



Ancient Silver Sentinels

Kelo Tree Dynamics in a Boreal Old-Growth
Forest in Northern Sweden

Stijn Qualm

Degree project • 60 credits

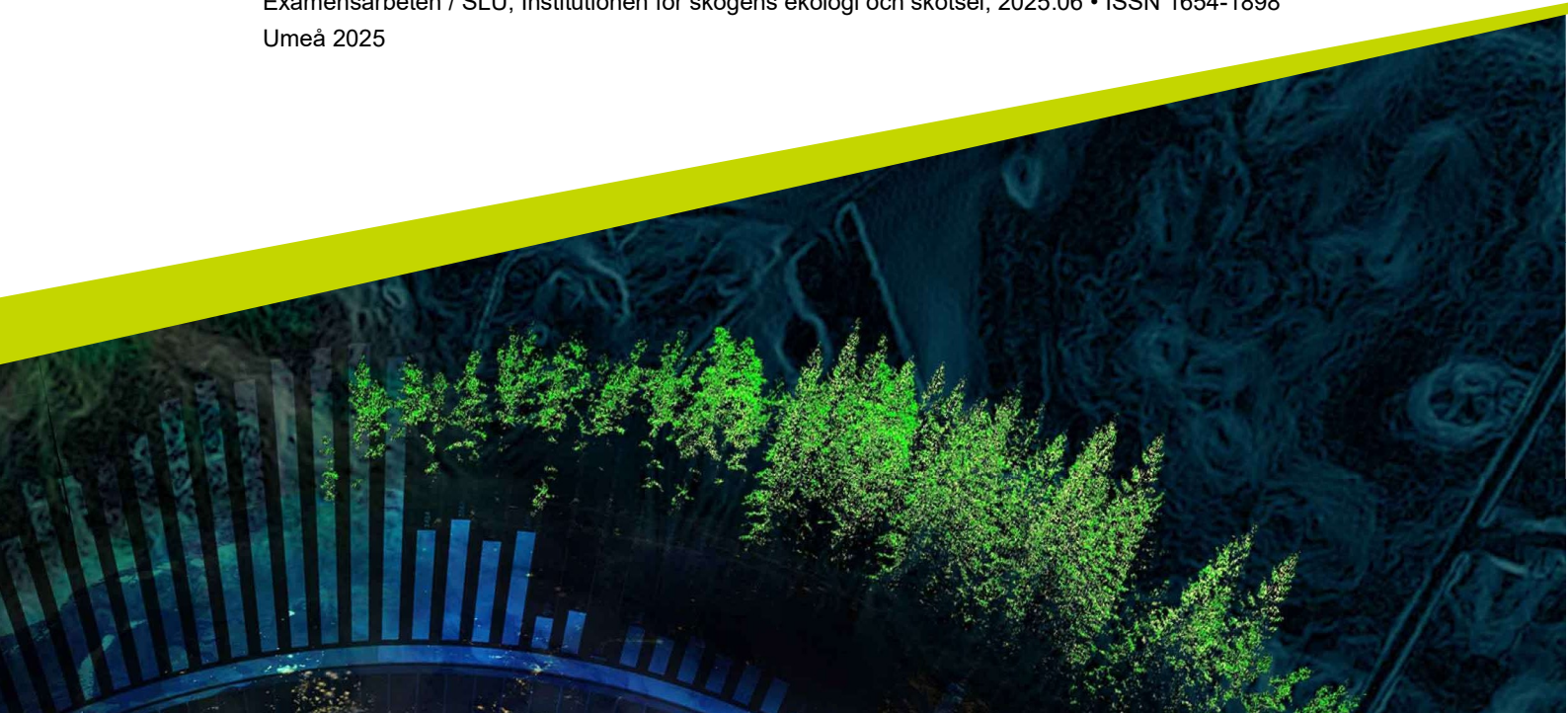
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Abstract

Deadwood is a key structural and ecological component in boreal forest ecosystems. One particularly distinctive type in northern Fennoscandia is dead standing Scots pines (*Pinus sylvestris* L.), known as kelo trees. Kelo trees play a crucial ecological role by offering habitat for specialized species and are primarily found in areas with minimal human disturbance. While previous studies have focused on Finnish boreal forests, little is known about kelo tree dynamics in other boreal ecosystem systems. Using dendrochronological field data, I assessed the age, year of death, and spatial distribution of 110 kelo trees in an old-growth forest within Tjeggelvas nature reserve (TNR) in northern Sweden. I found that they typically were clustered, died at an advanced age, and have remained standing for decades after death, however, some individuals died younger and showed no signs of reduced growth preceding death. Kelo tree recruitment in the study area did not follow previously assumed patterns in terms of recruitment rate and disturbance history, particularly due to the absence of fire. My findings suggest that kelo tree recruitment is influenced by a combination of long-term ecological processes and episodic stress events, and that the drivers and processes behind kelo tree recruitment vary between parts of Finland and this area in Sweden. However, these processes remain not yet fully understood, highlighting the need for further research. With climate change expected to increase small-scale disturbances, future kelo trees may emerge at younger ages and smaller sizes. Their ecological importance, slow recruitment rate, and low numbers in managed forests compared to the past show their high conservation value within natural Fennoscandian forests. Understanding the drivers of kelo tree formation under different disturbance regimes will be essential for informing conservation strategies in boreal forests facing climate-driven change.

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1. Introduction

Deadwood is a key structural and ecological component in boreal forest ecosystems (Löfroth et al., 2023; Vanha-Majamaa et al., 2007). The process of tree death can be complex, during which the tree's physiological state may weaken gradually over a period of up to several decades before the final death (Cailleret et al., 2017; Lännenpää et al., 2008). The process depends on factors such as tree species, age, size, competition, and site conditions (Aakala, 2010). Disturbances such as fires, storms, droughts, and insect outbreaks can contribute to tree death either directly or by weakening trees, making them more susceptible to subsequent disturbances and ultimately death (Aakala, 2010; Cailleret et al., 2017).

After death, the whole tree is considered to be Coarse Woody Debris (CWD) (House et al., 1987). Understanding the forms and functions of CWD, including its decomposition stages and structural roles, is crucial for evaluating ecosystem processes (House et al., 1987; Zhou et al., 2007). CWD is an important component of a forest, occurring in all decay and diameter classes within protected Fennoscandian boreal forests, particularly in the old-growth forests of northern Sweden and northwestern Russia (Siitonen, 2001). In such boreal forests it can comprise up to 50% of the total timber volume (Josefsson, 2009). However, within managed forests, the occurrence of CWD is much lower due to intensive forest management (Linder and Östlund, 1998; Similä et al., 2003), and has been removed often for fear of detrimental effects on forest stands, such as fires (Löfroth et al., 2023), insects, diseases (Josefsson et al., 2010) and harvested for firewood (Niemelä et al., 2002; Östlund et al., 2018).

There are several types of CWD, such as snags, lying deadwood, stumps, and standing dead trees (House et al., 1987), which all play a vital role in the forest structure (Aakala et al., 2007). Among the various forms of standing deadwood, one particularly distinctive type in northern Fennoscandia is dead standing Scots pines (*Pinus sylvestris* L.), known as kelo trees (Niemelä et al., 2002). Kelo trees are pines that have gone through self-preservation during their death process, and can be up to 500 years old at point of death (Kuuluvainen et al., 2017; Niemelä et al., 2002). They are decorticated, have dried-out wood, and have a distinct silvery colour. That, together with the loss of its foliage and fine branches over decades, leave it with a remarkable appearance (Figure 1).



Figure 1, A kelo tree with a visible Sámi bark peeling scar. Photo by the author.

Kelo trees can primarily be found in areas that experienced little to no human disturbances such as national parks, nature reserves and remnant old-growth forest patches (Niemelä et al., 2002). Kelo trees can often be found in clusters on flat ground, where they can comprise over half of the total number of dead standing pines (Kuuluvainen et al., 2017). However, in managed forests kelo trees have become very rare (Niemelä et al., 2002; Similä et al., 2003).

The forest conditions required for kelo tree development, such as forest fires and development into very old trees, are rare in managed forests (Niemelä et al., 2002). Current forestry methods do not allow for easy recruitment of kelo trees because the rotation period of stands is too short and the kelo tree recruitment process is very slow (Kuuluvainen et al., 2017; Niemelä et al., 2002), sometimes as slow as one new kelo tree per hectare per decade (Rouvainen et al., 2002).

A kelo tree's death process is unusually long and can take several decades (Niemelä et al., 2002), something that has not been observed in other tree species (Cailleret et al., 2017; Kuuluvainen et al., 2017). The processes of what causes a Scots pine to transform into a kelo tree instead of a regular dead standing Scots pine are not well understood (Kuuluvainen et al., 2017). However, it has been found that most kelo trees have experienced at least one forest fire (Niemelä et al., 2002) or other stressors and disturbances (Cailleret et al., 2017).

Another unique characteristic of kelo trees is their slow decomposition, which is thought to be the result of resin accumulation in the wood, drying of the wood, and a high ratio of heartwood to sapwood (Kuuluvainen et al., 2017; Niemelä et al., 2002). Furthermore, after the death of a Scots pine, blue-stain fungi inhibit the sapwood, making the wood unattractive to other decomposing fungi, which allows it to stand for up to 500 years more after death (Niemelä et al., 2002).

Traditionally, forest data has been collected through National Forest Inventories (NFIs), which also include information on deadwood (Fridman et al., 2014; Mcroberts et al., 2010). In Sweden, the NFI records deadwood across various stages of decomposition (Roberge et al., 2024), but it does not specifically identify kelo trees. Because of this limitation, there is need for more detailed, scalable methods to assess deadwood, especially rare forms like kelo trees. More precise mapping of kelo trees may improve our understanding of forest dynamics and the habitat availability they provide for associated species. Since the emergence of new techniques such as Unmanned Aerial Vehicles (UAVs), it has become more accessible to gather accurate forest data on large scales (Bater et al., 2009; Briechle et al., 2020). Using UAVs, forest properties such as forest structure and the amount of CWD can be remotely sensed (Gallardo-Salazar and Pompa-García, 2020; Heinaro et al., 2023). To my knowledge, these techniques have not been used in kelo tree studies.

Kelo trees play a crucial ecological role by offering habitat for specialized species (e.g. Larsson Ekström et al., 2023; Santaniello et al., 2017; Similä et al., 2003), and enhance biodiversity in pine-dominated forests (Ehnström, 2001; Niemelä et al., 2002). When kelo trees eventually fall over, they provide habitat to specialised fungi (Niemelä et al., 2002). Despite their ecological importance, comprehensive studies on the natural properties, dynamics, and spatial structure of kelo trees are limited, especially on larger scales in Fennoscandia (Kuuluvainen et al., 2017; Rouvinen et al., 2002).

This gap is notable given how unique kelo trees are, their significance within the ecosystem, and their decline in areas affected by modern forestry. While previous studies have focused on Finnish boreal forests, little is known about kelo tree dynamics in other boreal ecosystem systems. It is therefore important to contrast the few available studies on kelo trees with new research in other natural forests, with different disturbance histories and ecological settings, where numbers, temporal patterns, and spatial distribution in the landscape can be analysed.

In this study, I aim to provide insight into the age, year of death, and spatial distribution of kelo trees in an old-growth forest within Tjeggelvas nature reserve (TNR) in northern Sweden, which has experienced minimal anthropogenic influences. Here, I recorded and cored kelo trees in field plots. In addition, I employed an Unmanned Aerial Vehicle (UAV) to gather aerial imagery to

remotely sense the distribution of kelo trees within a larger study area, which was ground-truthed using the plot inventories.

In my study I want to answer the following questions:

1. How are kelo trees distributed in the forest landscape in relation to environmental factors such as topography, soil moisture, and the basal area of surrounding trees?
2. What are the life and death characteristics of kelo trees?
3. Can the number of kelo trees in a landscape be estimated by a combination of UAV photography and detailed plot inventory?

2. Methods

2.1 Study area

My study area is located east of lake Plähkkájävrr, within TNR (66°36'35.1"N 17°48'35.1"E; 300 km², Figure 2). TNR lies in Sweden's northern boreal zone and serves as a minimally impacted reference for natural forests in northern Fennoscandia (Josefsson, 2009; Östlund and Norstedt, 2021). It is dominated by a semi-open late-successional coniferous forest on dry, nutrient-poor soils. It primarily contains Scots pine (*Pinus sylvestris* L.), downy birch (*Betula pubescens* Ehrh.) and Norway spruce (*Picea abies* Karst.) (Josefsson, 2009). While TNR contains Norway spruce, I observed that these were not present within my study area during field work. Furthermore, I observed that the dominant tree species in my study area is Scots pine. In TNR Scots pine been found to commonly exceed 300 years of age, and the amount of dead wood is very high (Josefsson, 2009). The ground vegetation mainly consists of dwarf shrubs (*Vaccinium* spp. L., *Empetrum* spp. L), lichen and mosses such as reindeer lichen (*Cladonia rangiferina* L.) and red-stemmed feathermoss (*Pleurozium schreberi* Brid.).

Lake Tjeggelvas at ~450 m.a.s.l is in the centre of TNR, with the majority of the pristine forest at its northern shores. From its eastern shores, there is a gentle incline towards the east, where my study area is at ~510-560 m.a.s.l. The landscape includes mires, streams, and granite boulder fields that increase in density east and northwards from Lake Plähkkájävrr. The study area is located within Sápmi, which is the traditional territory of the indigenous Sámi people of northern Fennoscandia, who have inhabited the area shortly after the last ice age (Josefsson, 2009). A Sámi settlement that was used from the 17th century until the 20th century (Josefsson, 2009) is located approximately 1.5 km northwest of the study area, on the western shore of Lake Bläckkajaure. Sámi cultural remains in the form of bark peelings and hearths can be found throughout. Presently, the area is used as winter browsing grounds by reindeer herders from the Luokta-Mavas Sámi community.



Figure 2, The location of the study area in northern Sweden.

2.2 Study design and data collection

I selected a 700 m x 700 m (49ha) area where the forest was least disturbed by human activity according to Josefsson et al. (2010). The study design consisted of two components: the sampling of kelo trees and the collection of aerial imagery using a UAV.

Within the study area, I set up twelve 50 m x 50 m (0.25 ha) subplots that were spaced 150 m from each other, spread out over a 650 m x 450 m area. In each 0.25 ha subplot, I inventoried and cored every kelo tree that stands over 1.3 m tall and diameter greater than 10 cm at diameter at breast height (DBH) with a 5.15 mm increment borer. For each kelo tree I recorded its location with a GPS, DBH (in cm), height (in m), the remaining bark percentage, the presence of charred wood, fire scars, and decay class according to Aakala et al., (2007), and finally the trunk's silvery colour, following methods as described by Kuuluvainen et al. (2017). Furthermore, I determined the soil moisture class based on descriptions of Ågren et al. (2021) and whether the kelo tree was located on flat ground, a slope, or on a hilltop. Finally, to assess forest structure I used a relascope to measure the basal area of all living and dead pine and birch trees at the centre of each 0.25 ha subplot to determine its approximate forest density.

2.3 Dendrochronological analysis

After the cores were dry, they were glued to a wooden core mount and sanded with up to 1000 grit sandpaper. Then the cores were scanned at 3200-6400 dpi using an Epson Perfection V850 Pro scanner. Within the scanning software a sharpness filter and contrast correction were also used to improve the visibility of the rings. I then used CooRecorder 9.8.4 (Larsson and Larsson, 2024) to measure ring width and crossdate the samples with the regional master chronology using TTest values in CDendro 9.8.4 (Larsson and Larsson, 2024). The produced TTest values were not always perfect matches, therefore, I used pointer years from the area (Josefsson, 2009) to validate and determine the exact year of death. For my analyses I only used cores that matched the pointer years, resulting in 73 successfully dated kelo tree cores. To correct tree ages at breast height, I added 46 years based on local growth data for Scots pine in TNR (Lars Östlund, pers. comm.).

2.4 UAV image analysis

I captured RGB aerial imagery of the 49-hectare study area using a DJI Mavic 3 Multispectral drone, flying at an altitude of 80 metres with 80% front and side overlap. My initial objective was to apply machine learning techniques for the automatic detection of dead trees. However, upon examining the imagery, I

noticed that dead trees and boulders exhibited similar spectral properties, making it difficult to reliably distinguish between them based on spectral data alone.

To overcome this, I incorporated elevation data to supplement the classification process. I generated a high-resolution orthorectified image in combination with a digital elevation model (DEM) using PIX4Dmapper (“Pix4D S.A.,” 2023), which would potentially allow for the differentiation of dead trees and boulders based on elevation differences. From the DEM and collected UAV imagery, I generated a point cloud. However, the resulting point cloud lacked the resolution, density, and structural detail necessary to accurately represent tree structures, rendering the DEM unsuitable for my purpose.

Because of these limitations, I opted for a manual identification approach. Here I visually identified and counted standing dead trees from the orthorectified imagery using QGIS (QGIS Development Team, 2024). For ground-truthing, I used the 110 field-recorded kelo trees collected from the twelve 0.25-hectare subplots within the study area. These known kelo tree locations served as reference points for detection accuracy to evaluate and estimate the ratio of regular dead standing trees to kelo trees.

2.5 Statistical analysis

I used R (R Core Team, 2025) and RStudio (Posit team, 2024) for all statistical analyses and visualizations, and used the tidyverse suite (Wickham et al., 2019) for data manipulation, the creation of histograms, and scatterplots. I applied Kendall’s τ to assess monotonic associations between ordinal and continuous variables (decay class versus years after death). I chose Kendall’s τ due to non-normality in the year after death data and because the variable of decay class was ordinal.

Furthermore, I used Fisher’s exact tests to assess associations between the categorical variables of terrain type and soil moisture class. Three entries for soil moisture class and one entry for terrain type lacked data due to values not being recorded during fieldwork. These were retained as missing (N/A) to preserve data integrity.

Finally, I employed simple linear regressions to explore relationships between continuous variables (subplot basal area versus number of kelo trees). For these models, R^2 and p-values are reported. All hypothesis tests were two-tailed with a significance threshold of $\alpha = 0.05$.

3. Results

3.1 Kelo tree distribution and environmental factors

Across the 12 subplots, I recorded a total of 110 kelo trees, ranging from 5 to 13 kelo trees per subplot, with a mean of 9.2 (SD = 2.8). Out of the twelve subplots, seven had a geography that was predominantly sloped, while five were flat. Individually, kelo trees were most commonly found on slopes (64.5 %), followed by flat ground (20.0 %) and hilltops (14.5 %), missing data (n = 1) was excluded. They were also most frequently associated with mesic soils (60.9 %), followed by dry soils (35.5 %) and mesic-moist soils (0.9 %), missing data (n = 3) were excluded. A Fisher's exact test on kelo tree counts across slope and soil moisture combinations showed a statistically significant association ($p = 0.00088$), indicating that kelo trees were not randomly distributed across environmental conditions. Most kelo trees were found on sloped, mesic sites (43), while mesic-moist soil types across all terrain types contained least kelo trees (≤ 1) (Table 1).

Table 1, The number of kelo trees observed across combinations of terrain types and soil moisture classes. Missing data (n = 4) were excluded.

	Flat	Hilltop	Slope
Dry	8	6	25
Mesic	14	9	43
Mesic-moist	0	0	1

The overall mean basal area across the twelve subplots was $13.8 \text{ m}^2 \text{ ha}^{-1}$ (SD = 3.8), comprising $11.5 \text{ m}^2 \text{ ha}^{-1}$ of living trees and $2.3 \text{ m}^2 \text{ ha}^{-1}$ of dead trees. Of this, $13.6 \text{ m}^2 \text{ ha}^{-1}$ was Scots pine (98.7 %) and $0.2 \text{ m}^2 \text{ ha}^{-1}$ downy birch (1.3 %).

In addition, I found that the distribution of kelo trees within the study area varied, with most kelo trees recorded in the west of the study area, where the boulder fields were less dense. There was no apparent pattern in the age distribution within plots (Figure 5).

A simple linear regression showed a moderate positive relationship between subplot basal area and the number of kelo trees ($R^2 = 0.405$, $p = 0.026$) (Figure 3). In addition, I found only one kelo tree with a fire scar and five kelo trees with Sámi bark peelings.

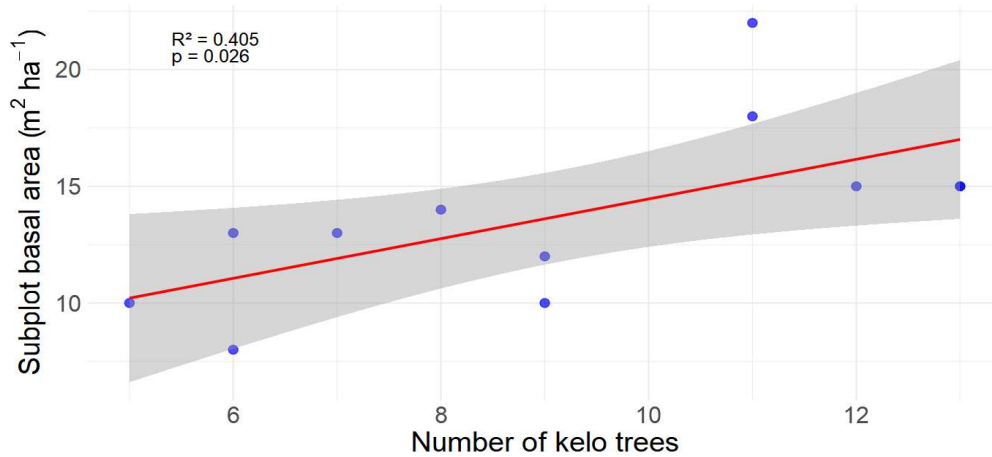


Figure 3, Relationship between subplot basal area ($\text{m}^2 \text{ha}^{-1}$) and number of kelo trees ($n = 12$ subplots). Each point represents a 0.25 ha subplot. The overall mean basal area is $13.8 \text{ m}^2 \text{ha}^{-1}$ ($SD = 3.8$), with an average of 9.2 kelo trees per subplot ($SD = 2.8$). $R^2 = 0.405$ and $p = 0.026$.

I found a DBH range between 12.3 cm and 44 cm with a mean DBH of 26.32 cm ($SD = 6.7$). The most common DBH of kelo trees was between 20-30 cm. The height of kelo trees was between 2.5 and 13.7 m. The most common height was between eight and ten metres tall, with a mean of 8.87 m ($SD = 2.4$). I found that most recorded kelo trees had a decay class of 6 (46.4 %) (Table 2). In addition, 40 % of the kelo trees had no bark remaining (Table 3). Furthermore, weathering had not yet deteriorated the sapwood of recorded kelo trees.

Table 2: Percentage of kelo trees per decay class.

Decay class	% of kelo trees
4	2.7%
5	39.1%
6	46.4%
7	10.0%
8	1.8%

Table 3: The amount of bark remaining on kelo trees.

Bark % remaining	% of kelo trees
0	40.0%
20	21.8%
40	13.6%
60	10.9%
80	13.6%
100	0%

3.2 Age of kelo trees

Of the 110 recorded kelo trees, I was able to core 96 trees, the rest had too much wood rot inside to be cored properly. I found an age range between 124 and 623 years with a mean age of 333.71 and a median of 322 years ($SD = 118.0$). The most common kelo tree age was between 300 - 325 years old (Figure 4).

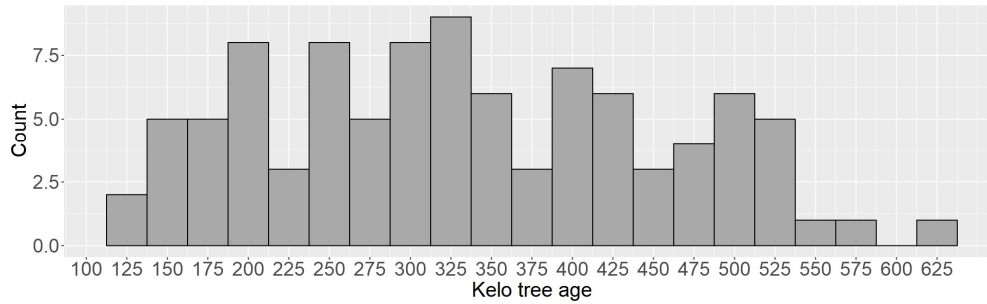


Figure 4, Age distribution of 96 cored kelo trees. Ages range from 124 to 623 years, with a mean of 333.7 years ($SD = 118.0$) and a modal class of 300–325 years. Ages corrected by adding 46 years to account for caving at breast height.

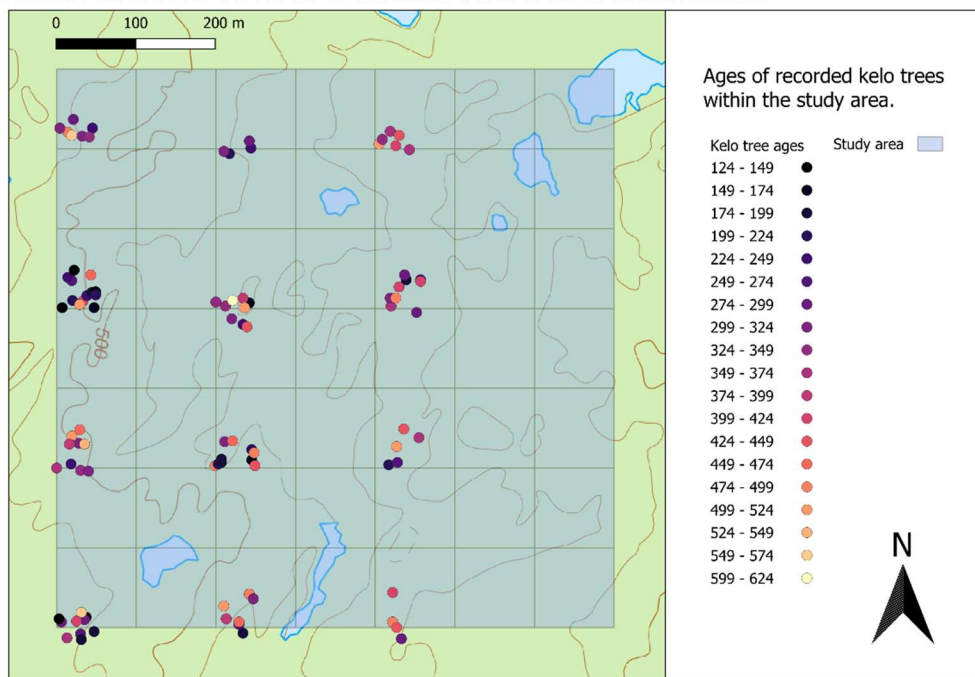


Figure 5, Map of spatial distribution of 110 kelo trees within the study area, color-coded by estimated age (124–623 years). Clustering is observed in the west where boulder fields are less dense. GPS error margins prevented exact subplot placement.

Of the 96 cored kelo trees I was able to dendrochronologically date 73 cores. Here I found that the earliest kelo tree death occurred in 1719 and the latest in 2020, with 64.4 % of deaths occurring after 1950 (Figure 6). In addition, I found that the range of which a kelo tree have remained standing after death was between 4 and 305 years, with a mean of 80.6 years ($SD = 79.8$). A Kendall's rank correlation test showed a significant positive association between years after death and decay class ($\tau = 0.53$, $z = 5.65$, $p < 0.001$), indicating that trees which had remained standing longer tended to be in more advanced decay stages.

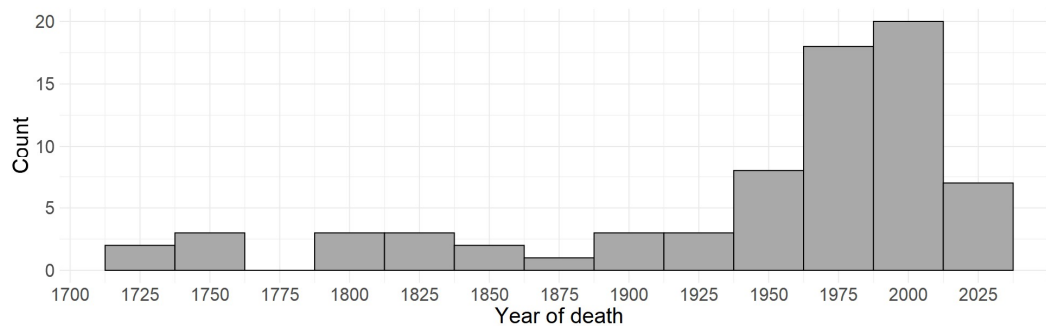


Figure 6, Temporal distribution of kelo tree deaths ($n = 73$) derived from dendrochronological dating, shown in 25-year intervals from 1719 to 2020. A majority (64.4%) of deaths occurred after 1950.

Kelo trees that died in the 18th and halfway into the 19th centuries were between 300 and 450 years old. In the latter half of the 19th century, the age range became larger. In the 20th and 21st centuries, the age at death ranged from 124 to 623 years. A simple linear regression revealed no statistically significant trend between year of death and age at death ($R^2 = 0.016$, $p = 0.285$) (Figure 7).

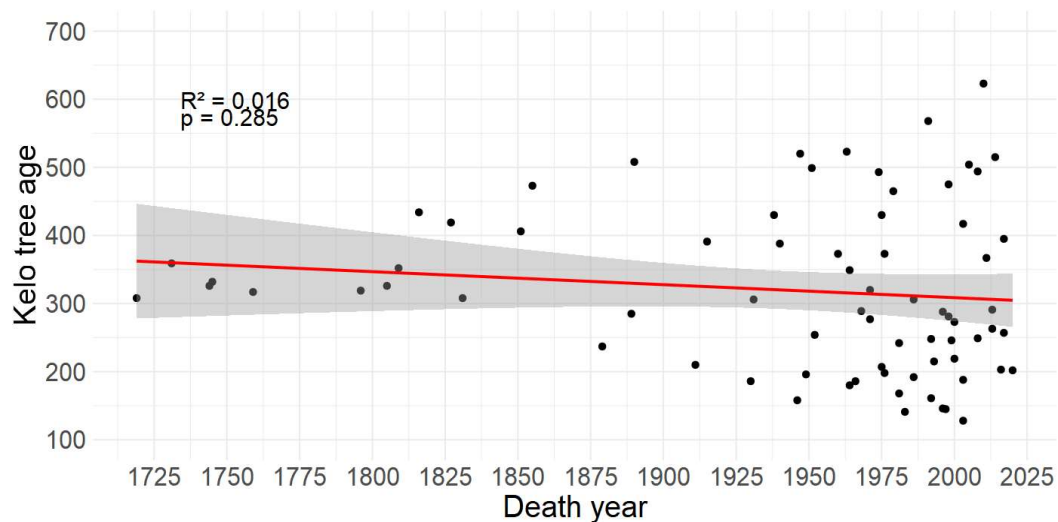


Figure 7, Scatter plot showing kelo tree age at year of death ($n = 73$). Trees dying in the 18th–19th centuries were 300–450 years old, whereas more recent deaths show a broader age range (124–623 years). $R^2 = 0.016$, $p = 0.285$.

I found distinct germination pulses throughout time: 1350-1375, 1425-1475, 1525-1550, 1750- 1800, and 1825-1850. The earliest germinating and oldest kelo tree started growing in 1372 and died in 2010. The youngest kelo tree germinated in 1875 and died in 2003. The most common germination years were between 1750 and 1800 (Figure 8).

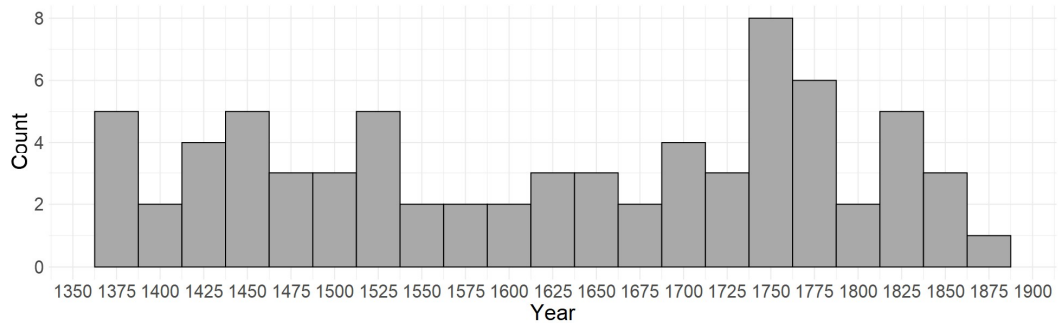


Figure 8, Germination year distribution of kelo trees ($n = 73$), estimated by subtracting age at death from death year. Pulses occurred around 1350–1375, 1425–1475, 1525–1550, 1750–1800, and 1825–1850, with a peak between 1750–1800.

3.3 Predicting kelo trees in the landscape

A total of 1,108 standing dead trees were identified within the 49-hectare study area, averaging 22.6 ha^{-1} , with no apparent clustering observed based on visual inspection. Using this method, I correctly identified 75 % of the 110 kelo trees that have been recorded in the subplots. Within the subplots, the minimum identification accuracy was 57 % and the maximum 91 %. On average, I was unable to identify 3 kelo trees per subplot.

4. Discussion

4.1 Kelo tree distribution and environmental factors

In this study most kelo trees were recorded on slopes (64.5 %), followed by flat ground (20.0 %). This is in line with findings by Niemelä et al. (2002) but contrasts with Kuuluvainen et al. (2017) and Rouvinen et al. (2002), who reported the reverse. Additionally, most kelo trees in my study grew on mesic sites (60.9 %), which is consistent with earlier findings (Niemelä et al., 2002; Rouvinen et al., 2002). On the other hand, kelo trees disfavoured wetter soils across all terrain types. The significant association between terrain type and soil moisture in relation to kelo tree distribution suggests that within this particular boreal ecosystem, kelo trees are more likely to occur in specific combinations of environmental conditions, in particular sloped mesic terrain, rather than being driven by terrain type or soil moisture alone.

Kelo trees recorded in my study area showed a clustered spatial pattern, which is consistent with previous findings (Kuuluvainen et al., 2017; Rouvinen et al., 2002) (Figure 5). However, I observed no apparent clustering in the distribution of dead standing trees identified through visual interpretation of UAV imagery. This discrepancy is likely explained by limitations in the remote sensing method I used. While I did not model all environmental drivers, I assessed site-level factors such as topography and soil moisture, which are known to influence Scots pine establishment (Aakala et al., 2023; Krakau et al., 2013). These factors may help explain the clustering pattern observed in the field.

Kelo tree density was higher in subplots with greater basal area, suggesting that forest structure may influence kelo tree distribution in this old-growth boreal forest. In my study area, I observed that the subplot basal area decreased there where boulder fields became notably denser (Figure 3). This is likely because higher boulder field density limits rooting availability and thus inhibits the establishment of new trees.

Both the mean basal area ($13.8 \text{ m}^2 \text{ ha}^{-1}$) and the number of kelo trees per hectare (36.7 ha^{-1}) were slightly higher compared to other studies (Kuuluvainen et al., 2017). High concentrations of kelo trees ($>20 \text{ kelo trees ha}^{-1}$) were already rare in the 1960s (Kalliola, 1966), and still are in the Fennoscandian forests (Niemelä et al., 2002; Similä et al., 2003). This clearly shows how unique the forest in TNR is today, since most kelo trees have disappeared in other areas that were subjected to low-intense forest use in the past, or more high-intense present day forestry. While normal dead standing Scots pine were not recorded in this study, I observed that the vast majority of the dead standing trees were also kelo trees, which is a higher proportion compared to other studies (Kuuluvainen et al., 2017).

Scots pine can host fungal infections that alter the heartwood's phenolic chemistry, a chemical compound that inhibits decay and is especially different in kelo trees (Venugopal et al., 2016). This chemical change has also been found to occur after forest fires. Over time, repeated infections may increase phenolic compound concentrations, making trees more resistant to decomposition and more likely to transform into kelo trees (Venugopal, 2016). Scots pine, comprising 98.7% of the overall mean basal area, was the dominant species in my study area. This suggests that in pine-dominated forests, fungal infections that alter phenolic chemistry could be more widespread, especially among older or weakened trees.

Altogether, my findings show that kelo tree distribution follows several broader patterns observed across the boreal landscape, including clustering and a preference for sloped mesic sites. At the same time, local-scale variation, particularly topographic elements such as boulder fields, influence where kelo trees can establish. These findings highlight that even in forests with high naturalness, site-specific constraints shape kelo tree dynamics.

4.2 Life and death characteristics of kelo trees

4.2.1 Age at death and mortality patterns

Scots pine typically reach maturity at 200–300 years old (Krakau et al., 2013). The kelo trees in my study area had a mean age of 333.71 years old, indicating that most died well beyond this maturity threshold. Rouvinen et al. (2002) showed that the kelo trees in their study also reached maturity. The two oldest trees in the study by Rouvinen et al. (2002) were 257 and 234 years old, this shows that most of the trees in my study died at an higher age. I also recorded 12 kelo trees that had not yet reached maturity, showing that while kelo formation generally occurs at advanced age, younger Scots pine can also develop into kelo trees.

Despite increased variation in the age of kelo trees at death during the 20th and 21st centuries (Figure 7), I found no statistically significant trend between year of death and age at death, suggesting that kelo tree recruitment has not become progressively younger over time. While some younger trees (<200 years old) have become kelo trees, this appears to be an exception rather than a shift in recruitment pattern. These findings support the view that kelo tree recruitment continues to occur predominantly at advanced ages (Niemelä et al., 2002).

Rouvinen et al. (2002) found that small-scale disturbances such as windthrows, pathogens, insects, and low-intensity fires kill individual trees or small groups of trees. Such disturbances are expected to become more frequent in the boreal forest (Shorohova et al., 2023), potentially limiting tree growth and leading to mortality before individuals reach maturity and large sizes (Löfroth et al., 2023). Yet for large Scots pines, the specific cause of death is often unclear (Palik and Pederson, 1996; Rouvinen et al., 2002). It has been found that old kelo trees can experience

several decades of reduced growth (Keto-Tokoi and Kuuluvainen, 2014; Niemelä et al., 2002). My observations support this, although only older trees appeared to have experienced slowed growth, whereas younger trees had no such decline, suggesting that younger individuals may have experienced a sudden death. This variability in pre-mortality growth patterns in Scots pine has been linked to drought-induced mortality, as well as the type, duration, and frequency of other stressors that caused death (Cailleret et al., 2017). While their findings were not specific to Scots pine, Cailleret et al. (2017) reported that gymnosperms and drought tolerant species, including Scots pine, generally exhibit prolonged periods of reduced growth preceding death. My findings indicate that the cause of death of kelo trees varies; some individuals are gradually weakened over time and others experience a sudden disturbance. With the expected increase of small-scale disturbances in boreal forests (Shorohova et al., 2023), future kelo trees may become smaller and younger as they die earlier, potentially before reaching maturity. Furthermore, kelo tree transformation may occur after death, possibly because of elevated phenolic concentrations in the heartwood from fungal infections, environmental stressors, or disturbance events (Venugopal et al., 2016).

Unlike other studies (Kuuluvainen et al., 2017; Niemelä et al., 2002; Rouvinen et al., 2002), I found almost no evidence of forest fires. This absence of fires has also been reported in TNR by Josefsson et al., (2010). Given this absence, my results may suggest that fungal infestations play a more prominent role in kelo tree recruitment than direct disturbances in this particular ecosystem. Nevertheless, disturbances still play an important role in tree mortality, but potentially act as secondary drivers behind the kelo tree recruitment process.

4.2.2 Time standing after death and decay

Kelo trees in my study area have remained standing on average for 80.6 years after death. These findings align with Rouvinen et al. (2002), who reported an average of 81 years. However, Niemelä et al. (2002) reported an average time of 128 years, although kelo trees in their study were subjectively selected. The long time standing after death of kelo trees recorded in my study is reflected by the physical characteristics of recorded kelo trees. Most trees were in decay classes 5 (39.1%) and 6 (46.4%) and the majority had little (21.8 %) to no (40.0 %) bark remaining (Tables 1 and 2). A positive correlation between years after death and decay class shows that trees that have been standing longer after death tend to be in more advanced stages of decay. Together, these findings support that the recorded kelo trees were already well into their transformation process.

4.2.3 Germination and recruitment dynamics

Kelo trees in my study area emerged during several germination pulses, notably around 1350–1375, 1425–1475, 1525–1550, 1750–1800, and 1825–1850, with a peak between 1750 and 1800 (Figure 8). Two of these pulses (1750–1800 and 1825–1850) were also identified by Josefsson et al. (2010), who dated trees in the same area. They additionally reported a recruitment pulse from 1635 to 1645, which was not reflected in my data. Josefsson et al. linked the 1750–1800 peak with a phase of rapidly increasing summer temperatures. Other studies from this region have shown that recruitment pulses are linked to higher summer temperatures (Zackrisson et al., 1995). These findings suggest that warm summers may enhance Scots pine regeneration.

Although kelo tree recruitment in natural forests is typically estimated at one kelo tree per hectare per decade (Rouvinen et al., 2002), my data show a much higher mortality peak in the latter half of the 20th century (Figure 6). This suggests that the recruitment rate of kelo trees in my study area was higher than previously assumed during this period. The underlying causes of this peak remain unclear. While senescence may account for the death of older individuals, it does not explain the mortality of younger trees or the pronounced mortality peak during the 20th century. Because only standing kelo trees were recorded and cored, and not those that had already fallen, some earlier deaths may have gone undetected. Including fallen kelo trees in the sampling could have revealed a more even distribution of mortality over time. Still, the overall recruitment rate during the 20th century would likely remain higher than previously reported patterns.

Together, my findings show that kelo tree recruitment and transformation are variable processes influenced by age, site-specific conditions, and disturbance history. While most kelo trees died at an advanced age, a smaller portion died suddenly and at younger ages, suggesting multiple pathways to kelo tree recruitment. While germination followed typical patterns, the irregular timing of mortality events in my data further supports findings by other studies that kelo tree dynamics are shaped by a combination of long-term environmental factors and episodic stressors, rather than a single dominant driver (Cailleret et al., 2017; Keto-Tokoi and Kuuluvainen, 2014; Kuuluvainen et al., 2017; Rouvinen et al., 2002).

4.3 Remote sensing for estimating kelo tree density

In my study, I initially attempted to identify and estimate the number of kelo trees through remote sensing using a UAV and machine learning. However, I encountered significant challenges due to the spectral similarity between boulders and dead trees, which made reliable identification difficult. Furthermore, the image quality was insufficient to generate the dense point cloud needed for a high

quality DEM. Additionally, the wide variety in decay stages, ranging from dead trees with finely branched canopies to tall snags, further complicated classification, a limitation also noted in other studies using direct detection (Pasher and King, 2009).

Due to these challenges, I ultimately resorted to manual identification. While easy to implement, it is extremely labour-intensive and influences the accuracy with which dead standing trees were identified. Other techniques, such as LiDAR and deep learning, achieve higher identification accuracy of dead standing trees (Jiang et al., 2023; Krzystek et al., 2020).

I developed a method that allowed for conservative estimations of dead standing trees, although it included a 27 % detection gap. Furthermore, since only kelo trees were recorded in field and not normal dead standing Scots pine, no estimation of the ratio between normal dead standing trees and kelo trees could be made based on the remotely sensed dead standing trees.

Interestingly, while shadows are generally considered as obstructive in remote sensing (e.g. Alavipanah et al., 2022; Mostafa, 2017), I found that tree shadows facilitated identification, in particularly for snags.

My findings indicate that while my method is cost-effective and relatively easy to implement, it can be further improved by collecting imagery at the start or end of the day. However, it is labour-intensive and other techniques offer higher detection of dead standing trees.

4.4 Broader interpretation of kelo trees in Tjeggelvas nature reserve

My study highlights the ecological and conservation values of kelo trees. They can be centuries old at death and can remain standing for a similar amount of time. Their longevity makes them important structural elements in boreal forests where they contribute to long-term carbon storage (Mukhortova et al., 2021) and ecological stability. They are important for biodiversity and form vital habitats for threatened species (Larsson Ekström et al., 2023; Santaniello et al., 2017; Tikkanen et al., 2006), especially when they eventually fall down (Keto-Tokoi and Kuuluvainen, 2014; Niemelä et al., 2002). The range of years in which kelo trees have died and remained standing after death show that their recruitment is continuous within boreal forests that have experienced limited human influences. Their ecological importance, slow recruitment rate, and low numbers in managed forests compared to the past show their high conservation value within natural Fennoscandian forests.

However, kelo tree recruitment in the study area did not follow previously assumed patterns in terms of recruitment rate and disturbance history, particularly due to the absence of fire. My findings suggest that the drivers and processes behind kelo tree recruitment vary between parts of Finland and this area in

Sweden, and remain not yet fully understood, highlighting the need for further research into the factors involved.

Climate change is expected to increase the occurrence of small-scale disturbances in boreal forests. Because of that, Scots pine mortality might increase, causing Scots pine to die when they are younger and at smaller sizes (Löfroth et al., 2023), this may in turn indirectly influence kelo tree recruitment, particularly under changing disturbance regimes. While my findings indicate that younger Scots pine can also transform into kelo trees, it remains unclear how frequently this transformation occurs in younger trees compared to older trees.

5. Conclusions

This study provides new insight into the spatial distribution, age, and recruitment dynamics of kelo trees within an old-growth forest in northern Sweden. Using dendrochronological field data, I assessed how environmental conditions, forest structure, and disturbance history influence the formation and continuity of kelo trees. Aerial imagery was explored as a supplementary method for large-scale kelo tree identification but proved limited in its ability to reliably identify kelo trees.

My findings confirm that most kelo trees die at an advanced age and can remain standing for a long time after death, highlighting their long-term role in forest structure, carbon storage, and biodiversity. A small number of younger kelo trees died without preceding growth decline, suggesting that multiple pathways exist for kelo tree formation. However, no significant trend was detected between age at death and year of death, suggesting that kelo tree recruitment has not progressively shifted to younger trees over time.

Furthermore, kelo tree recruitment in the study area was different from previously reported patterns, most notably the absence of forest fires and high mortality at the end of the 20th century. This shows the importance of local-scale variation in disturbance regimes and environmental conditions. Although most kelo trees were found on the west of the study area and in sloped mesic terrain, the relationship between site characteristics and kelo tree distribution remains complex.

Remote sensing using UAV imagery was limited by image quality and spectral similarities between kelo trees and other landscape features such as boulders, and by variation in decay stages of dead standing trees. While manual identification was possible, more advanced techniques such as LiDAR and deep learning may be necessary for more reliable large-scale mapping of kelo trees.

Taken together, the findings suggest that kelo tree recruitment is influenced by a combination of long-term ecological processes and episodic stress events. With climate change expected to increase small-scale disturbances, future kelo trees may emerge at younger ages and smaller sizes. Understanding the drivers of kelo tree formation under different disturbance regimes will be essential for informing conservation strategies in boreal forests facing climate-driven change.

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Popular science summary

Kelo trees: Ancient Sentinels of the Forest

Scattered across the primeval boreal forests of northern Europe, kelo trees are the standing dead remains of old Scots pines. Though dead, they play a vital role in forest ecosystems by providing long-lasting habitats for fungi, insects, and birds. These silver-grey trees can remain standing for hundreds of years after death. However, the conditions that lead to their formation are still not well understood.

My study looked at kelo trees in an old-growth forest in northern Sweden to better understand how and why they form. By combining fieldwork with remote sensing, I examined where kelo trees are found, how old they are, why they might have died, and how long they have been standing. Most were found on slopes and mesic soils, with some standing for centuries after death. Several kelo trees had died young and without signs of gradual decline in growth. This is surprising because it has been found that kelo trees are very old at point of death and that their growth reduces over a long period of time before death. This suggests that not all kelo trees follow the same path.

Unlike other areas in Fennoscandia, this forest showed no signs of fire. This is important because it is thought that forest fires contribute to kelo tree recruitment. This points to other causes, such as drought or insects, as possible drivers of kelo tree formation. As climate change is expected to increase these types of disturbances, more young pines might die and turn into kelo trees in the future. Understanding how and where kelo trees form helps us protect the forests that depend on them.

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