuuluvainen *et al.,* 2012), although warming of climate has also played a role (Henttonen *et al.,* 2017).

Forest inventories have been launched in many countries during recent decades, and time series on large trees and, less frequently, also old trees will accumulate. However, in several countries tree ages are not monitored. Also, the procedures used for determining tree age and the sampling intensities are varying. Chirici *et al.* (2011) elaborated the possibility of using other variables, including tree diameter as a proxy for tree age, when ages of individual sample trees are not measured. As most old trees are quite small, but most small trees are young in Finland, our results cast a shadow over this approach. In addition, our results show that the functional form of the dependence between tree *dbh* and age has changed over time since the 1970s. It should be noted that small old trees were especially abundant in the northern boreal zone. In Finland, small old trees are especially common on peatland forests, which are rare in many forested regions. It is possible that the balance tilts more towards old trees being also large in more temperate regions. Also, as pointed out by Chirici *et al.* (2011), additional variables describing site and stand conditions (e.g., regeneration method) can improve the predictive power of such models.

Densities of large and large old trees have, however, developed in a similar fashion in Finland, suggesting that large trees might serve as a useful indicator for large old trees. The relationship between large and large old trees may not remain unchanged over time, however. A forest owner aiming to maximize his profit from forestry is likely to produce higher densities of large trees in future as well, aided by the combination of efficient silviculture and warming climate. The profit-seeking forest owner will produce very few large old trees, however. In southern Finland, the rotation ages determined on economic grounds are generally 60-80 years. To reach an age of 150 years, the owner – almost always several successive owners – will have to postpone the final harvest by another 70-90 years. This involves economic sacrifices: old forests grow slowly (Assmann 1961), damage risks increase with aging (Schelhaas *et al.*, 2003) and very large opportunity cost are involved (the costs of not being able to reinvest the harvest revenues). There are forest owners valuing the non-monetary benefits from forests and willing to follow this path. It is hard to predict how the balance between these two owner groups will develop in future.

The design of each of the inventories involves potential problems for assessing the distribution of large trees. In NFI1, fixed-size 10 m × 50 m sample plots were used. As measuring such large sample plots was expensive, the number of plots was rather low, which affects the reliability of the estimates. From the 1960s to the 1980s, angle count plots (basal area factors 1-2) were used. In dense forests, large trees located far from the plot center can be missed due to poor visibility. Therefore, plots with a maximum plot radius have been used since 1992. For large trees, the maximum radius eliminates the errors caused by possibly unobserved trees, but detracts very little from the reliability of the estimates (Tomppo *et al.,* 2010).

Our study interval for old trees started from the early 1970s. The number of tree rings was determined visually in the field in NFI6 (1971-1976), though it was possible to send tricky cores to be measured in a laboratory. For slow-growing trees, counting rings in the field may have led to not noticing very narrow rings and consequent underestimation. Obviously, missing or double rings cannot be determined via cross-dating in field conditions. Data from NFI1 (1921-1924) included some cored tree ages, but detailed documentation about the sampling procedure was lacking. In future, it is possible to extend the study period for tree age, as field data from NFI2 (1936-1938) are in the process of being digitized.

The described development of large and old trees has occurred simultaneously with the transformation of the country from an agriculture-based society to an industrialized urban nation. In developed countries, forest resources, in particular growing stock volumes, have generally increased in recent decades. In Finland, the dependence of the national economy on forest industries has involved pressure for increasing wood production via intensive silvicultural measures. As a consequence, both the growing stock and the density of large trees have increased substantially, but no increase of old trees was observed, which suggests that additional measures are needed to preserve biodiversity. Our findings suggest that while the recent increase of growing stock, generally observed in developed countries is usually coupled with an increase of large trees, one should not automatically infer that a simultaneous increase of old trees has occurred. If sample-based data on tree ages are not available, a vital piece of the puzzle is missing.

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References

Ahti, T., Hämet-Ahti, L., & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici,* **5**(3), 169–211.

Assmann, E. 1961. Waldertragskunde. BLV Verlagsgesellschaft. München-Bonn-Wien. 490 p.

Bawa, K. S., & Seidler, R. (1998). Natural forest management and conservation of biodiversity in tropical forests. *Conservation Biology*, **12**(1), 46-55. doi: 10.1111/j.1523-1739.1998.96480.x

Bitterlich, W. 1948. Die Winkelzählprobe. *Allgemeine Forst-und Holzwirtschaftliche Zeitung*, **59**, 4-5.

Blicharska, M., & Mikusinski, G. (2013). Old trees: cultural value. *Science*, **339**, 904. doi: 10.1126/science.339.6122.904-b

Bowles, I. A., Rice, R. E., Mittermeier, R.A., & da Fonseca, G. A. B. (1998). Logging and tropical forest conservation. *Science*, **280**, 1899-1900. doi:10.1126/science.280.5371.1899

Bryant, J. P., Stuart Chapin, F. S. III, & Klein, D. R. (1983). Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Herbivore-plant interactions at northern latitudes. Proceedings of a Symposium Held 14-18 September, 1981, at Kevo, Finland. *Oikos*, **40**, 357-368. doi: 10.2307/3544308

Cecile, J., Silva, L. R., & Anand, M. (2013). Old trees: large and small. *Science*, **339**, 904-905.
doi: 10.1126/science.339.6122.904-c

Chirici, G., Winter, S., & McRoberts, R. E. (eds.) (2011). *National Forest Inventories: Contributions to forest biodiversity assessments*. Springer, Dordrecht Heidelberg London New York, 206 p.
doi: 10.1007/978-94-007-0482-4

Crowther, T. W., Glick, H. B., Covey, K. R., Bettigole, C., Maynard, D. S., Thomas, S. M., . . . Bradford, M. A. (2015). Mapping tree density at a global scale. *Nature*, **525**, 201-205.
doi: 10.1038/nature14967

Danell, K., Niemelä, P., Varvikko, T., & Vuorisalo, T. (1991). Moose browsing on Scots pine along a gradient of plant productivity. *Ecology*, **72**, 1624 1633. doi:10.2307/1940962.

Faison, E. K. (2013). Large old tree declines at broad scales: a more complicated story. *Conservation Letters*, **7**, 70-71.
doi: 10.1111/conl.12075

Henttonen, H. M., Nöjd, P., & Mäkinen, H. (2017). Environment-induced growth changes in the Finnish forests during 1971-2010 – An analysis based on National Forest Inventory. *Forest Ecology and Management,* **386**, 22-36.
doi: 10.1016/j.foreco.2016.11.044

Hewitt, G. (2000). The genetic legacy of the Quaternary ice ages. *Nature*, **405**, 907-913. doi:10.1038/35016000

Ihalainen, A., Koskela, T., Peltola, A., Kankaanhuhta, V., Torvelainen, J., Mäki-Simola, E.,… Aarne, M. 2017. Forest statistics. In: E-yearbook of food and natural resource statistics for 2016: statistical facts on agriculture, forestry, fisheries and hunting in Finland / eds. Kortesmaa, T & Jokela, A.. *Natural resources and bioeconomy studies*, **30**, 84 p. Natural Resources Institute Finland (Luke), Statistical services. URN: http://urn.fi/URN:ISBN:978-952-326-407-6

Ilvessalo, Y. (1927). Suomen metsät. Tulokset vuosina 1921-24 suoritetusta valtakunnan metsien arvioimisesta. Summary: The forests of Suomi (Finland). Results of the general survey of the forests of the country carried out during the years 1921-24. *Communicationes ex Instituto Quaestionum Forestalium Finlandiae*, **11** Valtioneuvoston kirjapaino, Helsinki, 617 p.

Jönsson, M. T., Fraver, S., & Jonsson, B. G. (2009). Forest history and the development of old-growth characteristics in fragmented boreal forests. *Journal of Vegetation Science*, **20**, 91-106. doi: 10.1111/j.1654-1103.2009.05394.x

Kauppi, P. E., Mielikäinen, K., & Kuusela, K. (1993). Biomass and carbon budget of European forests, 1971 to 1990. *Science*, **256**, 70-74. doi: 10.1126/science.256.5053.70

Kauppi, P. E., Birdsey, R. A., Pan, Y., Ihalainen, A., Nöjd, P., & Lehtonen, A. (2015). Effects of land management on large trees and carbon stocks. *Biogeosciences*, **12**, 855-862. doi: 10.5194/bg-12-855-2015.

Kauppi, P.E., Sandström, V., & Lipponen, A. (2018). Forest resources of nations in relation to human well-being. PLoS ONE 13(5): e0196248. doi: 10.1371/journal.pone.0196248

Keenan, R. J., Reams G. A., Achard F., de Freitas, J. V., Grainger A., & Lindquist, E. (2015). Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. *Forest Ecology and Management*, **352**, 9–20. doi: 10.1016/j.foreco.2015.06.014

Köhl, M., Lasco, R., Cifuentes, M., Jonsson, Ö., Korhonen, K. T., Mundhenk, P., . . . Stinson, G. (2015). Changes in forest production, biomass and carbon: Results from the 2015 UN Global Forest Resources Assessment. *Forest Ecology and Management*, **352**, 21–34. doi: 10.1016/j.foreco.2015.05.036

Korhonen, K. T., Ihalainen, A., Ahola, A., Heikkinen, J., Henttonen, H. M. Hotanen, . . . Viiri, H. (2017). Suomen metsät 2009–2013 ja niiden kehitys 1921–2013. *Luonnonvara- ja biotalouden tutkimus*, **59/2017**, 86 p.

Kouki, J., Arnold, K., & Matikainen, P. (2004). Long-term persistence of aspen – a key host for many threatened species – is endangered in old-growth conservation areas in Finland. *Journal for Nature Conservation,* **12**, 41-52. doi: /10.1016/j.jnc.2003.08.002

Kuuluvainen, R. T., Tahvonen, O., & Aakala, T. (2012). Even-aged and uneven-aged forest management in boreal Fennoscandia: A Review. *Ambio,* **41(7)**, 720–737. doi: 10.1007/s13280-012-0289-y

Lie, M. H., Arup, U., Grytnes, J.-A., & Ohlson, M. (2009). The importance of host tree age, size and growth rate as determinants of epiphytic lichen diversity in boreal spruce forests. *Biodiversity and Conservation*, **18**, 3579-3596. doi: 10.1007/s10531-009-9661-z

Lindeberg, J. W. (1924). Über die Berechnung des Mittelfehlers des Resultates einer Linientaxierung. *Acta Forestalia Fennica*, **25.5**, 1-22. doi: 10.14214/aff.7080.

Lindenmayer, D. B., Laurance, W. F., & Franklin, J. F., (2012). Global Decline in Large Old Trees. *Science*, **338**, 1305-1306. doi: 10.1126/science.1231070

Lindenmayer, D. B., Laurance, W. F., & Franklin, J. F. (2013). Old trees: large and small – response. *Science*, **339**, 905. doi:10.1126/science.339.6122.905-a

Lindenmayer, D. B., Banks, S. C., Laurance, W. F., Franklin, J. F. & Likens, G. E. (2014). Broad decline of populations of large old trees. *Conservation Letters*, **7**, 71-72. doi: 10.1111/conl.12079

Lutz, J. A., Furniss, T. J., Johnson, D. J., Davies, S. J., Allen, D., Alonso, A., …, Zimmerman, J. K. 2018. Global importance of large-diameter trees. Global Ecology and Biogeography 27:849-864. doi: 10.1111/geb.12747.

Mäkinen, H., Hallaksela, A.-M., & Isomäki, A. (2007). Increment and decay in Norway spruce and Scots pine after artificial logging damage. *Canadian Journal of Forest Research*, 37, 2030-2041. doi: 10.1139/X07-087

McLachlan, J. S., Clark, J. S., & Manos, P. S. (2005). Molecular indicators of tree migration capacity under rapid climate change. *Ecology*, **86**, 2088-2098. doi: 10.1890/04-1036

Metsätalouden kehittämiskeskus Tapio. (1994). *Luonnonläheinen metsänhoito*. metsänhoitosuositukset 1994. *Metsäkeskus Tapion julkaisu* 6/1994, 1-72. (In Finnish).

Myllyntaus, M., & Mattila, T. (2002). Decline or increase? The standing timber stock in Finland, 1800-1997. *Ecological Economics,* **41(2)**, 271-288. doi: 10.1016/S0921-8009(02)00034-4

Niemelä, P., Tuomi, J., & Haukioja, E. (1980). Age-specific resistance in trees: Defoliation of tamaracks (Larix laricina) by larch bud moth (Zeiraphera improbana) (Lep., Tortricidae). *Reports from Kevo Subarctic Research Station*, **16**, 49-57.

Nilsson, S. G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J. M., Linder, P., … Ranius, T. (2002). Densities of large living and dead trees in old-growth temperate and boreal forests. *Forest Ecology and Management,* **161**, 189-204. doi: 10.1016/S0378-1127(03)00084-7

Pretzsch, H., Biber, P., Schütze, G., Uhl, E., & Rötzer, T. (2014). Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nature Communications*, **5**, 4967. doi: 10.1038/ncomms5967

Rassi, P., Hyvärinen, E., Juslen, I., & Mannerkoski, I. (2010). *Suomen lajien uhanalaisuus, punainen kirja. The 2010 Red List of Finnish Species.* Ympäristöministeriö & Suomen ympäristökeskus, Helsinki, 685 p.

Ruohomäki , K., Virtanen, T., Kaitaniemi, P., & Tammaru, T. (1997). Old mountain birches at high latitudes are prone to outbreaks of Epirrita autumnata (Lepidortera: Goemetridae). *Environmental Entomology*, **26**, 1096-1104. doi: /10.1093/ee/26.5.1096

SAS Institute Inc. (2015). SAS/STAT® 14.1 User's Guide. Cary, NC: SAS Institute Inc. 10380 p.

Schelhaas, M.-J., Nabuurs, G.-J. & Schuck, A. 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biology 9, 1620-1633, dlk: 10.1046/j.1529-8817.2003.00684.x

Tiihonen, P. (1968). IV Valtakunnan metsien inventointi. 4. Suomen metsävarat vuosina 1960-63. Summary: Fourth National Forest Inventory in Finland. 4. Forest resources in Finland in 1960-63. *Communicationes Instituti Forestalis Fennica*, **66(3)**, 1-33.

Tomppo, E., Gschwantner, T., Lawrence, M., & McRoberts, R. E. (Eds.) (2010). *National Forest Inventories. Pathways for Common Reporting*. Springer, Heidelberg, Dordrecht, London, New York, 607 p.
doi:10.1007/978-90-481-3233-1

Tomppo, E., Heikkinen, J., Henttonen, H. M., Ihalainen, A., Katila, M., Mäkelä, H., Tuomainen, T. & Vainikainen, N. (2011). Designing and conducting a forest inventory - case: 9th National Forest Inventory of Finland. *Managing Forest Ecosystems* **21**. Springer, Heidelberg, Dordrecht, London, New York, 270 p.
doi:10.1007/978-94-007-1651-3

Tuhkanen, S. 1980. Climatic parameters and indices in plant geography. Acta Phytogeographica Suecica, vol 67. Almqwist & Wiksell International, Stockholm, 105 p.

VanDerWal, J., Falconi, L., Januchowski, S., Shoo, L., & Storlie, C. (2014). SDMTools: Species Distribution Modelling Tools: Tools for processing data associated with species distribution modelling exercises. R package version 1.1-221. https://CRAN.R-project.org/package=SDMTools.