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Identifying old Norway spruce and Scots pine trees by visual inspection: An analysis of the relationship between age, spatial distribution and morphological traits in trees

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Contents

Preface

I have would like to thank my supervisors Ole Bollandsås and Ivar Gjerde for all the help with making this thesis come to light. Additionally I would like to thank Alexander S. Bjelanovic and Kajsa Sivertsen with help with the fieldwork

Abstract

Old trees are important to biodiversity, yet they are in global decline. In Scandinavia, due to former forest management, old trees were declining, but now possibly on the rise. In Norway, identification of old trees has been incorporated as part of forest planning in the form of Old-tree habitats. The Old-tree habitats are management units, which in turn can be given the status of woodland key habitat. Forest planners delimit Old-tree habitats during fieldwork based on visual characteristics detailed in a field guide. This study aimed to evaluate if the Old-tree habitats on average contained higher densities of old Norway spruce and Scots pine trees compared to surrounding mature forests. Furthermore, the validity of the variables in the field guide was tested. In addition to tree variables, site variables detailing environmental conditions and proxies for anthropogenic influence were assessed.

The research design consisted of 373 trees sampled from 37 localities in four municipalities in southeastern Norway. On each locality, the age of the five oldest trees in an Old-tree habitat was sampled along with a corresponding reference plot situated in neighboring forests. Tree level variables and site variables were collected during fieldwork and through GIS. The age difference between the Old-tree habitats and surrounding mature forests were tested using a pairwise *t*-test. Three different types of age models were included: models for single trees, stand-level models fitted with tree variables, and stand-level models using site variables. These were mainly developed as mixed models

The Old-tree habitats were, on average 43 years older than neighboring mature forests. Old trees were present at each locality, but the density and age of the oldest trees in the Old tree habitats were higher than the reference plots. The single tree model for Norway spruce was weak, whereas the respective model for Scots pine had moderately explanatory power. The Stand level model tree based models for the species both explained a moderate amount of variance. The most consistent morphological trait for both models was bark structure, size-related variables were, however, generally weakly correlated with the age. The site-based models were weakly correlated with age.

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The results in this study strengthen the Old-tree habitats' credibility in retaining old trees. Registration of old trees without an increment corer should utilize morphological variables beyond size. However, forest planners should be aware of several pitfalls that can influence registrations.

Oppsummering

Gamle trær er viktig for det biologiske mangfoldet, likevel er de i nedgang globalt. Grunnet tidligere skogforvaltning var gamle trær i Skandinavia tidligere i nedgang, men denne negative trenden har muligens snudd. I Norge har registreringen av gamle trær blitt inkludert som en del av skogbruksplanleggingen igjennom MIS (Miljøregistrering i skog) livsmiljøet «Gamle trær». «Gamle trær» figureres ut ved hjelp av visuelle kjennetegn nedtegnet i feltinstruksen til MIS. Formålet med denne studien var å evaluere hvorvidt «Gamle trær» inneholdt flere gamle trær sammenlignet med hogstmoden skog i nærheten. Videre, ble validiteten til beskrivelsene av gamle trær i feltinstruksen vurdert. I tillegg til dette ble bruken av areal baserte variabler testet for å vurdere effekten av ulike miljøforhold og menneskelig påvirkning.

Forskningsdesignet bestod av 373 trær samplet fra 37 ulike lokaliteter i 4 kommuner i Sør-Øst-Norge. På hver lokalitet ble de fem eldste trærne samplet fra en prøveflate i en utvalgt «Gamle trær» figur, disse ble supplert med en tilsvarende flate i nærliggende hogstmoden skog. Trevariabler og arealbaserte variabler ble samlet ved feltarbeid og geografiske informasjons system. Aldersforskjellen mellom de eldste trærne fra prøveflatene i «Gamle trær» figurene ble sammenlignet med referanseflatene gjennom en parvis t-test. Tre ulike typer aldersmodeller ble utviklet: Enkelttremodeller med trevariabler, bestandsnivå modeller med trevariabler og arealbasert modeller på bestandsnivå. De ulike modellene ble hovedsakelig modellert ved bruk av mixed models.

De eldste trærne i «Gamle trær» figurene var i snitt 43 år eldre sammenlignet med nærliggende hogstmoden skog. Gamle trær var tilstede på hver lokalitet, men tettheten og alderen på trærne i «Gamle trær» var vesentlig høyere. Enkelttremodellene for alder forklarte middels mye av aldersvariasjonen til gamle furutrær, men forklarte lite av aldersvariasjonen til gran. På bestandnivå var imidlertid modellene for begge treslag mer jevnbyrdige, og forklarte middels mye av aldersvariasjonen. Den mest pålitelige tre baserte variabelen var barkstruktur, ettersom den var inkludert i alle trevariabel modellene. Størrelse-relaterte variabler forklarte generelt lite av aldersvariasjonen. De arealbaserte modellene på sin side forklarte lite av aldervariasjonen.

Resultatene fra denne studien styrker tiltroen til at «Gamle trær» faktisk ivaretar gamle trær. Ved bruk av visuell identifikasjon av gamle trær bør fokuset ligge på andre morfologiske trekk enn størrelsen alene. Skogsbruksplanleggere burde også være klar over de ulike faktorene som kan påvirke aldersregistreringene.

Introduction

Old trees and old-growth forests serve as important habitats for many species. The old trees contain a multitude of microhabitats such as hollow cavities, dead wood, and bark with higher pH and rougher structure compared to juvenile trees . These traits enable them to host a complex diversity of saproxylic beetles, arachnids, and lichens(Kirby & Watkins 2015; Lie et al. 2009; Nascimbene et al. 2009; Thunes et al. 2003). However, globally, old and large trees are in decline due to different causes such as forest harvesting, forest fires or simply for safety reasons in urban areas (Lindenmayer et al. 2014)

The boreal zone covers 27% of the global forest area (Fao 2020). Two-thirds of the boreal forests are under different forms of management, mainly with wood production in mind. Different parts of the boreal zone have to various degrees been subjected to forestry, where Fennoscandia is one of the most affected(Gauthier et al. 2015). Forestry has had profound effects on the age distribution of trees. In Northern Sweden, for example only one-third of the pre-1920 levels of old trees remain (Andersson & Östlund 2004).

In the coniferous boreal forest of Scandinavia, the age distribution of trees has varied throughout the last centuries. In Sweden and Norway, the number of old trees and old-growth forests have previously been reduced. Most of the Scandinavian forest has been subject to dimension harvests during the last centuries and there are virtually no so-called pristine continuous forests left. Even Trillemarka, a highly esteemed nature reserve in Norway is from untouched by human intervention (Storaunet et al. 2013).

The negative trend of old trees in mainland Scandinavia seems to have turned, albeit with some regional differences in the timing (The Swedish National Forest 2019; Tomter & Dalen 2018). In Northern Sweden for example, the reduction in old trees appears to have lasted until at least 1996 (Andersson & Östlund 2004). Such differences can be related to harvest patterns. Most of the oldest forest is concentrated in the mountainous region of northern region Norrland, and the northwestern parts of Svealand situated more in the middle part of Sweden (Nilsson et al. 2014).

The amount of old forest in Sweden has increased from the 1990s (Nilsson et al. 2014). Roughly twelve percent of the Swedish forest excluding reserves is now over 120 years. On a countrywide scale, the area of forest older than 120 years Sweden is slightly reduced from the 1950s, but it has recovered from the lowest point in the 1970s. However, only 3% of the forest excluding reserves is over 160 years old (The Swedish National Forest 2019). Similar forest data can be found in Norway. According to the Norwegian National Forest Inventory (NFI) around 18.3% of the Norwegian forest is older than 120 years. In the period from 1945 to 2014 these areas have increased by 150%. Three percent of the forest area is older than 160 years x (Tomter & Dalen 2018).

Despite the positive trend in stand age of the oldest forest in the national forest inventory, more direct measures need to be applied to locate individual old trees. The stand ages on the national forest inventory plots are based on the age of a representative tree in the dominating layer, and this is not a direct measure of the oldest trees in the plot (Tomter & Dalen 2018). An inspection of this discrepancy reported age differences exceeding 250 years between the oldest tree on the site and stand age (Gjerde and Sætersdal. Unpublished data). This potential age difference may warrant caution in the extrapolation of stand ages to indicate the presence of old trees. Registration of old trees was included in the Norwegian NFI plot methodology in 2003. This was done to improve the forest monitoring of important habitats for biodiversity on a national scale.

Old trees are included in the habitats in the Norwegian forest habitat inventory based on the Complementary Hotspot Inventory (CHI) approach (Gjerde et al. 2007). The original aim of CHI was to map habitats for biodiversity as an integrated part of forest planning in the actively managed forests. It is a habitat-based approach combining species-rich sites covering a spectrum of different species compositions. CHI consists of 12 habitats, usually with a minimum size of 0.2 hectares that are considered of particular importance to the overall biodiversity. The Norwegian PEFC forest management standard states that such registrations are to be carried out in forest properties over 10 hectares. Areas delimited with this methodology serve as the basis for woodland key habitats through a selection process (PEFC Norge 2015). Old trees are a resource that takes a long time to replenish, and in addition to woodland key habitats conservation efforts are aimed at protecting the remaining old trees in the landscape.

The Norwegian Ministry of Agriculture and Food has requested a more detailed methodology for registering old-growth forests. If the goal is to ensure well-informed decision-making related to forest management, more detailed knowledge about the spatial distribution of old-growth forests recognizing its importance for several threatened species. At the same time, another stated aim has been to increase the Norwegian forest harvest (Landbruks og matdepartementet, 2016). To approach this request, two new questions need to be addressed: What is an old-growth forest? What is an old tree?

Old-growth forests are difficult to define accurately (Bauhus et al. 2009). One synonymous definition practiced in Norway is to use the total age of the forest stand as a measure for what is called "Old-age forest" (*Gammelskog* in Norwegian). The different dominating tree species have different species-specific age thresholds. The stand age for Norway spruce(*Picea abies*), Scots pine(*Pinus sylvestris*) and all the broadleaved trees must respectively be at least 140-160, 160-180 and 90-120 years of age to be called old-age forests (Landbruks og matdepartementet, 2016). Defining old-growth forests as forests rich in elements such as old trees, dead wood and structural diversity puts more emphasis on the ecological aspects (Bauhus et al. 2009). As the name states, old trees are a vital component and will be the focus of this study.

As with old-growth forests, the definition of what can be called an old tree varies. At one end of the scale it is possible to define old age absolutely. Ancient individuals have been found among species adapted to extreme longevity. Bristlecone pine, the oldest known living tree species has a confirmed individual>4900 years (Currey 1965). Another approach is to judge the age of individuals in relation to the expected longevity of a given species (Lindenmayer et al. 2014). Regardless of the definition of old, the maximum age of a given tree species generally far exceeds the optimal economic rotation cycle.

Both broadleaf and coniferous trees are included in the CHI-habitat "Old trees". Broadleaved trees are defined as old when their diameter exceeds a species-specific threshold. Norway spruce and Scots pine are defined as old when they reach 150 and 200 years of age respectively. A detailed description of different morphological traits such as bark structure, crown shape and

bark color is provided in the field manual to discern old individuals from young individuals of these two species (Baumann et al. 2001). From now on the term Old-tree habitat will be used to emphasize when it is the habitat in the CHI methodology which is referred to and not old trees in general.

To generalize from the Old-tree habitat requires control measures to make sure that it has empirical support. As of today, no such measures have been taken to support the validity of the method. The current Old-tree habitat methodology is primarily based on expert opinions, and its accuracy relies on the forest planner. Therefore, it is difficult to make assumptions today regarding the effectiveness of conservation measures for protecting old trees. There is a need to investigate if the current practice of delimitation of Old-tree habitat is sufficient for locating areas with old trees.

Size is often associated with tree age, making size a possible proxy of the age and abundance of old trees. However, tree size is highly dependent on site productivity. Trees that grow on more fertile locations will reach larger diameters faster than trees growing on comparatively poorer sites. Two trees of the same size are, therefore, not necessarily the same age. This is vital to keep in mind as the expected longevity of conifers such as Scots pine and Norway spruce trees are generally negatively correlated with growth rate (Bigler & Veblen 2009; Bigler 2016; Castagneri et al. 2013; Kaufmann 1996; Rötheli et al. 2012).

Spatial distribution and site characteristics appear to hold valuable information on the age of forests. In China large scale patterns have been found between the age in ancient trees and elevation (Liu et al. 2019). Similar, but weaker patterns have also been found for Mountain pine(*Pinus montana*) (Bigler, 2016) and Norway spruce (Rötheli et al. 2012) in the Swiss Alps. Studies on Norway spruce sampled from the Trillemarka-reserve in Norway have reported similar findings (Castagneri et al. 2013). A study examining the spatial distribution of CHI habitats in 10 selected municipalities stretching from southern Norway to central Norway supported the idea of distinct spatial patterns as the main bulk of CHI-habitats were situated on high productive sites. The Old-trees habitats in contrast were more associated with sites low in

productivity. Furthermore, the old trees additionally tended to be far away from roads and on higher elevations (Sætersdal et al. 2016b).

While old trees have been subject of intensive studies in relation to biodiversity and dendrochronological research there are surprisingly few published studies done to quantify predictors for the age of old Norway spruce and Scots pine. Only one published article reporting predictors for old Norway spruce beyond height and diameter were found (Rötheli et al. 2012), while no such articles were found for Scots pine. There were however several research articles studying age characteristics of other pine and spruce species in-depth (Bigler 2016; Brown et al. 2019; Van Pelt 2008; Weisberg & Ko 2012) Documenting fine-grained information of species-specific and age-related morphological traits from Norway spruce and Scots pine may further improve the accuracy of the practical identification of old trees.

The most precise approach for the determination of tree age is to count visible growth rings on an extracted increment core. However, there are disadvantages to core extraction. One of these is the potential damage it may cause the trees (Tsen et al. 2016). Another argument is related to the labor costs from fieldwork. Forest planners are expected to cover sizeable areas a day depending on site conditions. The process of coring can be further divided into two components, the coring itself, but also the task of counting growth rings. Counting rings by eye can also prove arduous if there are many narrow rings. In conclusion to core one or several trees every time an old tree habitat is delimited is time-consuming.

Identifying old trees without an increment corer requires an integrative approach. It is possible to some extent to compensate for the effect of different site productivities on the age-related growth patterns(Alberdi et al. 2013). However, utilizing other morphological traits in addition to size alone can improve the accuracy of age predictions (Brown et al. 2019; Weisberg & Ko 2012). Old trees often develop different characteristics such as a coarser bark texture, right-oriented spiral grain, dead branches and thick branches that can be used to separate them from younger trees. Bark structure, visible spiral grain and crown flatness may prove useful for Scots pine. Bark structure has been included in age models for other pine species such as Single leaf pinyon pine(*Pinus monophylla*) (Weisberg & Ko 2012). Spiral grain reflects a general

pattern of coniferous trees in the northern hemisphere. The orientation of the tracheids start of as left-oriented and as they grow, while the orientation gradually becomes more right-oriented with age (Kubler 1991; Skatter & Kucera 1998). Crown flatness would represent a decrease in height growth with increasing age.

This thesis was divided into three research questions. The first was to assess if the oldest trees in the delimited CHI habitat Old-trees were on average older than nearby comparative forest. The second research question was related to if descriptions from the current old tree CHI field guide for Norway spruce and Scots pine could be quantified and empirically supported, and which other morphological variables in addition to size that should be included? The third research question was related to whether spatial distribution patterns could explain the age in old trees.

Forty locations in southeastern Norway of the CHI habitat old trees were sampled to approach the research question. These were paired with reference plots outside the CHI figures as a means of comparing with the surrounding forest around. Models were made both on a single tree level and a stand-level to enable a sensible model selection. The results of the study were later discussed with an applied focus to illuminate the practical implications.

Study area

Four municipalities from South-eastern Norway were chosen for the study: Nore og Uvdal, Sør-Aurdal, Aurskog-Høland, and Sauherad(Now a part of Midt-Telemark). These were deemed representative of the managed forest landscape in southeastern Norway. The former two municipalities are situated in the boreal zone, while the latter are on the edge of the boreonemoral zone.
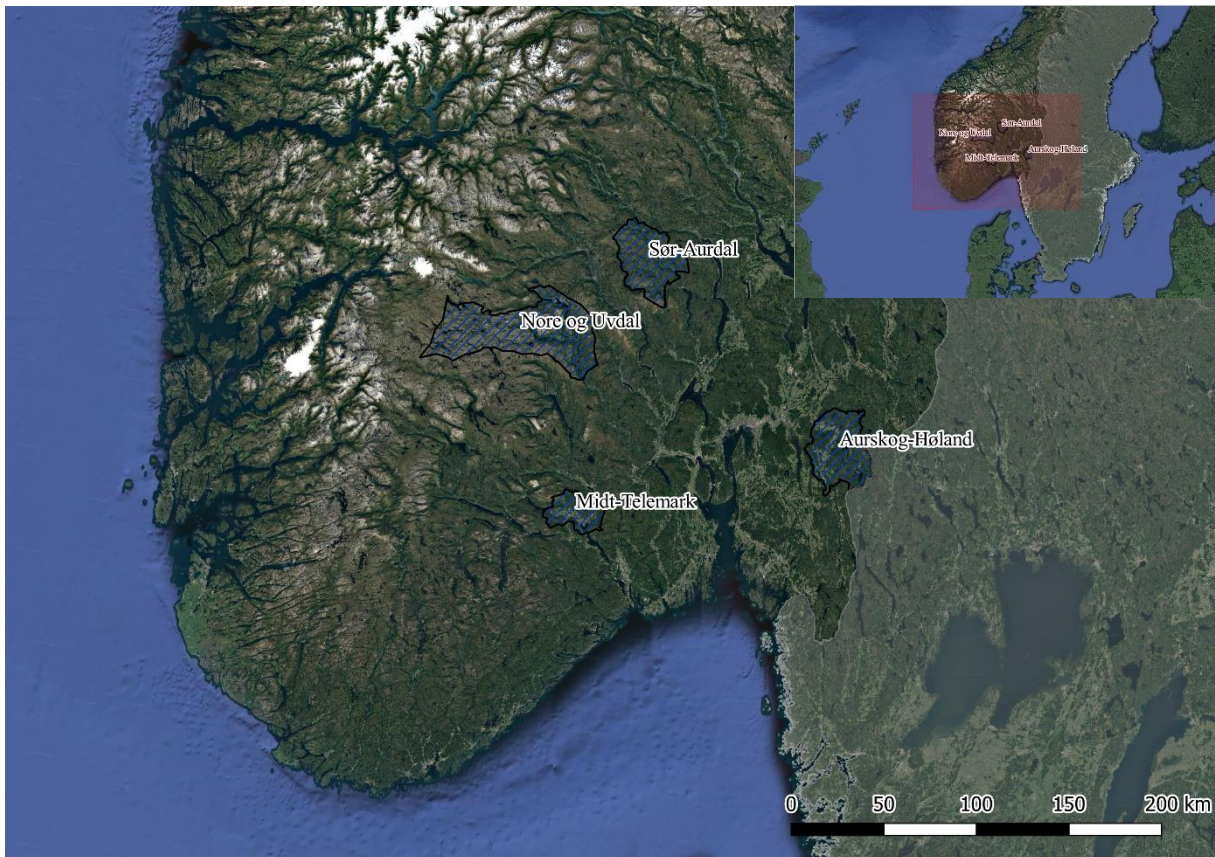
Map of the four different municipalities included in the study area. Background map generated using opensource google maps in Qgis ("QGIS Geographic Information System," 2020)

Fieldwork

Ten Old-tree habitats were randomly selected from the CHI registry in each of the four municipalities. The fieldwork of the study was carried out over two field seasons: August-October 2018 and August-September 2019. The purpose of the random selection was done to avoid sampling bias. Knowing that Old-tree habitats were overrepresented far away from roads and on low site indexes (Sætersdal et al. 2016a) made it crucial to not just select areas for the sake of easy access.

Study plots of 0.162 ha in size were laid out at the center each of the Old-tree habitats, in which five of the presumably oldest living spruce or pine trees were carefully chosen from within the plot in accordance to the descriptions in the CHI field guide. The plot size and the number of trees were chosen to reflect the minimum threshold for delimitation of the CHI habitat Old-trees of at least 30 trees per hectare (Baumann et al. 2001). Every study plot from the Old-tree habitats was accompanied by a corresponding reference plot outside the delimited area. The aim of the reference plots was to sample old trees from comparable nearby forests. To qualify as a reference plot, they had to belong to a forested area within 200-500 meters distance from the Old-tree habitats, and the elevation along with similar species distribution. The total number of study plots numbered 80, and in sum consisted of 40 pairs, hereby denoted as localities.

The core extraction procedure was carried out after GPS-marking the sample trees. An extraction height of 0.5 meters was chosen as an appropriate compromise between nearing the total age, while still being able to turn the handle and detect butt rot. Trees with heart rot, however, were drilled at 1.3 meters to salvage more complete growth rings in the core sample.

Registered variables

Variables were collected from descriptions provided in the CHI field guide(Baumann et al., 2001) and quantified. In addition, site variables were added such as site index, distance to road, slope and elevation. Site index is a measure of forest stand productivity based on dominant tree height and age. The inclusion of site index was due to other studies indicating potential predictive power (Alberdi et al. 2013; Sætersdal et al. 2016a) . Many variables were the same for the two species. Some adaptations were necessary to account for the morphological differences between the species. Some variables were not registered for spruce, these were spiral grain and hanging branches. Others were registered differently, such as bark structure, bark color, branch thickness and crown shape. Complete lists of all variables along with their descriptions are found in tables 1 and 2.

Site variables

The main purpose of registering the site variables was to describe different site factors that may influence growing conditions for the sampled trees. These were all variables that could easily be procured in the field or from forest inventory maps. Site index and vegetation type indicate

productivity. Vegetation types were classified with the methodology developed by (Larsson, 2000). The topographic position is the combination of aspect and local topography. Together, the combination of vegetation type and topographic position indicates the humidity conditions on the locality (Baumann et al. 2001). All GIS work was done in Qgis (*QGIS Geographic Information System* 2020)

1 List of site variables

Site variables	Methodology
Basal area	Basal areas was registered as Relascope sum around each sample tree , which is equal to the basal area in m^2 per hectare. The relascope consisted of a 50 cm long chain with an opening. All the trees counted in the stand that exceed the relascope opening from on spot is mathematically equal to the m^2 per hectare around in the area (Fitje 1996).
Forest structure	The number of recorded trees in distinct layers in a 7-meter radius around each sample tree. This was divided into one-storied layer, two-storied and multi-storied
Vegetation type	Vegetation type were registered around each sample tree. These were grouped into productivity according to the tree species.
Site index	Site index H40 from forest inventory plan. The number reflects the site index of the dominating tree species at a breast height age at 40 years (Tveite 1977; Tveite & Braastad 1984)
Topographic position	A four-level factor from 1 to 4 derived from local topography. 1 signifies a top, 2 A south facing hill, 3 a north facing hill and 4 flat terrain or hollow
Distance to the nearest road	Distance of each sample tree to the nearest suitable forest access road
Elevation	Elevation found using GPS point on national height model data. The lowest elevation in the sample was 149 meter above sea level, while the highest was 1034 meters.
Slope	Slope in percent from a 10-meter radius buffered around each sample tree

Tree variables

Tree variables were included to describe the sampled trees. Some traits, such as visible right-oriented spiral grain predominantly occur in older trees. Crookedness on the other hand may provide information regarding a tree's attractiveness as timber. The occurrence of heart rot was also recorded for each tree due to its role as a possible confounding variable. A challenge with some of the collected variables could be subject to unconscious bias, which could affect the registration. If a tree turned out to be old or young, it could have swayed some decisions afterward in the field due to confirmation bias. A conscious effort was made only to record such variables after the core extraction to reduce this bias effect.

Tree variables	Methodology
Age	Age estimated from growth rings
Height	Breast height(1,3 meter)
Diameter at 1,3 m	Cross calipered diameter measurement. Registered at the detail level of half a cm.
Diameter Height ratio (DH:ratio)	The diameter in cm divided on the height in meters
Crown length in %	The length of the crown recorded from the first living branch to the top in % of the total tree height
Crown shape	A leveled factor from 1-4. For spruce this signified crown wideness. For pine it was a composite variable of crown wideness along with crown flatness.
Rot	Free of rot = 0, rot present = 1
Stem taper %	Stem taper from 1,3 meters to 2,3 meters height in percent
Bark structure	A leveled factor from 1-5 describing increasing bark roughness in spruce. In pine it is a leveled factor from 1-5 describing the development of tightly connected bark plates.
Bark color	A leveled factor from 1-5 describing the color change on the stem from brown to increasingly light gray in spruce. For pine it is a leveled factor from 1-5 describing the color change from orange to gray.
Spiral grain	Visible spiral grain is represented binomially: 0 = no spiral grain and 1 = visible spiral grain
Branch thickness	For spruce this is the diameter of the thickest branch in cm in the first 2,3 meters of the stem. For pine it is the thickest branch in the crown recorded in four levels: 0-5 cm, 5-10 cm, 10-20 cm and >20 cm.
Hanging branches	Binomial variable where 1 means that the majority of the branches are inclining downwards.
Crookedness	A leveled factor from 1-5. 1 is straight, while 5 is very crooked and unsuitable for timber
Broken top/spike knot	Visible spike knot after a top breakage
Number of main stems	Number of stems below 1,3 meters height
Visible wounds	Visible wounds on the stem were registered binomially
Dark pendant lichens	Leveled factor from 0-2 where 0 is no dark pendant lichens present, 1 is present and 2 signifies 10 dark pendant lichens longer than 10 cm on the richest 1 M^2
Lightly colored pendant lichens	Leveled factor from 0-2 where 0 is no lightly colored pendant lichens present, 1 is present and 2 signifies 10 lightly color pendant lichens longer than 10 cm on the richest 1 M^2

Laboratory work - Dendrochronology

Growth rings were counted using lintab 6 and the dendrochronology software TSAP-Win x (Rinntech). Cores lacking piths were corrected for using a plastic template of the transversal section (Applequist 1958). The remaining distance to the pith was estimated using the mean width of the 10 closest year rings. Of the trees included in the sample only 8 trees had more than 4 cm miss to the pith, these were either characterized by large ring widths throughout their life or confirmed old by all the counted rings. Lastly, the estimated number of growth rings in the samples was adjusted according to the mean distance of the core extraction height. Two growth rings were added for every 10 cm in core extraction height to approximate the remaining growth rings (Kuuluvainen et al. 2002). Several core samples from Nore og Uvdal were unfortunately corrupted, and from 400 core samples, 373 were included in the final sample.

The oldest sampled spruce was estimated to be 353 years old while the oldest pine tree with pith in the sample was 452 years old. An older pine estimated to be 520 years was included in the sample. Another pine was possibly even older (>550 years old), however as it had a large hollow inside the age it was excluded. Below in table 3 is the summary statistics for the age distribution in both species. Table 4 is a summary of the amount of trees that qualify as old

table 3 Summary statistics for the age distribution in all the sampled spruce and pine trees

Tree species	N	Maximum	Minimum	Median	Mean
Spruce	182	363	62	178	190
Pine	191	520	64	212	225

table 4: Summary of the number of old trees in the different study plots divided onto the two age thresholds

Age threshold	CHI	Reference	Age threshold	CHI	Reference
> 150 years	167	126	> 200 years	113	65
< 150 years	18	63	< 200 years	72	124
Total trees	185	189	Sum	185	189

Table 4: A list of all the tree variables

Statistical analysis

The analysis can be divided into three main parts: First, a preliminary analysis to determine which statistical distribution best reflected the age. The next part was a pairwise *t*-test to test the difference in the mean age of the oldest trees on each plot pair. Lastly prediction models for the age in old spruce and pine trees were made. Three types of models were made for each species: 1) single tree models dependent on tree variables, 2) stand-level models dependent on field variables and 3) models from site variables. All the analyses were performed in the statistical software R (R Core team, 2018) and the presented figures were made using the package "*ggplot2*" (Wickham 2011).

Preliminary analysis

A Shapiro-Wilk test showed that the age distributions of the sampled trees were not normally distributed. Both were visibly skewed. For a visualization of the two distributions see Figure 1 and 2. A log transformation did not improve the skewness. Further inspections were done utilizing functions embedded in the package "*fitdistrplus*", a package that offers useful diagnostic tools for identifying the appropriate distribution (Cullen & Frey 1999; Delignette-Muller & Dutang 2015).

Three candidate distributions: gamma, normal and Weibull were chosen for further examination. Skewness describes the degree of which the distribution leans in one direction. Kurtosis corresponds to the how much the tails of the sample distribution differs from the normal distribution. Together these can provide information regarding the distribution in the sample. A skewness-kurtosis plot function "*descdist*" in "*fitdistrplus*" could therefore aid in process of elimination (Cullen & Frey 1999; Delignette-Muller & Dutang 2015). The selected distributions were then compared using the inbuilt graphical functions for cumulative density functions and plotted empirical quantiles against the theoretical quantiles. Maximum likelihood estimates of the fit were used to calculate the AIC information criterion, a measure for the amount of information lost (Akaike 1973). The Gamma distribution, suited for values that are positive and skewed provided the best fit for Norway spruce(table 5 in results) (Crawley 2013)and was therefore chosen for the single tree models. Weibull and gamma were indistinguishable for Scots pine, therefore gamma was chosen to enable comparisons across species.
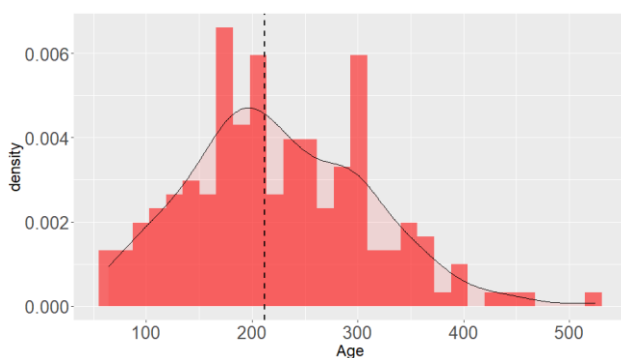

Figure 1: The age distribution of the pine trees in the sample represented in a density plot supplied with a histogram. The binwidth of the columns is 30 years, and the median is represented with a dotted line
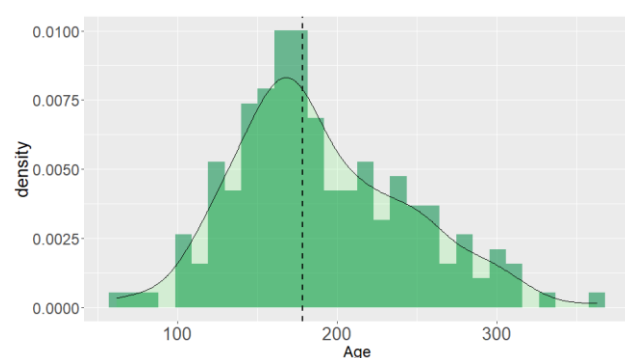
Figure 2: The age distribution of the sampled spruce trees represented in a density plot supplied with a histogram. The binwidth of the columns is 30 years, and the median is represented with a dotted line

Evaluation of the age of the oldest trees in the Old-tree habitats

A pairwise t-test was used to test the age difference between the on each locality. The Old-tree habitats and the reference plots were treated as pairs under the assumption that they would tend to share forest history and site conditions. The mean age of the trees sampled in each study plot was calculated. One of the assumptions of the pairwise t-test is normality. No violations of the normality assumption were found, which meant that the analysis could proceed as planned. The test was formulated the following way:

Null hypothesis: The mean of the age difference is equal to 0

Alternative hypothesis: The mean of the age difference is not equal to 0

To truly test such a hypothesis would mean to extract core samples from all the trees in the delimited areas and directly measure if the density of Old-tree habitats upheld the set age thresholds. Such a research design would, however, be too costly and, for the same amount of funding, would cover a smaller area reducing its potential to be generalized. Therefore, a second solution was opted for; to restrict the research design and a representative area in southeastern Norway.

Prediction models for age

A mixed modeling approach was applied to account for the spatial autocorrelation between the sample trees and the locality. Refraining to take care of this dependency is known to lead to an increased rate of type I errors. This is when the null hypothesis is falsely rejected (Musca et al. 2011). Localities were represented in all the models as random intercepts. The amount of variation explained by the random clustering effects was quantified through the intra-class correlation(ICC) (Crawley 2013). All the prediction models were fitted in the package "*lme4*" in R (Bates et al. 2015).

Single tree models

The single tree models were modeled using generalized linear mixed models fitted with the gamma distribution (GLMM). Generalized linear models provide flexibility by accounting for error structures that are not normally distributed nor have non-constant variance. This is done by relating the sums of the linear predictors to the response through a link function (Nelder & Wedderburn 1972) .A log-link was used to ensure positive age values, an assumption of the gamma distribution(Crawley 2013).

Stand models

Field stand models and site models were fitted with linear mixed effects using the mean age of trees of the same species on each study plot. These values were normally distributed which meant that they did not need to be modeled as GLMM. Lastly, all variables were included as means except, vegetation types which were included as the percentage of the stand with the given vegetation type.

Effect size

Two types of pseudo-R^2's aimed at describing the different levels of variance explained by linear mixed models were used as measures of the goodness of fit. The marginal R^2 (R^2_m) is a measure of the variance explained by the fixed effects in the model. The conditional R^2 (R^2_c) on the other hand also includes variance explained by the random effects. Supplying both were seen as advantageous as they provide an intuitive comparison of the explanatory models and the relative contribution of the random effect (Nakagawa & Schielzeth 2013). The two R^2 measures can be represented this way:

Formula 1: Explanation for all the symbols**:** σ_f^2 = *fixed effects variance.* σ_a^2 = *random effect variance.* σ_e^2 = *residual variance* (Nakagawa & Schielzeth 2013)*.*

$$R_m^2 = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_a^2 + \sigma_e^2}$$

Formula 2: *explanation see formula 1*

$$R_c^2 = \frac{\sigma_f^2 + \sigma_a^2}{\sigma_f^2 + \sigma_a^2 + \sigma_e^2}$$

Estimating R^2 for Gamma GLMM is however not as straightforward as with LMM. The stand models were modeled using linear mixed models, and the two formerly described R^2's could be used. The residual variance σ_e^2 for Poisson and binomial distributions, can be accurately estimated (Nakagawa et al. 2017) . Estimating the residual variance σ_e^2 for Gamma GLMM, however is a different matter. This difference is related to overdispersion, the variation which exceeds the distribution's variance, which is called the distribution specific variance x (Crawley 2013). When utilizing the Poisson and binomial distributions, overdispersion can be separated from the distribution specific variance using an overdispersion coefficient estimated from the model. This separation is however, not possible with the gamma GLMM; it must be derived from the latent scale (Nakagawa et al. 2017).

The error distribution need to be taken into account (Nakagawa & Schielzeth 2013; Nakagawa et al. 2017) . This has been done using the trigamma function on the variance in the latent GLMM scale. The reason why this works is that it is equivalent to the gamma variance in a logarithmic scale and used when in cases where the GLMM is fitted with a log link. Trigamma

is the logarithmic second derivate of the gamma function (Nakagawa et al. 2017). Put simply the trigamma method provides the best approximation for the residual variance.

$R^2_{m.gamma}$, $R^2_{c.gamma}$ (Formulas have been supplied below). and intraclass correlation (ICC) were calculated in R based on this method using the "*r2.squared.glmm*" function in the package "*MuMIn*" and "*icc*()" in the package performance (Barton 2020) . For more details regarding this method see Nakagawa et al. (2017)

Formula 3: Explanation for all the symbols**:** σ_f^2 = *fixed effects variance.* σ_a^2 = *random effect variance.* σ_e^2 = *residual variance.* $ln(\psi(v))$ = *log link on the trigamma function applied to the gamma variance* (Nakagawa et al. 2017)

.

$$R^2_{m.gamma} = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_a^2 + \ln(\psi(v))} \approx \frac{\sigma_f^2}{\sigma_f^2 + \sigma_a^2 + \sigma_e^2}$$

Formula 4: *explanation see formula 3*

$$R^2_{c.gamma} = \frac{\sigma_f^2 + \sigma_a^2}{\sigma_f^2 + \sigma_a^2 + \ln(\psi(v))} \approx \frac{\sigma_f^2 + \sigma_a^2}{\sigma_f^2 + \sigma_a^2 + \sigma_e^2}$$

Variable selection
All variables were inspected for potential interactions, second-order terms along with an emphasis on models that made biologically sense. Inclusion in regression models showed that heart rot was a significant predictor for the age in spruce trees on both on a single tree level and a stand level. Regardless, rot was not registered for use directly in the models, but its potential effects on the rest of the predictors.

Model selection
Model selection was done through a combination of backwards forwards stepwise variable screening, and AICc of different promising models. If there were no clear distinction in AICc and AICc weight between the different candidate models multiple models are shown in the results.

During the model selection process, it became clear that the two best site models LMM models for spruce were singular, meaning that the random effect of locality did not explain any variance. These models were further examined, and met the assumption of normality, independence and were identically distributed. Thus, a choice was made to simplify the models into linear regression models.

Results

Statistical distributions

For both tree species the age distributions were significantly different from the normal distribution on a single tree level. Scots pine (p-value = 0.02312) and spruce (p-value = 0.002872).

table 5 Akaike's information criterion for the fitted distributions

Species	Gamma	Weibull	Normal
Norway spruce	1976	1989	1985
Scots pine	2236	2236	2248

Age comparison between old tree habitats and reference plots

The oldest trees in the Old-tree habitats were significantly older compared to the reference plots. The mean of the age differences between the plots was 43.3 years (t-value = 4.77, p-value = 2.9 e-05, 38 pairs). The 95% confidence interval was CI (24.9, 61.6). For a boxplot comparison between the old tree habitats and the reference plots see Figure 3. A general trend was that localities with a high mean age in the Old-tree habitats had reference plots with correspondingly old trees (R^2 = 0.2, p-value < 0.05, figure 4) Notable exceptions did, however, occur.

Seven of the in total 38 pairs had reference plots which exceeded the age in the old tree habitats. None of these seven discrepancies could be attributed to differences in the species composition. The most extreme examples could be found in two pairs located in Nore og Uvdal and Sauherad respectively. In the example from Nore og Uvdal the mean age of the oldest trees in the old tree

habitat was 191 years and the reference plot was 270.7 years. In the Sauherad locality the old tree habitat plot had a mean age of 281, whereas the reference plot had 340. Nevertheless, these Old-tree habitats still fulfilled the age thresholds. A complete list of the study plot pairs containing the mean of age of the oldest trees, locality number, the municipality is available in appendix A.
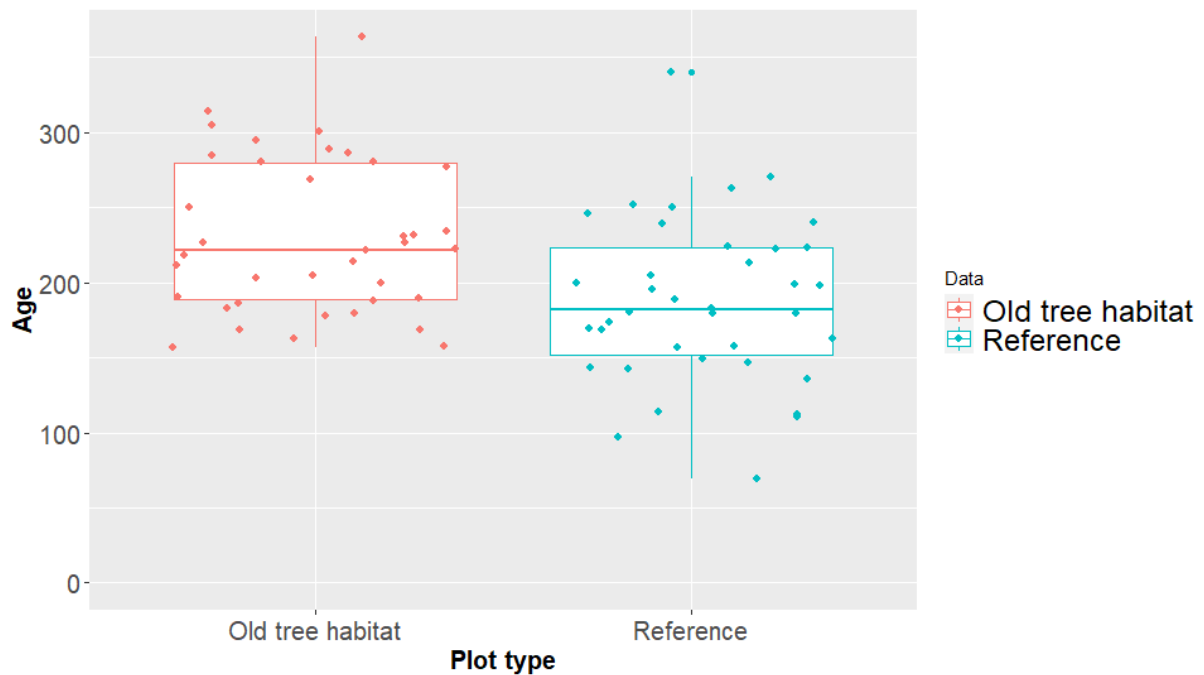

Figure 1: A boxplot comparison of the mean age of the oldest trees on each plot where the line shown in each box is the median. The observations have been jittered using geom_jitter() in ggplot2 to avoid overplotting (Wickham, 2011).
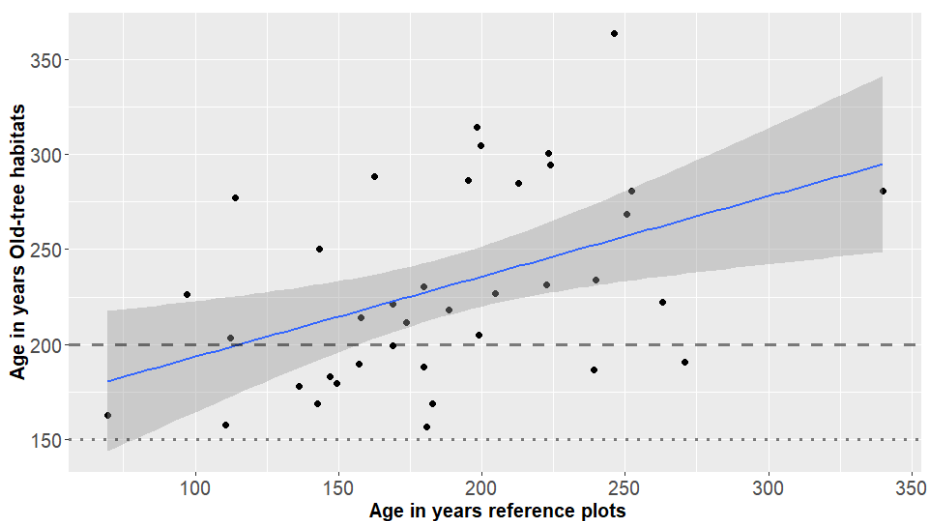
figure 4: The linear regression between the mean age of the oldest trees on the old tree habitats as a response and reference plots as the explanatory variable. The slashed line represents the age threshold for pine (slashed line, 200 years) and spruce (dotted line, 150 years) given that there was no correlation between the study plot pairs on each locality.

Age models

The main focus is on the variables included in the models. For a list of variables which were significant alone but not included in the final models see table 6

Single tree models for age

Spruce

The single tree spruce model only explained a small amount of the variance in age ($R^2_{m.glmm}$ = 0.24). The explained variance by the model improved somewhat by including the random effect of locality ($R^2_{c.glmm}$ = 0.32). Both **bark structure** and **bark color** correlated with the age, although also intercorrelated. Of these, the best predictor was the measure of an increasingly rough bark structure with age. The only size-related variable was **height**, which correlated negatively with age. This negative relationship is likely due the positive correlation between **site index** and tree **height** (Kendall rank correlation = 0.478, p-value = 2.2e-16). The ICC was considerable in the full model (0.69). The full model can be found in table 7.

Pine

The pine model had moderate explanatory power ($R^2_{marginal\ glmm}$ = 0.53, $R^2_{conditional\ glmm}$ = 0.68, full model table 8) and consisted of a more complex model compared to the spruce model. The effect of random clustering on pine trees was very strong (ICC for the full model = 0.91). Such clustering may have been caused by the fact that some localities consisted of one pine tree and four spruce trees. The fixed effects included in the models were all related to morphological traits and growth patterns.

The only included size variable was a logarithmic transformation of the composite variable **DH: ratio**. The original untransformed variable was strongly linear until around 3 in **DH: ratio** (figure 8), after which the age did not further increase along with the **DH: ratio**. A log transformation smoothed some of this trend and reduced multicollinearity with **branch thickness**.

Most of the included variables were not size related. Two of the most consistent variables were **bark structure**. **Visible spiral grain** occurred mostly in Scots pine trees over the age of 200 years. Two additional crown morphology variables were included: **Branch thickness,** which increased with age and **Hanging branches,** which indicated that old scots pine trees had branches inclining downwards.

table 6 The most influential tree variables which were significantly correlated with age alone, but not included in the final models. Discussion regarding were ordered thematicially within the discussion

Variables	Relation with age
Crown length in percent	Positively correlated with age in Norway spruce
Crown shape	Positively correlated with age in Scots pine
Visible spike knot	Positively correlated with age in Scots pine
Bark color	Positively correlated with age in both species, only included in field stand model for Scots pine
Elevation	Positively correlated with age in both trees species. For figure see figure x
Diameter	Weak correlation for Scots pine, not significant for Norway spruce
Height	Negative correlated with age for both species, but only included in the single tree model for Norway spruce.

Spruce

table 7: The most parsimonious single tree field model for spruce. All the variables are in their logarithmic state. To use the model first calculate it, the raise it using exp(). The fixed effects are shown in the first half of the table. Bark structure was added in the model as dummy variables where the number indicated the order of the bark structure classes. height is a continuous variable. Random effect related information is displayed in the bottom half. The html table output from tab_mod has been used as a template, the estimates, however, come from lme4(Bates et al., 2015)

Model spruce	Age		
Predictors	*Estimates*	*Std.Error*	*p*
(Intercept)	5.094759	0.132344	**< 2e-16**
Barkstructure [2]	0.335950	0.097896	**0.001180**
Barkstructure [3]	0.456639	0.094194	**4.50e-06**
Barkstructure [4]	0.571948	0.103558	**9.82e-08**
Barkstructure [5]	0.674659	0.171965	**0.000146**
Height	-0.016075	0.004832	**0.001606**
Random Effects			
ICC	0.69		
$N_{Locality}$	24		
Observations	182		
Marginal R^2_{glmm} / Conditional R^2_{glmm}	0.24 / 0.32		

Pine

table 8: The most parsimonious single tree field model for pine. All the variables are in their logarithmic state. The fixed effects are shown in the first half of the table. Bark structure, branch thickness, spiral grain and downwards facing branches (down_branch) is added in the model as dummy variables. The numbers in the Bark structure and Branch thickness were added indicates the order of the classes. Log(DH:ratio) is continuous. Random effect related information is displayed in the bottom half. The html table output from tab_mod has been used as a template, the estimates, however, come from lme4(Bates et al., 2015)

Model pine	Age		
Predictors	*Estimates*	*Std.Error*	*p*
(Intercept)	4.57259	0.09809	**2,00E-16**
Barkstructure [2]	0.15980	0.05447	**0.003352**
Barkstructure [3]	0.27618	0.06106	**6.10e-06**
Barkstructure [4]	0.47209	0.08689	**5.53e-08**
Barkstructure [5]	1.10705	0.23650	**2.85e-06**
Crookedness	0.07157	0.02025	**0.000408**
Visible spiral grain	0.12635	0.04022	**0.001681**
Branch thickness [2]	0.13197	0.05798	**0.022835**
Branch thickness [3]	0.21407	0.06608	**0.001198**
Branch thickness [4]	0.12391	0.08701	**0.154409**
Down_branch	0.08020	0.03705	**0.030403**
Log(DH:ratio)	0.18757	0.06635	**0.004698**
Random Effects			
ICC	0.91		
N $_{Localities}$	26		
Observations	191		
Marginal R$^2_{glmm}$ / Conditional R$^2_{glmm}$	0.55 / 0.70		

Linear models for age on a stand level
Field models
Spruce

As opposed to the single tree model, this model consisted of **bark structure, crookedness** and provided moderately explanatory power (R^2_m = 0.49, R^2_c = 0.58, full model table 9).). **Bark structure** was again the most influential variable. The age of the oldest trees on a plot increased with an increase in **bark structure**. Furthermore, plots with older trees tended to have straighter stems on average (not **crooked)**

Pine

The final field stand model explained marginally more variance compared to the single tree models to ($R^2_{m=}$ 0.57, R^2_{c} = 0.74, full model table 10). Furthermore, the field model contained fewer variables than the single tree model. The model included **bark structure**, **bark color**, a logarithmic term of the **DH: ratio,** and **crookedness**. In contrast to the single tree model. bark color explained more variance than **bark structure**

Site variables

The site models were all weakly correlated with age. ($R^2_{adj.spruce}$ = 0.30/ 0.31 vs $R^2_{m.pine}$ = 0.22). Several site variables were not included in the final models due to multicollinearity and no. **Site index** and **elevation** two of the most influential were intercorrelated (Kendall rank correlation spruce = -0.66, *p*-value = 4.5e-09). Of the two variables **site index** explained most of the variance in the site models (Kendall rank correlation for spruce = -0.4, *p*-value = 3.8e-04, figure 8 for visualization), and thus was the choice for the final models. See Table 11 for Spruce and Table 12 for pine.

Spruce models

Two candidate models, both linear regression models(see model selection under methods for explanation) containing **site index** were selected as the AICc were indistinguishable. In addition to site index model 1 included a second-order term of **site index**, which represented a negative non-linear effect of **site index** on the age. Model 2 on the contrary included site index in addition to two **slope** parameters. These **slope** parameters consisted of a negative main effect along with an interaction term between **site index** and **slope**.

Pine Site Model

The fixed effects correlated poorly with tree age, and only marginally improved by including the random effects variance. Similar to spruce model 2, the pine model also included negative increase with increasing **site index**. Nonetheless, opposed to the spruce model 1, an increase in the **slope** parameter leads to an increase in maximum age.

Spruce stand models tree variables tables

Table 9: The most parsimonious linear mixed effect tree variable stand model for spruce according to AICc. The fixed effects are shown in the first half of the table. Both bark structure and crookedness are continuous. Random effect related information is displayed in the bottom half.

Model	Age		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	84.68	36.18 – 133.18	**0.001**
Bark structure	52.81	37.09 – 68.53	**<0.001**
Crookedness	-21.14	-39.37 – -2.90	**0.023**
Random Effects			
σ^2	833.88		
τ_{00} locality	179.02		
ICC	0.18		
N locality	24		
Observations	45		
Marginal R^2 / Conditional R^2	0.49 / 0.58		

Pine stand models tree variables tables

table 10: The two potentially most parsimonious linear mixed effect tree variable stand models for pine according to AICc. The fixed effects are shown in the first half of the table. All the variables are continuous and two models only differ with the diameter terms. Random effect related information is displayed in the bottom half. The html table output from tab_mod has been used as a template, the estimates come from lme4(Bates et al., 2015)

	Model		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-65.50	-154.1 – 23.09	0.147
Bark color	25.94	6.63 – 45.26	**0.008**
Bark structure	23.93	2.76 – 45.10	**0.027**
Crookedness	26.53	1.84 – 51.22	**0.035**
DH:ratio	100.20	45.10 – 155.29	**<0.001**
Random Effects			
σ^2	1422.36		
$\tau_{00 \text{ locality}}$	915.59		
ICC	0.39		
N $_{\text{locality}}$	26		
Observations	46		
Marginal R^2 / Conditional R^2	0.57 / 0.74		

Site variables spruce

Table 11: The two most parsimonious linear regression site models for Norway spruce. The variables are continuous. The random effect of locality did not explain any additional variance and therefore discarded.

	Model 1				**Model 2**		
Predictors	*Estimates*	*CI*	*p*	*Predictors*	*Estimates*	*CI*	*p*
(Intercept)	404.91	286.85 – 522.96	**<0.001**	(Intercept)	349.56	276.14 – 422.98	**<0.001**
Site_index	-37.32	-60.98 – -13.66	**0.003**	Site_index	-14.63	-21.32 – -7.95	**<0.001**
Site_index^2	1.46	0.36 – 2.56	**0.010**	Slope	-5.32	-9.02 – -1.61	**0.006**
				Site_index * Slope	0.46	0.15 – 0.77	**0.005**
Observations	45			Observations	45		
R^2 / $R^2_{adjusted}$	0.33 / 0.3			R^2 / $R^2_{adjusted}$	0.37 / 0.31		

Table 12: The most parsimonious linear mixed models with site variable pine. The fixed effects are shown in the first half of the table. All the variables are continuous. Random effect related information is displayed in the bottom half. The html table output from tab_mod has been used as a template, and the estimates come from lme4(Bates et al., 2015)

	Model		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	300.44	222.69 – 378.18	**<0.001**
Site_index	-11.12	-18.58 – -3.67	**0.003**
Slope	1.31	0.13 – 2.48	**0.030**
Random Effects			
σ^2	3213.15		
$\tau_{00\ locality}$	610.30		
ICC	0.16		
$N_{\ locality}$	26		
Observations	46		
Marginal R^2 / Conditional R^2	0.224 / 0.348		

Discussion

Preliminary analysis: Modelling the age of old trees

Determining the right statistical distribution was vital when the goal was to make statistical inferences about the old trees. Assumptions of a normal distribution on a single tree level would lead to wrong estimates for both studied species as the variance was not constant (Crawley 2013). The age structure of Norway spruce was clearly not normal, and according to the AIC values best explained by the gamma distribution. Scots pine was also significantly different from the normal distribution, but the AIC values for Weibull and gamma were indistinguishable.

There appears to be no consensus regarding which statistical distribution is best for the age of old trees. Various studies have utilized different distributions ranging from Poisson (Rötheli et al. 2012), lognormal (Bigler 2016; Liu et al. 2019) and normal distribution to model age according to what fit their data best. However, while distributions differ, several of the distributions have in common that they are skewed. A skewed probability may possibly reflect the probability of individual trees reaching old age. Surviving long enough to reach old age is likely an exception to the rule rather than the norm (Munné-Bosch 2018). Trees face many perils in their lifetime (including harvesting), and many do not even reach the sapling stage

(Long et al. 2004). Even with the intention of sampling old trees, such life expectancy patterns may potentially have carried into the studied trees.

The age of the Old-tree habitats

Are the oldest trees in the delimited Old-tree habitats on average older than nearby comparative forests?

The five oldest trees in the Old-tree habitats were on average 43 years older compared to surrounding mature forests, strongly indicating that the methodology has located old trees. The mean age of the Old-tree habitats and the mean age of the reference plots were correlated, indicating a common local forest history. A correlation between the study plots strengthens the representability of the reference plots as proxies of the surrounding mature forests. On a given locality, Old-tree habitats mean age was relatively older, which indicates that the selected area might represent the oldest forest in a given area. Furthermore, the Old-tree habitats were not just relatively older (table 4), they also had markedly more old trees than the reference areas over the 150-year threshold. The oldest trees in the Old-tree habitats were less affected by the 200-year threshold. This threshold effect means that many of sampled trees from Old-tree habitats were truly old, while the oldest trees outside were generally younger. However, for methodological reasons, generalizations of the practice should be based on the entire dataset.

Testing the contents of Old-tree habitat requires that the fact that the Old-tree habitats first have delimited by a forest planner is taken into account, who decided in the field that these areas contained old trees. Furthermore, in this study five of these trees were sampled from a study plot placed within this area. Even though the same CHI field manual was used, yet, there are no guarantees that the trees sampled in this study are the same as the forest planner had in mind while delimiting out the given Old-tree habitat. Nevertheless, there is some value of discussing potential factors affecting the age structure within the Old-tree habitats. There were reference study plots that qualified the Old-tree habit age thresholds, but for some reason were not delimited by the forest planners. Additionally, there were seven exceptions in which the reference study plots were older than the Old-tree habitats (see figure 3). These for mentioned exceptions were likely the interplay of several factors, one of which is related to CHI methodology.

The delimitation thresholds for the habitats in the CHI methodology are meant to be adjusted to the local forest conditions. In other words, the required age for the Old-tree habitat will be relative to the overall age in the given planning area (Baumann et al. 2001). CHI aims to cost-effectively delimit ecologically representative areas in the production forests as part of forest planning (Gjerde et al. 2007; Gjerde et al. 2018). A central principle of the CHI methodology is the ecological term of *complementarity*, which states that conservation measures should complement each other by capturing different communities and different species composition along environmental gradients (Sætersdal et al. 2004; Vane-Wight et al. 1991).

A common situation is that one or more of the 12 CHI habitats is scarce or abundant in a given planning area. CHI aims to represent the various forms of species diversity within a given planning area. Through the approval of a certified forest ecologist adjustments can therefore be made (Baumann et al. 2001). In the instance of Old-tree habitats, such adjustments are made by increasing or decreasing the age thresholds and the area needed for delimitation. Increasing age thresholds will exclude areas that otherwise would have been registered following the generic age thresholds.

Sampling effects

Sampling effects might have affected the age and spatial thresholds required for delimiting an Old-tree habitat. Differences in tree species composition is another naturally defined factor which could lead to younger trees in the old tree habitats due to differences in the maximum age of the species (Castagneri et al. 2013; Finnish Forest Research 2007). However, no such effects were found in the seven localities in which the oldest trees on the reference plots exceeded the age in the old tree habitats. Nevertheless, if such differences had been found they still might uphold the species-specific threshold. Another reason for older reference plots might have been that the density of old trees per ha and that the spatial threshold of 0.2 ha for Old-tree habitats was not fulfilled (Baumann et al. 2001). Such effects are not possible to determine based on means alone.

Old trees: Present at different spatial scales in the production forests

For both tree species, almost all the localities had one or several old trees present. Another way of judging the success of the Old-tree habitats is to compare the number of old trees within them. Old trees were located at different study plots regardless if they were in Old-tree habitats or reference areas (Figure 5 and 6). However, the Old-tree habitats supported higher densities of old trees than the surrounding forests. These differences grew even further when applying the 200-year threshold (table 4). The aggregated distribution of the old trees extended to larger spatial scales.

Local forest conditions were reflected on a locality level. The age structure of the oldest trees was clustered on each study plot (figure 5 for the age of each spruce tree and figure 6 for pine). Furthermore, at each locality level, the mean ages of the oldest trees on the Old-tree habitats were correlated with the mean ages of the oldest trees in the reference plots (figure 5). Which may reflect a weak, but significant effect of local forest history. Furthermore, tree age appears to correspond in localities in proximity (figure 5 and figure 6). The age structure of the oldest trees therefore appears to span beyond the stand scale.

At the broadest spatial scale of this study, the municipality level, the mean ages of the oldest trees were surprisingly similar. The mean age of the oldest trees for each species within each municipality followed each other closely. Furthermore, all the municipalities were of comparable ages, however of these, Aurskog-Høland, showed the highest variation. This geographic area is known to contain fewer Old-tree habitats than Norway as a whole (Hylen et al. 2018). During the CHI registration the age thresholds had to be readjusted from 200 for Scots pine to 180 and 150 to 140 for Norway spruce (Gjerde & Sætersdal 2015). Nevertheless, even in Aurskog-Høland, there were old trees far exceeding the age thresholds. This indicates the presence of old individuals spread out in the production forest, even in more intensively managed areas. Information about old trees spanning different spatial scales may guide future decision-making.

Conservation efforts range from single tree retention, protection of entire stands as woodland key habitats and establishment of large reserves (Gjerde et al. 2007; Norge 2015). Of these, retention forestry (Franklin 1989) is the conservation approach in Norway which governs the

largest spatial scales. The individual sizes of the retained patches are small on their own, but the in sum the largest as it is required by the forest certifications (Norge 2015). Retention forestry leaves a minimum of 5-10% of the original stand postharvest. This is opposed to traditional clearcutting, where all the trees are removed (Gustafsson et al. 2012). Retention forestry aims to maintain biodiversity in the production forest by emulating natural disturbances. Biological legacies are left in the form of structural elements. Examples of such structural elements are living trees, dead wood either spread out in the stand or groups (Gustafsson et al. 2012).

If the aim is to maintain old-growth traits over time through the retention of structural diversity in the production forest (Bauhus et al. 2009), more accurate identification of the old trees can guide the selection of the right conservation tool. The most common forest certification in Norway PEFC states that there should be left at least ten living trees per hectare. These trees are supposed to be selected predominantly from the oldest trees within the stand (Norge 2015). The following models for age may therefore also prove useful not only for forest planners but also for forest managers and entrepreneurs.
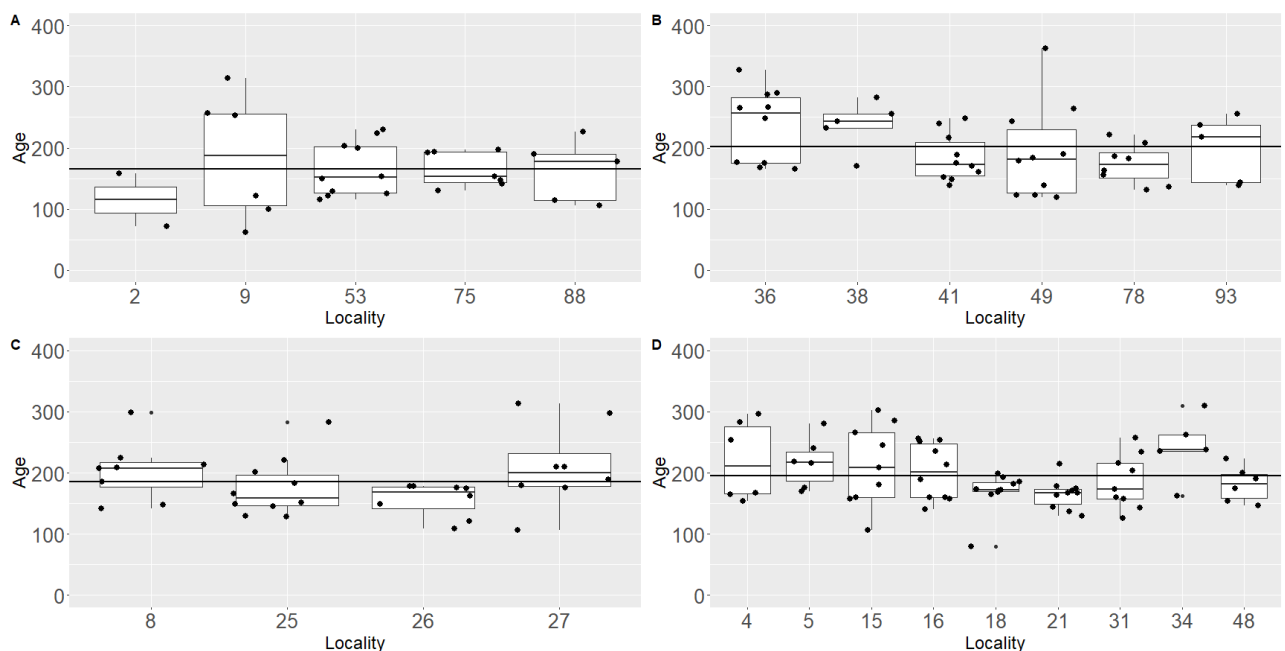

Figure 5: A boxplot comparison of spruce trees sampled on the different localities. The black line is the mean in the municipality, while the line in each box is the median. To avoid overplotting, the observation has been jittered using geom_jitter() in ggplot2 (Wickham, 2011). Each window is one municipality: A = Aurskog-Høland, B = Nore og Uvdal, C = Sauherad, D =Sør-Aurdal. The numbers on the x-axis are the numbers of the localities which were numbered then randomly picked out for sampling.
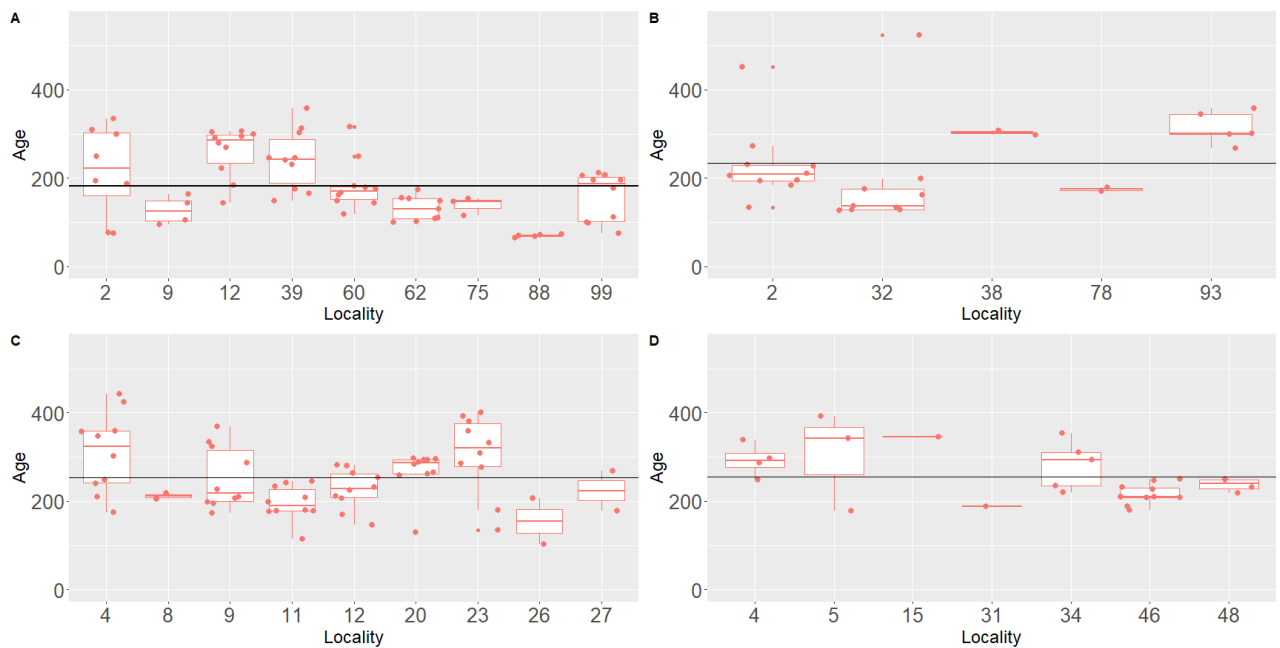
Figure 6: A boxplot comparison of pine trees sampled on the different localities. The black line is the mean age in the municipality, while the line in each box is the median. To avoid overplotting, the observation has been jittered using geom_jitter() in ggplot2 (Wickham, 2011). Each window is one municipality: A = Aurskog-Høland, B = Nore og Uvdal, C = Sauherad, D =Sør-Aurdal. The numbers on the x-axis are the numbers of the localities which were numbered then randomly picked out for sampling.

Models for age

Within the last decades, a growing body of literature has provided a deeper understanding of the factors as to why certain trees live long lives. One of these is the realization that the decline in tree growth over time might be related to maximum size rather than age alone (Munné-Bosch 2018). To provide a well-rounded description of the morphological basis for age models, it is necessary to contextualize the results in light of ontogeny: the development of an organism throughout its lifespan, the environment and anthropogenic influence.

Taking a step from theory towards application requires understanding factors that can complicate field registration of old trees. Furthermore, to potentially improve the CHI field guide (Baumann et al. 2001), several variables listed in the handbook descriptions not included in the final models will be emphasized in the following discussion. Variables that have potential pitfalls are also discussed to ensure an ecological sound registration.

Single tree models and field stand models

Can descriptions from the current old tree CHI field guide for Norway spruce and Scots pine be quantified and empirically supported, and which other morphological variables in addition to size should be included?

Tree size and age

Height

In this study, both studied tree species heights were negatively related to age. Only for pine, indications of a positive non-linear relation with height was found. Nevertheless, the positive relation was limited to the youngest trees. The height growth of a tree is assumed to generally follow a sigmoid pattern (Long et al. 2004). The height growth is first slow, only later increase exponentially until it finally stagnates again. When this saturation in height growth occurs, varies between tree species. Pioneer trees such as birches typically quickly gain height early on in life, followed by an early decline in height growth (Tveite & Braastad 1984). Norway spruce, a late succession species, maintains vigorous height growth for longer (Tveite 1977). Scots pine stands in an intermediate position between the birch and spruces. Tree size as an indicator for tree age becomes less useful over time as a saturation effect occurs as the tree ages (Weisberg & Ko 2012). At first glance, the height and age should always be positive; still, that is not always given.

A negative correlation between tree heights and age may reflect the site index of the area and successively the growth rates of the trees. Even though there was a negative relation with height in the single tree spruce models, this was weak, and it held no explanatory power on a stand level. It is well established that slow growth generally increases tree longevity, likely due to a shift into higher investment in defense compared to primary growth (Bigler & Veblen 2009; Bigler 2016; Castagneri et al. 2013; Kaufmann 1996; Rötheli et al. 2012). Less productive sites imply slower tree growth, which in turn leads to longer life spans. Moreover, it cannot be excluded that localities characterized by higher site indexes may have been subject to more frequent harvesting.

Old trees are subject to many external factors that can reduce their height. For some tree species such as Sitka spruce (*Picea sitchensis*), age seems to be highly correlated with the height.

However, around 200 years of age, depending on site index, this age-height relation weakens. The oldest Sitka spruce trees, however, generally feature broken tops and other structural complexity in the crowns, which ultimately reduce their height (Van Pelt 2007). Kuuluvainen et al. (2002) reported similar findings in Scots pine, Norway spruce and broadleaved trees in an old-growth forest in Finland. In this old-growth forest, the oldest trees were never the tallest. He attributed the reduced height to snow break, as the likelihood of an old tree to have experienced snow breakage will be higher compared to that of a young tree. A lightning strike is another factor that can lead to broken tops (Aamlid et al. 1991).

Diameter

In this study diameter was not directly included in any of the models. For Norway spruce it was not significant at all. The results in this study aligned with the idea that the relationship between size variables such as between tree age and diameter are weak or moderate at best. Previous studies of Norway spruce and Scots pine have reported correlations ranging from positive to negative and which also vary between localities (Castagneri et al. 2013; Kuuluvainen et al. 2002). A large scale study of old conifers in the Rocky Mountains in the USA showed that the correlation between age and diameter only applied to trees under 150 years (Brown et al. 2019). Furthermore, there are even more dimensions to this. High early growth rates in trees are negatively correlated with maximum life span and which in turn leads to larger diameters. Such absolute diameter differences have been reported to remain until the time of death (Bigler & Veblen 2009; Bigler 2016; Rötheli et al. 2012).

Diameter Height ratio

The diameter was not directly included in the models, but its relevance came in the form of the composite variable DH: ratio. This variable was included in both field models for Scots pine. For Scots pine DH: ratio was stronger in variance explained than either height or diameter. The DH: ratio had a moderately strong linear relationship until around 2.5 in DH: ratio (figure 7), before a saturation like that of the diameter occurred. A logarithmic transformation was attempted to linearize it. The DH: ratio has been suggested as an alternative size measure (Weisberg & Ko 2012). The benefit of this variable is the avoiding of absolute height and diameter, but instead relying on the innate proportions of the tree itself.
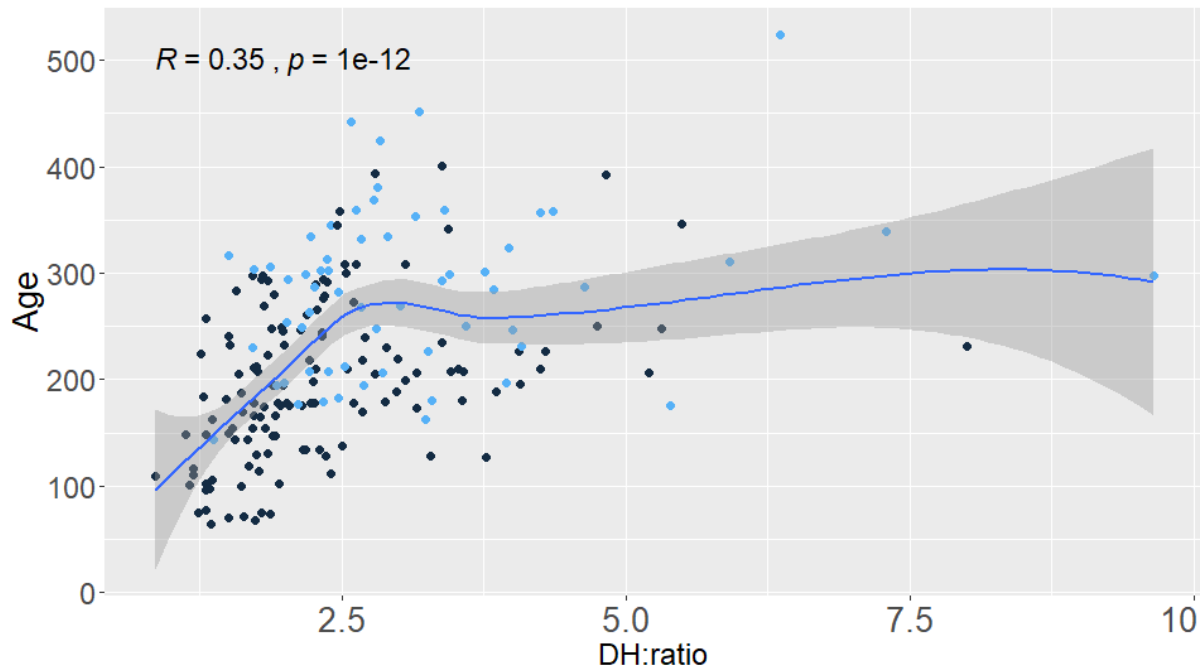
Figure 7: Kendall rank correlation displayed for the age of pine trees and their DH:ratio. The line is represented using loess. The dark grey area around the estimated line is the 95% confidence intervals for DH:ratio. The presence of visible spiral grain is illustrated with blue.

Other morphological features

Crookedness

The crookedness was included in both field models for Scots pine, possibly because they were deemed unsatisfactory quality and left untouched from harvests. The tree-level variable crookedness was included to quantify the selection effects of dimension harvests. In Northern Sweden 75% of the Scots pine trees that were above the age of 159 years all had diameters between 10 and 30 cm (Andersson & Östlund 2004). The weak correlations between age and size measures may likely be heavily modified by forestry the last centuries. Trees with straight stems and free of knots in the bole were regarded as higher in timber quality. As to why the spruce tree age appear negatively correlated with crookedness one can only speculate.

Spiral grain

Visible spiral grain appears to be a consistent characteristic of old Scots pine on a single tree level. It predominantly occurred in trees above the threshold of 200 years, and therefore perhaps a suitable separator of old pine trees from younger trees (Figure 7). Similar patterns have been reported for Ponderosa pine (*Pinus ponderosa*) (Van Pelt 2008). As the potential of spiral grain as an indicator of age is so apparent from the data, it is worth understanding which

situations can affect the practical implementation of visual registrations. The degree to which spiral grain occurs is regulated in trees by genetics (Steffenrem et al. 2016). However, its function is debated.

Untangling the causal mechanisms of spiral grain has proved challenging. Many studies have been conducted on the topic and yet reached different conclusions (Kubler 1991). Currently, there are two main hypotheses: the water supply hypothesis (Kubler 1991) and the wind stability hypothesis (Skatter & Kučera 1997; Skatter & Kučera 1998). Both hypotheses have approached the phenomenon from different angles.

The review by Hans Kubler concluded that the spiral grain improves the flow of nutrients and water along the stem and into the crown. Straight-grained trees can only supply water directly above the roots. A Spiral pattern may benefit the trees by covering larger parts of the crown. Kubler also stated that spiral grains provided more flexibility against wind, but deemed this secondary to the increased water and nutrient availability (Kubler 1991). Old Ponderosa pine trees growing in adverse conditions tend to exhibit spiral grain more often than young individuals (Van Pelt 2008).

Another hypothesis poses that the primary function of spiral grain is to make conifers more stable against the wind (Skatter & Kučera 1997). On the northern hemisphere, trees are exposed to prevailing winds, mainly from the west. Furthermore, they tend to have asymmetric crowns facing the south to optimize the interception of sunlight (Skatter & Kučera 1998). Under such conditions, right-oriented spiral grain improves the resistance against stem breakage. Mechanically it can be compared to the increased strength in a rope twisted with the knitted orientation (Skatter & Kučera 1997).

A study of bristlecone pine species reported conflicting results, contradicting both the water supply hypothesis and the wind resistance hypothesis (Skatter & Kučera 1997; Skatter & Kučera 1998). There were next to none correlation between spiral grain and environmental factors (Wing et al. 2014). Additionally, the trees sported predominantly left-oriented spiral

grain. Nevertheless, there were few factors which cast doubt if this study indeed can refute any of the hypothesizes. The studied Bristlecone pine trees lacked asymmetric crowns, a vital component of Skatter and Kučera's hypothesis. Another point was the fact that bristlecone pine rarely suffers broken stems. Right-oriented spiral grain might therefore not represent a benefit for the trees. This discrepancy may suggest that the spiral grain patterns may not necessarily be beneficial for all conifers (Wing et al. 2014).

There were some challenges with generalizing the use of spiral grain as a predictor of age. The spiral grain pattern may be hard to spot on the bark, as the fissures in the bark do not necessarily follow the same pattern due to the expansion and contractions due to heat from the sun (Kubler 1991). Spiral grain also occurs in Norway spruce (Gjerdrum et al. 2002), and it is likely that the same would hold for this species. Unfortunately, experiences from the field found spiral grain on Norway spruce challenging to spot with the naked eye.

The presence of right-oriented grain on Scots pine trees was, however, easier to observe. Scots pine trees with bark-free spots and dead branches were more easily classified. Dead branches, was suggested by (Weisberg & Ko 2012) as a predictor for old age, however, this might be a confounding variable. However, despite all the challenges related to causality, and practical implementations, Scots Pine individuals with a prominent spiral grain were older.

Both mentioned hypotheses, the water supply hypothesis and wind resistance hypothesis serve as plausible explanations for the occurrence of spiral grain. Scots pine trees were more often than Norway spruce situated on dryer localities. Older trees also sported asymmetric crowns (own observation). Under the mentioned conditions, spiral grain may have helped individual trees survive for longer.

Bark phenology: Barking up the right tree

Both bark structure and bark color were influential variables for both species and unsurprisingly intercorrelated as they are inevitably linked. Collectively these variables can be referred to as bark phenology, a term that reflects the interaction between genes and the environment. Bark

structure was the most recurring variable of the bark phenology variables. Bark structure was included in all the field models, advocating for its use.

For Norway spruce the bark structure variable in field models on a stand level were moderately related to age. Bark structure along with crookedness explained 48% of the variance of the five oldest trees on a given plot. The observed strength of the link between age and bark structure on a single tree level appears to be lower in spruce trees. This falls in line with other studies reporting variation in bark morphology such as color brightness in addition to length and size of bark scales have been reported to vary widely between localities (Dinulică et al. 2019) .

The bark of a tree serves multiple purposes, one central function of the outer bark is to protect trees from outside threats from drying out and from infections (Morris & Jansen 2017). In other words, the morphology of the bark cannot be understood without including factors beyond age itself (Dinulică et al. 2019; Laasasenaho et al. 2005; Sonmez et al. 2007). Age is not the only regulating factor. Diameter outside the bark, height, and environmental effects such as aspect and climate zone all affect it one way or the other (Dinulică et al. 2019; Laasasenaho et al. 2005; Sonmez et al. 2007).

Spruce bark roughness is closely related to bark thickness, which in several spruce species is known to increase with age (Dinulică et al. 2019; Laasasenahoet al. 2005;   Sonmezet al. 2007) . However, the value of bark structure to indicate age differs between spruce species. In Sitka spruce, height, volume, and crown complexity caused by wear and tear over the years seem to be better indicators of age (Van Pelt 2007). Nevertheless, from this study, bark structure was by far the best predictor for age in Norway spruce.

Bark structure, however, appears to be a consistent predictor for several pine species, such as Single leaf pinyon pine (Weisberg & Ko 2012) and Ponderosa pine (Van Pelt 2008). Results from Ponderosa pine are also arguably more transferable to Scots pine as both can reach high stature and along with similar bark. In both species, increasing age leads to increasingly large interlocking plates in the bark, which the strength of the correlation with age exceed that of the age-diameter (Van Pelt 2008). On a stand level, the explanatory power of bark structure,

although still included in the model, however shifted towards a relative higher variance explained by bark color.

Bark color appears to be less reliable, with weak correlations, albeit significant correlations reported for Norway spruce (Dinulică et al. 2019). Bark color in Norway spruce varies along elevational gradients, where lowland populations tend to be browner in color. Norway spruce situated in the mountain forest tends to be grayer (Eremin 1977; Tjoelker et al. 2007). These color differences manifested as lower levels of yellow in the bark on the northern side of the trunk with increasing age (Dinulică et al., 2019) . For pine species comparisons, one should be careful with generalizing the bark color. Ponderosa pine bark generally becomes redder with increasing age. In contrast to Ponderosa pine, Scots pine appear to turn grayer with age (Van Pelt 2008).

Crown and branches

The crown morphology differs between young and old trees. Flat, wide and diminished crowns accompanied with few thick drooping branches have been suggested as indicators of old age, especially concerning pine species (Brown et al. 2019; Castagneri et al. 2013; Kaufmann 1996; Van Pelt 2008; Weisberg & Ko 2012). The oldest Scots pine indeed seemed to align with such ideas as they were characterized by thick branches inclining downward. Both variables were included in the single tree models for Scots pine.

The age of the trees increased with branch thickness until an optimum size. This change in morphology has been related to an increase in hydraulic resistance in older trees limiting the water flow in the tree, which in turn reduces the upward expansion of the (Kaufmann 1996). The thickest branches (> 20 cm in diameter) indicated a lower age than trees with branches of 10-20 cm thickness. However, as the largest branch thickness was insignificant, one should be careful to assume any optimum size based on the results in this study.

Other included crown morphology variables, beyond branch thickness and inclining branches were not as easily implemented into any of the age models for Scots pine. Crown shape was not included as the variation explained by crown shape in pine was highly situational. Much of the

variation in crown flatness in Scots pine was explained first and foremost by locality, spike tops and an interaction term between these. Dependencies are hard to include in age models, where the goal is to include variables which can be applied on a general basis.

Spike tops may be caused by stochastic events such as snow break, lightning, and fungi attacks (Aamlid et al. 1991) . The interaction between crown shape and spike top interaction meant that the crowns of Scots pine trees with a spike top were pointed. The increased pointiness arose from the establishment of newly grown tops. When registering in the field, such instances may call for closer inspections to be sure.

The final field models for spruce models did not include any crown variables, despite other studies including it. While crown length also was correlated with age in this study, the relationship was weak and vanished in models. Crown shape, on the other hand, was insignificant for Norway spruce even by itself. It should be noted that the thin, long, and diminished crowns easily can give the impression that a tree is old, but unfortunately, these are also traits commonly found in alpine Norway spruce (Tjoelker et al. 2007). Rötheli et al. (2012) in their study only sampled spruce trees on an elevation of 1200 meters and higher. In contrast, the sampled elevations in this study spanned from 149-1034 meters above sea level. More research is arguably needed to ensure general crown morphology traits that indicate old Norway spruce.

Site models: fantastic trees and where to find them
Spatial distribution patterns explain the age in old trees.

Different productivity measures, that covered a broad spectrum of spatial scales, were all tested but only partly explained the oldest trees' ages: elevation which governs temperatures, topographic position on the stand level, a composite of aspect, and local topography (for the scale see table 2). Site index measuring tree productivity on a stand level and vegetation types were recorded around the sample trees to quantify within plot differences in productivity.

The inclusion of vegetation type did, however, not reveal any within-site differences. The addition of vegetation types provided a productivity measure that could examine the principle of longevity under diversity. Longevity under diversity states that individual trees often grow older on harsh microsites (Schulman 1954). Two of the included vegetation types, "Lichen forest" (in Norwegian *Lavskog*) and "Cowberry-bilberry forest" (in Norwegian *Bærlyngskog*), were deemed a possible measure for harsh microsites as both indicate thin and dry soils (Larsson 2000). Nevertheless, the differences from vegetation types were negligible, and instead reflected the general preference of pine on drier localities versus spruce on more mesic localities.

None of the resulting site models were strong, but site index was the productivity variable that explained the most variance for Norway spruce (Figure 8 C) and Scots pine. The good thing about site index is that in Norway, it is, at least in a rudimentary form, readily available from forest resource maps. Site index is, however, not a perfect tool.

Significant errors can occur as the age of old trees far exceed the intended use of site indexes. The site index is defined by the dominating tree species, which limits the possibility of making accurate estimations for other species on the locality. Prediction models for site index can, on the other hand, account for some of these challenges (Sharma et al. 2012). Regardless, if forest resource maps are available with site indexes, arguably, it may serve useful as decision support for the registration of old trees. Brown et al. (2019) demonstrated that site index, to some extent, could separate the older Ponderosa pine trees from the youngest in instances where the morphological traits were ambiguous in terms of age.

The explanatory strength of the spatial variables varies on a species basis. A study of the spatial distribution of the oldest trees in China found a moderately strong positive correlation between longevity in trees and elevation across species (Liu et al. 2019). The age of the broadleaved European beech (*Fagus Sylvatia*) in the Alps and Apennines seems to be strongly related to both elevations and with a preference for calcareous soils (Di Filippo et al. 2012). Longevity in mountain pine in Swiss alps, however, also found other topographical variables such as aspect and slope significant (Bigler 2016). For Ponderosa pine in the Rocky Mountains, site index and

elevation were weak predictors alone but were useful in differentiating between young to moderately old trees (Brown et al. 2019). Common for all the tree longevity models with spatial variables seems to be the inclusion of variables that employ the negative age-growth relation.

Earlier studies have only reported a weak correlation with elevation as the only significant site variable of the age of old Norway spruce (Castagneri et al. 2013; Rötheli et al. 2012), however, for forest planning site index may be superior. None of the aforementioned studies included site index. Nevertheless, as illustrated in figure 8, the site index was inversely related to increasing elevation, meaning that these variables are intercorrelated. Given that the site index explained the most variance in age of the two intercorrelated variables, a choice was made to include site index instead of elevation. Sætersdal et al. 2016a also reported a similar relation between site index and elevation when examining the spatial distribution of CHI habitats and attributed this to the effect of the decreasing temperatures on productivity.

Slope was the other variable also included in site models, but with differing effects between the tree species. Old-tree habitats have earlier been reported to be overrepresented on slopes, although differing between municipalities (Sætersdal et al. 2016a). This study backed the relevance of slope on age, but sampling old trees directly on a species level revealed a species-specific response. The longevity of the oldest pine trees increased with steeper slopes, while the spruces were in contrast negatively impacted. These differences may be due to different root systems.

Landscape-level anthropogenic effects were difficult to trace in this study. None of the site variables intended to quantify this seemed to have impacted the longevity of the trees. Arguably, the accessibility of the forest stand can be an indirect measure. Elevation, in addition to its environmental impact, along with the weak, but significant correlations with slope, can also possibly reflect low profitability in terms of forest harvest (Bollandsås et al. 2004). Nevertheless, to which degree previous harvesting have impacted the age of old trees today remains unknown. One might speculate that the lack of pristine forests in Norway have eroded the chances of a baseline comparison without human influence.
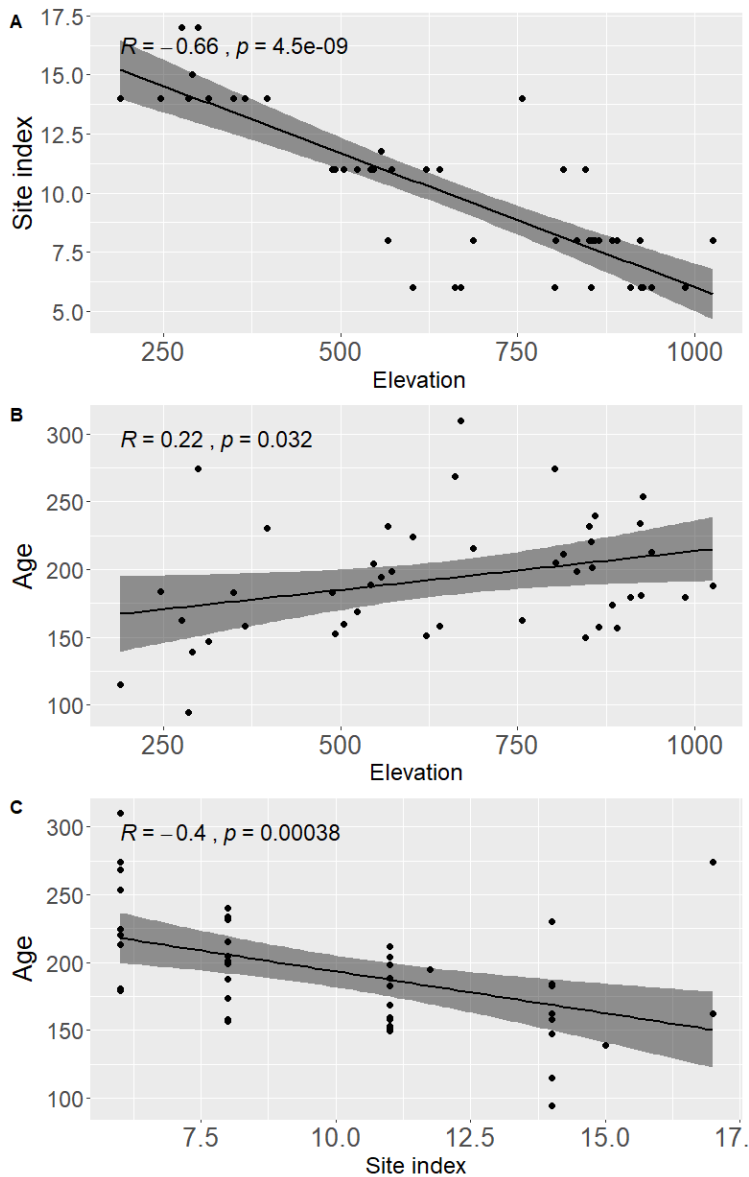
Figure 8: Kendall rank correlation displayed for the mean of the oldest spruce trees on a given plot. Plot A shows the multicollinearity with between site index and elevation, B shows the age plotted against the elevation and C the correlation between age and site index. The dark grey area around the estimated line is the 95% confidence intervals

Potential sources of error

The main sources of error were related to the core samples, the lack of cross dating and heart rot. Cross dating would have improved the age estimates, however, there were no available chronology for the purpose to cross date. Another challenge during the study was the occurrence of heart rot in spruce. The rot posed a dilemma regarding the research. On one end, avoiding trees with rot would increase the certainty from the core sample. Then again, avoiding such trees would introduce bias in the selection of sample trees and end up with questionable validity. Arguably some more variance is preferred compared to bias.

Future research

The list of examined variables in this study was not exhaustive. Future research should focus on other morphological traits not covered in this study. One such variable is the lack of visible branches on the lower stem, included in other studies (Brown et al. 2019). Furthermore, the strongest variables in the age models should be tested further if they truly represent general age patterns in old Norway spruce and Scots pine trees. To improve the confidence in variables such as bark structure may call for more quantitatively testing. An example of this is the size of the bark scales along with the distance of the fissures in Scots pine bark, which have given good results on ponderosa pine (Van Pelt 2008).

Future application of the models

Based on the age models I propose the use of a scoring system in the field where the trees can be rated based on their features, similar to what Robert Van Pelt has constructed for old trees in Washington (Van Pelt 2008). Not only does this simplify the registration, but if recorded for each Old-tree habitat it may aid the selection process of which Old-tree habitats should be anointed the status of Woodland Key habitats . Quantifying the forest planners confidence in the presence of Old-trees may also serve useful when planning the size of future reserves.

Conclusion

This study has looked at the old trees at different levels from the tree level to a landscape scale, inspired by the political goal of obtaining more information regarding the oldest forest. A few main patterns occurred in the results. The current practice of the old tree habitats has on average preserved older trees than those present in neighboring mature stands, and most of the investigated Old-tree sites fulfilled the intention of preserve trees older than 150 (Norway spruce) and 200 (Scots pine) years.

Regarding prediction of age for Norway Spruce and Scots Pine it was easier to determine the age of pine than spruce without an increment corer on a single tree level. However, on a stand-level, it was possible to acquire more insight for spruce.

Based on the results in this study, visual inspection should emphasize morphological characteristics beyond that of size. Scots pine can be visually aged based on crown morphology, spiral grain, crookedness, and how large their diameter is compared to their to their height. Old spruce should preferably be registered on a stand level. Areas dominated by spruce trees with thick bark may host old individuals. An important conclusion of the study is the realization that one should rely on multiple traits in terms of determining the age.

Site variables may hold some use, but should not be the sole reason for delimition of Old-tree habitas. Site variables, such as site index and slope were generally weak, but may prove useful as extra decision support in times of uncertainty. Nevertheless, there are considerations to make beyond age itself. Species richness has been shown to increase with an increase in site productivity (Gjerde et al. 2005). Furthermore, if old trees situated on high productive areas indeed are rare, in terms of complementarity delimitation of such areas may be a goal.

Appendix A

Complete list of the mean age of the oldest trees divided into pairs. The locality numbers stem from the random sampling process of old tree habitats

Municipality	Locality	Old tree habitat	Reference
Aurskog-Høland	2	277.4	114.0
Aurskog-Høland	9	226.3	97.1
Aurskog-Høland	12	294.5	224.1
Aurskog-Høland	39	222.3	263.2
Aurskog-Høland	53	182.8	147.1
Aurskog-Høland	60	199.3	169.0
Aurskog-Høland	62	157.8	110.7
Aurskog-Høland	75	177.9	136.1
Aurskog-Høland	88	162.6	69.5
Aurskog-Høland	99	203.4	112.4
Nore og Uvdal	2	190.7	270.7
Nore og Uvdal	32	250.0	143.4
Nore og Uvdal	36	233.9	239.9
Nore og Uvdal	38	268.7	250.4
Nore og Uvdal	41	188.0	179.6
Nore og Uvdal	49	211.6	173.7
Nore og Uvdal	78	189.8	157.0
Nore og Uvdal	93	314.2	198.3
Sauherad	4	280.7	340.0

Sauherad	8	230.5	179.9
Sauherad	9	304.6	199.6
Sauherad	11	221.3	168.8
Sauherad	12	231.6	222.6
Sauherad	20	280.5	252.2
Sauherad	23	363.4	246.1
Sauherad	25	169.0	182.8
Sauherad	26	169.0	142.6
Sauherad	27	186.4	239.2
Sør-Aurdal	4	284.9	212.9
Sør-Aurdal	5	286.2	195.4
Sør-Aurdal	15	288.6	162.6
Sør-Aurdal	16	204.9	198.8
Sør-Aurdal	18	156.7	180.7
Sør-Aurdal	21	179.5	149.5
Sør-Aurdal	31	214.0	157.7
Sør-Aurdal	34	300.4	223.2
Sør-Aurdal	46	226.9	204.7
Sør-Aurdal	48	218.3	188.7

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