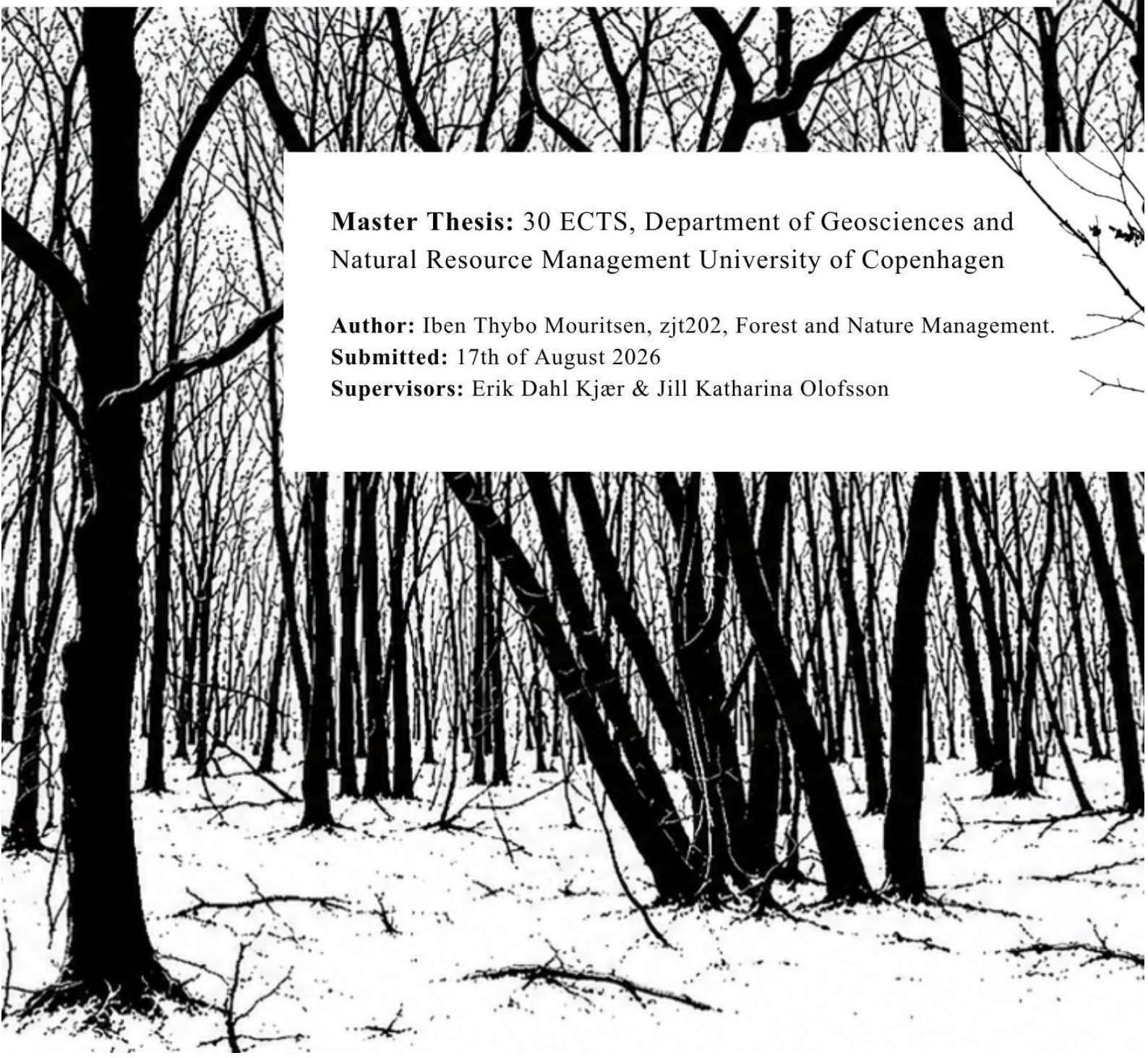
KØBENHAVNS UNIVERSITET
INSTITUT FOR GEOVIDENSKAB OG NATURFORVALTNING

DEVELOPMENT OF DANISH OAK SHRUBS

Effects of coppicing on Structural Development and Genetic Composition In Kollemorten & Tinnet Oak Shrub



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Supervisors: Erik Dahl Kjær & Jill Katharina Olofsson

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Title: Development of Danish Oak Shrubs: Effects of Coppicing on Structural Development and Genetic Composition in Kollemorten and Tinnet Oak Shrubs

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Abstract

Danish oak shrubs (Danish: egekrat) are semi-natural forest systems shaped by centuries of ecological disturbances and historical management practices, such as coppicing. This thesis investigates the structural development of oak shrubs after coppicing. Additionally, the genetic composition and spatial distribution of *Q. robur*, *Q. petraea* and admixed individuals are investigated within the coppiced systems and adjacent open grassland. The study was conducted in Kollemorten and Tinnet Oak Shrub using plots representing up to 83 years since coppicing, together with reference areas. The results showed a development towards high forest with increasing time since coppicing.

Tree height increased during the first approximately 35 years, while several characteristic shrub features were most pronounced 10-30 years after coppicing and later declined. Coppiced areas generally had higher shrub scores than reference areas. Genetically, *Q. petraea* dominated the older, closed stands, while individuals with higher *Q. robur* ancestry were more common in open and grazed areas. Overall, the results indicate that coppicing alone is not sufficient to maintain the characteristic open, crooked and multi-stemmed structure of Danish oak shrubs. Continued management with coppicing and potentially selective cutting and grazing is therefore needed to preserve these systems.

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Introduction

Danish forest land cover has been heavily influenced by human intervention and was historically reduced to only 2% of the land area. Consequently, Danish forests have largely developed through human intervention, shaping the structure and species composition of today's forests. One of the few forest types believed to have maintained continuous forest cover in Denmark is the oak shrub system. Although oak shrubs have been affected by management such as grazing, coppicing and selective cutting, many Danish oak shrubs are believed to be remnants of the original forests (Friis Møller et al., 2002; Vaupell, 1863). The one factor that has the greatest influence on the development and species composition of Danish oak shrubs today is forest management (Strandberg et al., 2005). However, the management types that upheld the cultural oak shrub systems have disappeared with the modernisation of the forestry and agriculture industry. A study of Danish oak shrubs has demonstrated that succession of unmanaged oak shrubs leads to dark, beech-dominated forests with drastically reduced species numbers and the development of thick organic layers on the forest floor. Oak shrubs are known for their cultural, historical, botanical and ecological significance, and have been studied by many botanists and foresters, such as Knud Gram(Gram et al., 1944), Enrico Dalgas (Dalgas, 1883), Adolph Oppermann (Oppermann, 1932) and many more. They have all described oak shrubs with some recurring key features, such as low growth, multiple stems and strong crookedness. A central question is whether these unique characteristics are a result of one or multiple of the disturbances that affect oak shrubs, such as soil conditions, climate, grazing, forest fires or coppicing management. Studies have suggested selective felling, coppicing and grazing as management to preserve a diverse flora and efficient nutrient cycling resembling historical states (Friis Møller et al., 2002; Strandberg et al., 2005). Ultimately, the research confirms that continued intervention is required to protect the unique ecological character of open oak woodlands from becoming a high forest. Exactly how to attain this is, today, poorly understood. Not many studies have looked into precisely how to reach the characteristic low, crooked growth of the oak shrubs. This leaves managers with questions regarding whether there should be multiple forms of management and how often there should be interventions. In central Jutland, in Tinnet and Kollemorten shrub, the Danish Nature Agency has tried to facilitate continuous coppicing, to try to imitate the old forest management system as a way to preserve the oak shrubs; however, studies have not been conducted to explore the outcome of these efforts. Another central question is about the distribution and interaction between the species *Quercus robur* and *Quercus petraea*, both of which appear in oak shrubs in Denmark. Do the two species coexist in these habitats? Do they naturally hybridise? And how does this affect the physical form of the trees? This thesis investigates the development of forest structure and species composition within the coppiced oak shrubs of Kollemorten and Tinnet Oak Shrub. Here I look into a chronosequence of coppiced areas that have been coppiced and have since been left untouched. I explore whether the structure and species composition differ in these plots and compare this to uncoppiced reference areas. This study will shed light on the impact of non-intervention on the characteristic oak shrub features and genetic composition. This insight is used to explore the necessary management and frequency of coppicing to prevent a shift toward high forest conditions and contribute towards a sustainable management practice that can preserve the ecological and cultural heritage of Denmark's unique oak scrub.

Hypothesis

The preservation of Danish oak shrubs (Danish: egekrat) requires interventions with historical management methods, such as coppicing. If left unmanaged, Danish oak shrubs will gradually lose the structural characteristics of an oak shrub and develop the structural characteristics of a high forest, such as increased tree height, single-stemmed, straight growth and canopy closure. Furthermore, the genetic composition of the oak shrubs is expected to show a non-random spatial distribution, where trees with predominantly *Quercus petraea* ancestry become more frequent in closed-canopy areas, while trees with predominantly *Quercus robur* ancestry are expected to dominate the younger, open stands.

Research questions

1) Is there a transition in the terms of tree height and form over time from shrub towards high forest if the forests are left unmanaged?

2) Is the current coppicing management sufficient to preserve the oak shrub characteristics: low, crooked, multi-stemmed growth?

3) Do the oak trees form a species complex where both *Quercus robur* and *Quercus petraea* are present? If so, do they produce hybrids?

4) Is there a relationship between genetic admixture and the spatial distribution of oak trees in closed oak shrub stands versus open areas?

To address these questions, I have studied Kollemorten and Tinnet Oak Shrub, two shrubs that used to be part of the same big oak shrub system. I have developed a set of parameters to describe the tree shapes and used these as a scoring system to put a value on the oak trees' crookedness. This score, combined with tree height, years since the last coppicing event and stem number, was used to assess tree size and form in oak trees. The sampled trees were located in recently coppiced, old coppiced, and uncoppiced parts of the forests, as well as in areas along forest edges and in adjacent open areas undergoing oak colonisation. I have sampled DNA from 170 of the trees and tested their species identity. I have linked the observation to the site (Kollemorten versus Tinnet), to the age of the coppicing, and the fine-scale location of the trees, comparing central parts of the shrub, edges and open areas. Finally, I discuss the implications of the findings for future management of the oak shrubs.

Background

Origin of Danish Oak Shrubs

Structurally, Danish oak shrub ranges from low, shrublike stands to taller, almost high forest formations. However, the oak shrub is distinguished by its crooked growth form, multi-stemmed structure and signs of historical disturbance (Friis Møller et al., 2002). The oak shrubs have developed through natural and cultural dynamics with heath- and grassland on one side and high forest on the other. Ecologically, oak shrubs are shaped by the poor soil conditions and long-term human and natural disturbances such as grazing, coppicing, cutting, wind exposure, frost, fire and salt stress in coastal areas. These factors suppress the natural succession towards high forest and favour stress-tolerant, light-demanding species. Many oak shrub sites are considered continuity woodlands, meaning that they may never have been cleared completely, even though they have been used by humans over long periods of time, and therefore genetically can be direct descendants of the ancient forests (Friis Møller et al., 2002). Other oak shrubs are secondary successional shrubs that developed through natural regeneration and expansion on open, nutrient-poor land. In the 16th to 18th centuries, the Danish landscapes were exposed to frequent felling and intensive grazing, which led to degradation and impoverishment of the forests. This led to shrub formations that were maintained through long-term human and natural disturbances such as grazing, coppicing, cutting, wind exposure, frost, fire and salt stress in coastal areas. Heavy exploitation combined with burning converted some areas into heathland, which back then was seen as an irreversible condition, partly due to podsolization (formation of mor and hardpan). The relationship between the different landscape and nature types is dynamic. Figure 1 illustrates this dynamic connection between forest, oak shrub, and heath on high, dry ground.

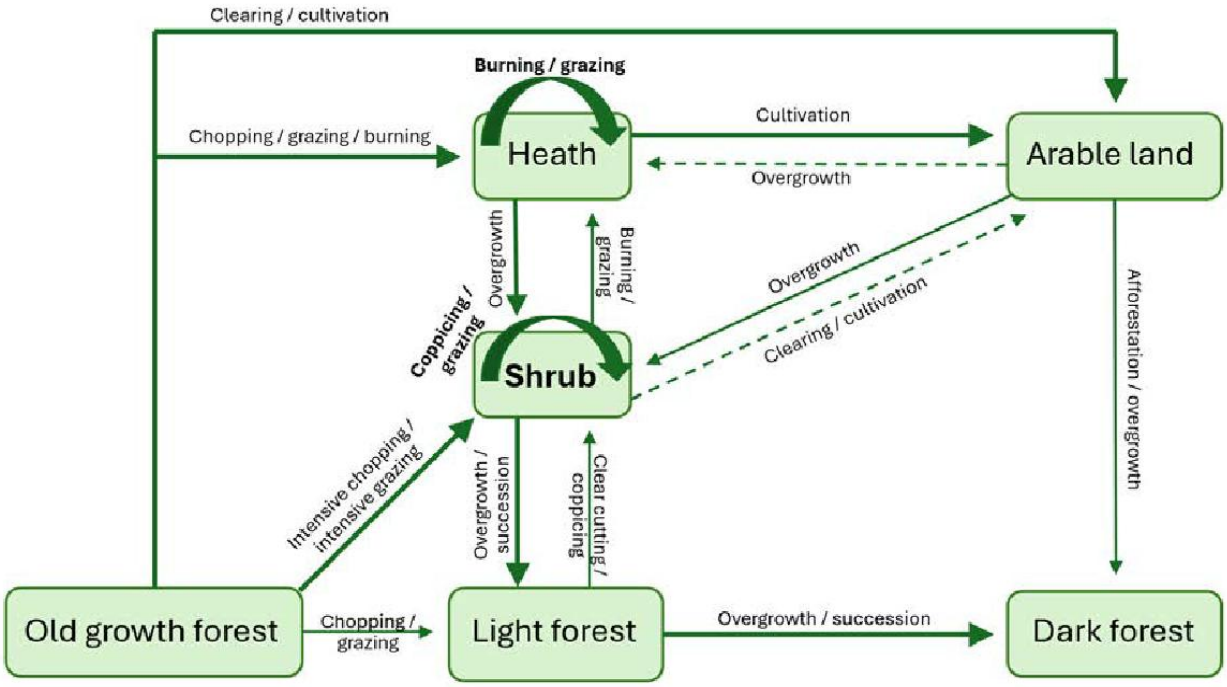


Figure 1. Development of oak shrub through dynamic processes of forest, shrub and heath through management or natural succession. Thicker lines represent stronger tendencies. Figure originally from Friis Møller et al. 2002, adapted by Mathilde Lundt Larsen (Lundt Larsen, 2025).

Historically, the development went from high forest towards heath, driven by human activities such as frequent felling, grazing, coppicing, burning and clearing for agriculture. Today we see a development towards high forest, as many of the mentioned activities have ceased with the development of modern agriculture. In contrast to earlier theories suggesting permanent degradation, these systems are reversable. The shift to high forest is also reflected in the soil, where studies have documented depodsolization (the reversal of podsolization processes) following the establishment of oak within heathland vegetation. Apart from human activities and natural disturbances, soil type and quality are key drivers of the speed and direction of these transitions. For example, figure 1 shows that a transition from modern agriculture to heathland is unlikely due to the higher nutrient levels in the soil (Friis Møller et al., 2002). In contrast, many of today's oak shrubs are standing on top of ancient fields, burial mounds and historical traces of settlements, showing that these areas have shifted between agricultural land, heathland and different forest states over thousands of years.

Protection and definition of Danish oak shrubs

The obligation to protect Danish oak shrubs was established in the 1989 amendment of the Danish Forest Act (Danish: *Skovloven*). Here, the oak shrubs were designated as protected forest (Danish: *fredsskov*) and were prevented from being converted into high forest (Skovloven, 1989). In 1996, an amendment was introduced for the registration of conservation-worthy oak shrubs to strengthen their

protection. In this law text, there are no strict legal requirements to actively maintain oak shrubs in their characteristic form, but actions that significantly alter or damage the oak shrubs' characteristics were restricted. The mentioned characteristics were: low, crooked and multi-stemmed growth. However, the exact definition of crooked growth or how tall the trees should be before they were no longer defined as low growth was not specified. The explanatory notes to this legislation defined oak shrubs as areas larger than 0,5 ha that consist predominantly of naturally regenerated oak trees that are geographically located on poor soils in Jutland. Furthermore, they should be characterised by a dominance of oak, often accompanied by species such as *Populus tremuloides*, *Tilia cordata, etc*., and/or characterised by management impact in the form of grazing, coppicing as well as harsh environmental conditions during early growth, such as frost or heavy winds (Appendix 4.d, (Skovloven, 2009; Møller et al., 2002)). In 2004, conservation-worthy oak shrubs were written into the Danish Forest Act (*Skovlovens § 26-28, LOV nr 453*, 2004). These were also geographically defined oak shrubs, and a concrete definition of the natural characteristics of oak shrubs was not provided in any of these amendments.

Even though many have tried to define oak shrub as a nature type (Dalgas, 1883; Fritzbørger, 1992; Gram K et al., 1944; Vaupell, 1863; Worsøe, 1982a) the exact definition is still being discussed, and oak shrubs may lack one or more of the listed characteristics and still be defined as an oak shrub. In summary, the recurring descriptives of oak shrubs are: low, semi-natural, oak-dominated vegetation types that are often located on nutrient poor soils (Friis Møller et al., 2002). The definitions are based on both structural characteristics, origin, management history, species composition, natural disturbance and geographical location.

Tinnet and Kollemorten Oak Shrub are believed to be some of the few continuity woodlands with direct genetic descendants of the prehistoric forests (NST Forvaltningsplaner, 2025; Worsøe, 1982a). Because of this, and the historical coppicing management, the area is deemed to have high biological and cultural value. Therefore, several of the areas have been designated as forests of high nature value under the Danish Forestry Act (Skovloven, LBK nr 690 af 26/05/2023 §25 stk. 1, Table 4). Forests of high nature value are nature-wise particularly valuable forests (Danish: *Naturmæssigt særlig værdifuld skov).* The Danish Nature Agency has made a management strategy for 2025-2040, where parts of both Tinnet and Kollemorten fall under a larger plan area designated as set-aside forests (Danish: *urørt skov*) in 2021. Set aside in this regard does not mean non-intervention management, but rather a more active strategy, where timber production is seized and the area is set aside for biodiversity. The management plan states that to maintain the shrub characteristics and to support the rare species, historical management forms, such as coppicing and grazing, will be continued and even expanded. Furthermore, in the period from 2025 to 2031, active restoration will take place, which includes creating more canopy gaps, increasing the amount of deadwood and *veteranizing* the trees (mimicking the natural decay process by damaging the trees). Kollemorten have previously been designated for gene conservation of *Q. petraea*, to ensure the genetic integrity of this specific population. This meant that planting trees from other gene pools was prohibited within 500 metres to minimize the mixing of genes with non-native individuals (NST Forvaltningsplaner, 2025).

Danish oak shrubs are not only protected under the Danish Forest Act but may also be included in the European Union's Natura 2000 network as habitat type 9190, described as *"Old acidophilous oak woods with Quercus robur on sandy plains"*(*Natura 2000 Viewer*, 2026). This means that the area should be held in a "*favourable conservation status*" based on the protection basis (Natura 2000 Viewer, 2026). Areas of Kollemorten and all of Tinnet Oak Shrub fall under habitat 9190. However, the Natura 2000 definition of habitat 9190 does not fully correspond with the characteristics of Danish oak shrubs, as it describes an oak woodland dominated by *Q. robur* rather than specifically defining an oak shrub habitat.

In Denmark, oak shrubs typically consist of naturally regenerated *Q. robur*, *Q. petraea* and hybrids of these two species. Furthermore, none of the unique ecological and physiological characteristics of the Danish oak shrubs is described in the Natura 2000 habitat classification. Therefore, although Danish oak shrubs are under legal protection through both the Danish Forestry Act since 1989 and, in some cases, the Natura 2000 network, their ecological, physiological and historical management is not covered by the current European habitat classification. This could be because the Danish oak shrub is a unique nature type also at a European level due to its species complex (E. D. Kjær, pers. comm.), with few, if any, examples found elsewhere in Europe. This increases the importance of documenting the presence of the two species in the Danish oak shrubs.

Coppicing

Coppicing is a historical forest management type that is considered one of the oldest types of silviculture (Fritzbørger, 1992). It is based on the ability of certain deciduous trees to produce new shoots from the stump and/or roots after being cut down. In Denmark, this management type has been used for centuries to get wood in small dimensions, for firewood, poles for fencing, charcoal production and bark for tanning practices (Friis Møller et al., 2002). In Western Jutland, some oak shrub coppice systems have been dated back to the 12th century (Fritzbørger, 1992). Coppicing usually involves area felling (Danish: *fladehugst*) where most trees in a specific area of the forest are cut down approximately 20-25 cm above the forest floor. Coppicing removes apical dominance and forces new shoots to develop from dormant buds positioned around the stump rather than from a single vertically oriented stem. As neighbouring shoots compete for light, stems frequently develop irregular angles and bends instead of the straight monoaxial stems favoured in timber production (Figure 2). Repeated cutting over several centuries amplifies this effect, producing the twisted and irregular stem architecture that has become characteristic of many historical oak shrubs, creating a multi-stemmed tree. A few trees would usually be left in the overstory to be harvested at a later time as timber of bigger dimensions (Worsøe, 1982b). The coppicing would typically be followed by a thinning regime, where certain stems were cut down after approximately 30 years. This was to widen the space between the stems, leaving many of the earlier multi-stemmed trees as single-stem trees. These were then coppiced when they reached an acceptable DBH (Diameter at Breast Height), creating a coppicing cycle of around 60 years, depending on how fast the trees were growing (Friis Møller et al., 2002). The length of coppicing cycles would vary based on soil conditions (Danish: *bonitet*), with cycles ranging from 20-30 years up to 50-80 years. The open space between the trees

left space for the sun to reach the forest floor. This was particularly important because the farmers needed grass to grow in between the trees to feed their cattle and horses, which typically grazed within the coppicing systems (Worsøe, 1982a). The only exception to this was the first few years after coppicing, when the farmers would fence the area to let the oak trees regenerate.

Continuous coppicing management plays a role in creating the crooked, shrub-like nature of the oak shrubs. After repeated coppicing, combined with browsing, the trees grow lower, often multi-stemmed and more crooked than non-coppiced oak trees would (Buttenschøn et al., 2018). There is no definitive maximum number of times an oak shrub can be coppiced. However, with every coppicing there are some stumps that do not survive. A Danish report, Naturplejeportalen – Rapportudgave, (Buttenschøn et al., 2018) reports that 5-10% of stumps may die with each coppicing. This number increases with age, as the ability to regenerate from a stump decreases significantly when the tree ages and stem diameter increases. After the tree reaches a diameter of 25 cm, the success rate drops (Buttenschøn et al., 2018). Repeated cutting can also lead to growth point aging (Danish: *vækstpunktforældelse*) where new stems behave like the aged parts of an old tree, contributing to the crooked appearance (Friis Møller et al., 2002).

The characteristic growth form is not only shaped by the cutting of trees, but also by the long term grazing, that historically is part of the coppicing system. The browsing, trampling, and mechanical damage from animals rubbing against stems or breaking branches can change the tree's architecture and promote irregular, crooked growth. Repeated trampling around the root collar can cause damage that stimulates the growth of dormant buds, which in turn can lead to root collar thickening around the base of the tree (Friis Møller et al., 2002). Repeated browsing also removes young shoots and buds, suppressing apical dominance and stimulating the development of new shoots from dormant buds. This can create a low, horizontal, irregular crown, with many bends and forks. Grazing also kept the competition from faster growing tree species down and kept the understory open (Vaupell, 1863). Old, coppiced areas are also recognized by the soil mounds that are found around the tree bases. These are formed by old, stumps rotting away after being cut, creating a little mound around the new stems (see Figure 2).



Figure 2. Tree coppiced in 1983, in Kollemorten Oak Shrub, plot 6. Garmin GPS mark 68 (see Appendix 1.b.), shrub score 7. The white stripes mark the soil mound. The stem on the left is a potential root shoot, due to its angle and position (Worsøe, 1982b). Image background blurred with Microsoft Designer.

Biodiversity, Management and Threats

Both *Q. petraea* and *Q. robur* are light-giving species. Therefore, several light-demanding species are connected to oak-dominated ecosystems, such as oak shrubs. Oak shrub as a nature type contains a variety of woodland species, such as *Populus tremula* (aspen), *Tilia cordata* (small-leaved lime), *Sorbus aucuparia* (rowan), *Betula spp*. (birch) and occasionally *Alnus glutinosa* (black alder), *Fraxinus Excelsior* (ash) and *Fagus sylvatica* (beech). In the understory, species such as *Frangula alnus* (buckthorn), *Juniperus communis* (juniper), *Crataegus spp*. (hawthorn), and *Corylus avellana* (hazel) can be found (Friis Møller et al., 2002). Another species often found in oak shrubs is the vine *Lonicera periclymenum* (honeysuckle), which adds to the crooked expression of the oak trees, as they grow around the stems and branches (Buttenschøn et al., 2018). It is believed that the presence of

Tilia cordata can be an indication that the oak shrub is a remnant of prehistoric natural forests, as a continuity oak shrub (Friis Møller et al., 2002). In addition to woodland species, Danish oak shrubs support several species connected to open, disturbed woodland habitats that are protected under both Danish and international legislation. These consist of fungi, lichens, beetles, birds and butterflies. In Kollemorten and Tinnet Oak Shrub, several species that are protected under the EU Habitats Directive are found, including *Triturus cristatus* (great crested newt), *Pelobates fuscus* (garlic toads), and *Rana arvalis* (moor frogs) (Arter.dk, 2026). Anisomeridium biforme has also been found, which is a lichen categorised as endangered (EN) on the Danish red list, a list that gives an overview of the endangerment status of species based on criteria from IUCN (*Den Danske Rødliste*, 2026).

The shrub-like growth in Danish oak shrubs is essential for maintaining the biodiversity found in these systems. The irregular form, veteran trees and deadwood that can be found in these areas contain many of the 64 microhabitats found in the *Catalogue of Tree Microhabita*ts made by the European Forest Institute (Kraus et al., 2016). These microhabitats are characteristic of old-growth forests and are important for biodiversity, especially saproxylic species that depend on deadwood. Twenty-seven out of sixty-four microhabitats were located in Kollemorten and Tinnet Oak Shrub (Appendix 4.a).

The main threat to the preservation of Danish oak shrubs is abandonment of traditional management (Friis Møller et al., 2002). Sixty kilometres north of Tinnet and Kollemorten Oak Shrub lies *Hald Ege*, an oak forest that has developed into high forest, and which historically had been an oak shrub. Coppicing and grazing management ceased as the forest was protected in 1909 when it was bought by the Danish government, and from then on free succession led to the area developing into high forest. A study made in Hald forest in 1999 (Tybirk & Strandberg, 1999) showed how the cessation of management combined with historical nitrogen deposition affected biodiversity negatively. The study found a 26% reduction in the number of species, with the most significant reasons being decreased light to the forest floor, decreased disturbance and increased nitrogen deposition from the atmosphere, which adds nutrients to the otherwise nutrient-poor soils. This, combined with the lack of disturbance, fragmentation of the oak shrubs and invasion of shade-tolerant species such as *Fagus sylvatica* (European beech), *Acer pseudoplatanus* (sycamore maple), *Prunus serotina* (black cherry) and conifers such as Picea abies (Norway spruce) and *Picea sitchensis* (sitka spruce), is threatening the oak shrub systems. Without active management, most oak shrubs tend to become taller, denser and darker, gradually losing the structural and compositional characteristics that define the habitat. Furthermore, climate change, with rapidly changing weather causing summer droughts, leads to stress and increased seedling mortality(Eaton et al., 2016; Muhamed et al., 2013). A study from 2013 found that the understory in oak systems shifts from being *negative competition* to the oak seedling to being a *positive facilitation* for the oak seedlings, as the understory protects the seedlings from high temperatures and drought stress (Muhamed et al., 2013). This is consistent with the “stress gradient hypothesis” (SGH), where plant interactions are typically negative when conditions are good, but become positive when stress from the environment, such as climate change, increases (Bertness & Ragan, 1994).

Therefore, management and restoration of Danish oak shrubs are crucial. Today, this is done through grazing, coppicing and/or selective cutting to preserve the oak dominance, the biodiversity through lighter, more open conditions and the historical and cultural value that this management imparts to the trees and the landscape (Strandberg et al., 2005).

Differences between Quercus robur & Quercus petraea

Both *Q. robur* and *Q. petraea* have their natural range in much of Europe, and both species are found in most Danish oak shrubs (Gram et al., 1944). Figure 3 depicts the natural range of the two species, and portrays the large overlap, making the two species sympatric in much of their natural range. *Q. robur* has the widest distribution of any European oak species, extending from the Atlantic coast to western Russia and from southern Norway, Sweden and Finland down to the Mediterranean, and is especially abundant in lowland areas with moist fertile soils. Compared to the range of *Q. petraea*, the range of *Q. robur* stretches further out to the north/east, while *Q. petraea* has a smaller range both to the east and the north, where it is largely absent from Finland and either absent or fragmented in Russia. *Q. petraea* is more often found in well-drained, acidic, and nutrient-poor soils on hillslopes and in mountainous areas. The exact placement of the southern range can be difficult to determine, due to the occurrence of hybrids with *Q. pubescens* and *Q. frainetto* (*EUFORGEN*, 2025). In Denmark, it is believed that *Q. petraea* is less common than *Q. robur*, with only scattered populations in the north and west Jutland (Figure 4 (*EUFORGEN*, 2025). However, it has also been found that there may be a significant proportion of genes from *Q. petraea* in the northern part of the species' distribution (Olofsson et al., 2023).

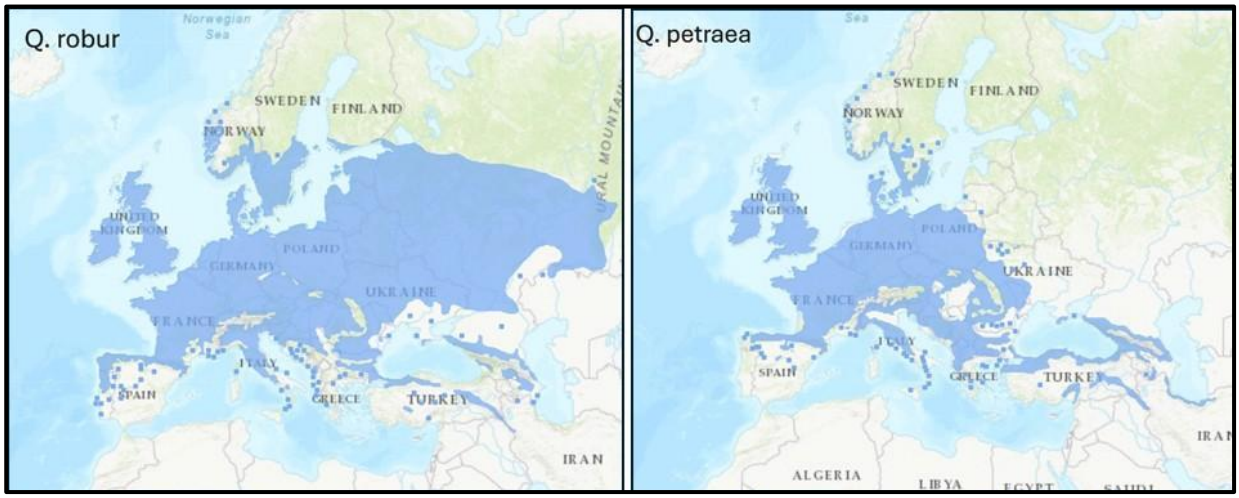


Figure 3. Distribution maps of Q. robur *(left) and* Q. petraea *(right), source: www.euforgen.org. (Caudullo et al., 2017).*



Fig. 17. *Quercus petraea* (MATTUSCHKA) LIEBL.
▼: oprindelig plantet. (Originally planted).

Fig. 18. *Quercus robur* L.

Figure 4. Distribution of Q. petraea *(left) and* Q. robur *(right) in Denmark. ("BOTANISKTID-64-1968-1969", 1968). Explanation of the maps distribution markers see Appendix 1.c.*

In year 2000 the total forest area of oak in Denmark was around 30.000 to 40.000 ha. Apart from European Beech (*Fagus sylvatica*), the sessile oak (*Quercus petraea*) and pedunculate oak (*Quercus robur)* are the most common broadleaf species in Denmark. Worldwide, there are reports of 200-500 different oak species, including hybrids, depending on how the subspecies are divided (Olrik & Kjaer, 2007). Twenty-four of these species have their ecological range in Europe (J. Kleinschmit, 1993). Within the subgenus Quercus (White oaks), *Q. petraea* and *Q. robur* are the most common in Northern Europe (Olrik and Kjaer, 2007). Of these two species, *Q. robur* is the most common in Denmark however, the old natural stands, found in Jutland, contain a large proportion of *Q. petraea* (Jensen, 2000).

Oak has played an important cultural role in Denmark, as well as an economic role throughout silvicultural history. The species has often been mentioned in legends and old folktales as a symbol of strength, durability and solidarity (Eaton et al., 2016; Friis Møller & Staun, 2017). The oak can live more than 1000 years and can, under the right conditions, grow to be over 40 meters tall (Eaton et al., 2016). However, in Denmark we see that they often reach their maximum height between 25 and 30 meters (Appendix 4.b) (Nord-Larsen et al., 2009). It has been used in both boat and house building, and acorns have been imported to Denmark for hundreds of years from different European seed sources (Jensen, 2000), therefore, the genetic origin can be difficult to determine. These two

oaks are monoecious (having both male and female flowers) and are pollinated by wind (Eaton et al., 2016).

The two oak species *Q. petraea* and *Q. robur* are closely related and are known to hybridise and produce fertile offspring. Studies found that the hybridisation is asymmetric, as it is significantly easier for *Q. petraea* pollen (father) to fertilise *Q. robur* flowers (mother) than the other way around. However, both the formation of *Q. petraea* (mother) x *Q. robur* (father) hybrids and *Q. robur* (mother) x *Q. petraea* (father) hybrids are found. Research has shown that the first generation (F1) of hybrids are highly fertile. Even when "pure species"[1] pollen is available, the hybrids can pollinate and backcross with both parental species successfully. The fertile hybrids can lead to backcrossing with both *Q. petraea* and *Q. robur* (Olrik and Kjaer, 2007). Repeated backcrossing leads to admixture, and the individuals can no longer be called hybrids.

During introgression, there is movement in the nuclear genes from one species to another. Introgression is the result of repeated hybridisation and backcrossing over several generations, with a transfer of specific genes, mixing the gene pools (Strandberg et al., 2005). The process of nuclear gene flow often starts when a *Q. robur* is pollinated by *Q. petraea*, resulting in fertile first-generation hybrids that can backcross with either parental species. During backcrossing, first-generation hybrids can carry 50/50 proportions of genetic material from both parents and can cross with individuals of one pure parental species, producing offspring with, e.g., 75% of one species and 25% of the other (Figure 5) (Strandberg et al., 2005).

[1] Pollen from pure parental individuals of oak trees that are not hybrids but are genetically non-admixed

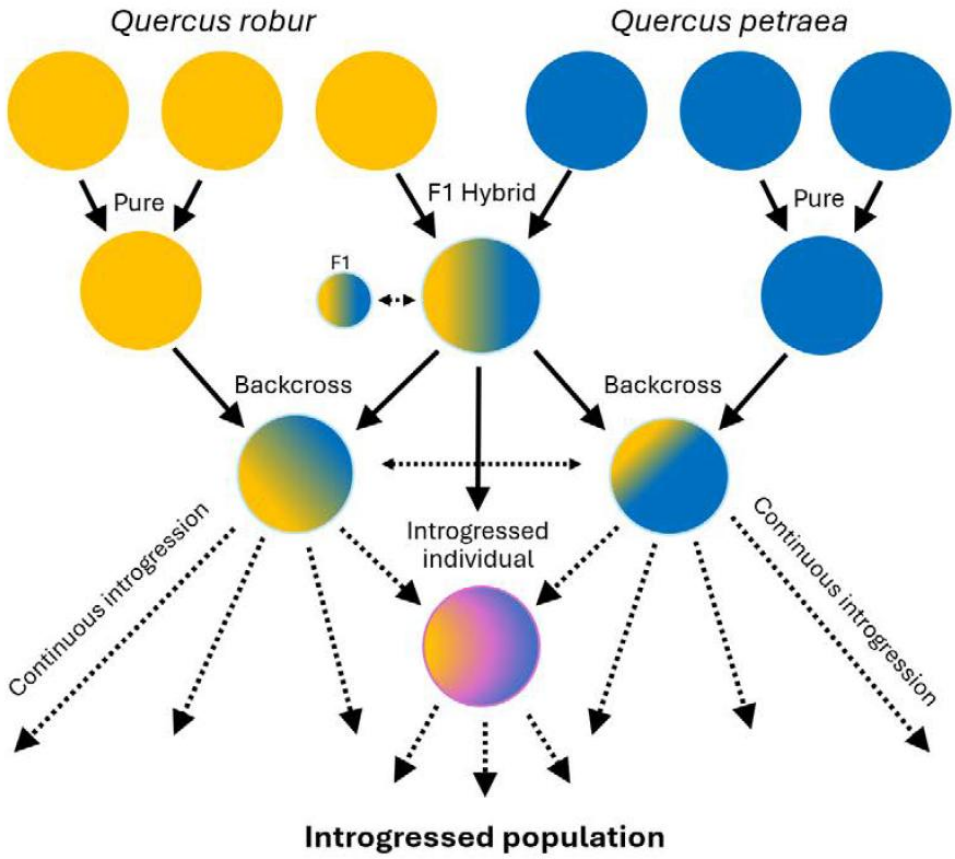


Figure 5. Mixing of DNA in hybrids with backcrossing leading to introgression in individuals and introgressed populations in Q. robur and Q. petraea. Hybrids are fertile and can create hybrids with both pure individuals, other hybrids and introgressed individuals. Figure adapted and developed from Olrik and Kjær (2007), by Mathilde Lundt Larsen (Lundt Larsen, 2025)

The first generation of the offspring of *Q. petraea* and *Q. robur* has some reproductive barriers. The hybrid of *Q. petraea* x *Q. robur* has some difficulties, while the hybrid *Q. robur* x *Q. petraea* is more successful (Olrik and Kjaer, 2007). Although the two species are closely related and capable of producing fertile hybrids, they remain mostly distinct with differing characteristics in morphology, ecology and physiology. Studies based on observations from Danish oak provenance trials found significant differences in the two oak species in both morphological and ecological traits (Table 1) (Jensen, 2000).

The two tree species have high intraspecific variation, and a collection of botanical descriptions, made by Moritz Willkomm in 1887, found that *Q. robur* have the highest variability of all broad-leaved tree species when it comes to leaf shape, structure, colour and size (Willkomm, 1887). Despite this high intraspecific variation, certain traits are more common in *Q. robur* than *Q. petraea* and vice versa. The shorter leafstalk, ear-shaped leaf base, more irregular lobes and veins that often run straight into the sinuses (gaps) between the lobes are all traits more often found in *Q. robur* leaves. The leaves of *Q. petraea* are, in contrast, more regular in both overall shape and the shallower lobes, and have a hairier underside (Høeg, 1992). Morphological differences in the two species include both seeds, leaves, stem straightness, number of epicormic shoots and branch architecture (Table 1). The acorns also differ, as the acorn of *Q. robur* sits on a long stalk and is bigger than the one of *Q. petraea* (Friis

Møller & Staun, 2017). This can be important in the process of seed dispersal, which is often done by birds and mammals, as the bigger acorn has better chances in the open grassland (Eaton et al., 2016).

Stem structure is one of the traits that is under the strongest genetic control, and it is therefore often a good indicator of which species the observer is standing in front of (Jensen, 2000). *Q. petraea* is a popular choice in forestry, due to its straighter stem growth with fewer epicormic shoots. *Q. robur* generally has a less straight stem and produces up to five times as many epicormic shoots as *Q. petraea*. This is an adaptive characteristic of oaks that enables them to regenerate their branches and canopy following a disturbance or damage by browsing (Jensen, 2000). This aligns with *Q. robur* behaving to a higher degree as a pioneer species, while *Q. petraea* is regarded as a climax forest species. However, both of these oak species possess the ability to behave as both a pioneer and a climax species (Eaton et al., 2016; Friis Møller et al., 2002). Moreover, Danish *Q. robur* has thicker branches that are crooked, horizontal and thick, while *Q. petraea* grows thinner branches with a more acute angle and finer architecture (Eaton et al., 2016).

When looking at the differences in ecological traits and niches, the two species have a large overlap in ecological amplitude. However, the further we get from the two oaks' ecological optimum, the more visible are the differences (Eaton et al., 2016). *Q. petraea* is found to be more competitive on poor, sandy soils, whereas it is rarely found naturally on loamy, fertile soils. Jensen et. al. (2000) hypothesised that this absence on richer soils might be because *Q. petraea* grows more slowly than *Q. robur* in the first year, leading it to be outcompeted on rich soils (Jensen, 2000). J. Kleinschmit (1993) argues that adaptation to the more specific site conditions of *Q. petraea* (dry, nutrient-poor environments) requires a higher degree of specialisation that can only be continued if the tree has a stronger resistance to introgression. *Q. robur* often occurs in richer soils and is therefore able to maintain a wider and more diverse gene pool as its distribution is wider (J. Kleinschmit, 1993). German field trials on different provenances have shown that height growth of the Spessart oak (*Q. petraea*) was 12–15% greater than that of local Danish pedunculate oak (Q. robur). This growth superiority was found on both loamy and sandy soils (Jensen, 2000). It should not, however, be concluded that *Q. petraea* is superior in growth, as German provenance trials show no significant difference in overall growth between the two species (Kleinschmit & Svolba, 1995) and growth trials on juvenile oak trees show that *Q. robur* grows faster in the early years, perhaps due to the bigger acorn (Kleinschmit, 1993). Observations made on the differences in phenology show that *Q. petrae*a may flush earlier than *Q. robur*, which would flush two to four days later. This is, however, affected by whether the provenances are from coastal regions that flush later or continental regions that flush earlier. The two species have different levels of resilience when it comes to wind and frost conditions.

While both *Q. robur* and *Q. petraea* are light demanding, *Q. petraea* is more shade tolerant and show a superior ability to regenerate within high forest systems (Fritzbørger, 1992). This can result in a non-random distribution, where *Q. robur* is mainly found in exposed forest edges and open land, while *Q. petraea* is found in the sheltered interior of the forest (Lundt Larsen, 2025).

Table 1. Morphology and ecology of Q. petraea *and* Q. robur *compared. Sources:* (Vedel & Møller, *Træer og buske i landskabet,* 2002), (Frederiksen et al., Dansk Flora, 2019), (Brander, Træer og buske i by og land, 2017), (Worsøe, *Kan Egen Danne Rodskud,* 1982b), (Fritzburger, *Danske Skove, 1992),* (Petersen, *Forstbotanik, 1920),* (Jensen, *Provenance Variation in Phenotypic Traits in Quercus robur and Quercus petraea in Danish Provenance Trials, 2000),* (J. Kleinschmit, *Intraspecific variation of growth and adaptive traits in European oak species, 1993),* (Høeg, *Om Mellemformerne mellem Quercus robur L. og Q. sessiliflora Martyn, 1992),* (E. Eation et al., *Quercus robur and Quercus petraea in Europe: distribution, habitat, usage and threats, 2016).*

	Q. robur	***Q. petraea***
Crowns	Crowns are usually irregularly forked with widely spaced, vigorous, crooked branches mainly in a horizontal plane. Monoaxiality is rare.	More regular crown with thinner branches, which are more evenly distributed and at a more acute angle.
Leaf	Short leaf stalk (2-5mm). Ear-shaped/lobed leaf base. More irregular, deeper leaf lobes. Wider towards the tip. Veins often run straight into the sinuses (gaps) between lobes. Smooth leaves.	Long leaf stalk (8-15mm). Wedge-shaped (Danish: kileformet) leaf base. More regular/rounder, shallower leaf lobes. More even shape. Softer, hairier undersides (especially along veins). Hairs often stellate hairs or 2-branched.
Stem	Less straight stems. Stem disappearing in the crown.	Straighter stems.
Branches	Thick, crooked, and horizontal. Less acute angle, sometimes hanging down and hiding the main stem. Thick, also in the top.	Thinner than *Q. robur*. More regular spacing. Often has a more acute angle than the branches of *Q. robur.* Decreases in size with height.
Wood	Darker and more compact heart- and sapwood.	Lighter and less compact heart- and sapwood.
Bark	Thicker bark with a coarse and furrowed structure.	Thinner and less coarse bark structure. Tend to exfoliate.
Roots	Young plants have a superior root system that is less sensitive to waterlogging than other oak species. *Q robur* roots can penetrate compacted soil and improve it.	More intensive root systems for *Q. petraea.*
Bud	More spread out, less clustered. Later bud set. Thick and more rounded.	Often clustered at the ends of shoots. Pointy and thin.
Acorn	On long stalks (2–8 cm). Bigger with dark longitudinal strips.	Almost stalkless, very short stalk. Smaller, germinates earlier.

Epicormic shoots	Produce three to five times more epicormic shoots.	Produce three to five times less epicormic shoots.
Flush	Flush 2-4 days later than *Q. petraea.*	Flush 2-4 days earlier than *Q. robur.*
Growth	Faster growth in the first year.	Slower growth in the first year. Trials have shown faster growth on dry, sandy soil, compared to *Q. robur*.
Frost	Suffer visible damage that reduces their height and volume growth in spring frost.	More hardy against frost on sandy soils. Less affected by spring frost (more frost tolerant).
Wind	A pioneer species that colonize open land and forest edges, where it can withstand the windy conditions.	*Q. petraea* shows a superior ability to resist sudden exposure to strong winds, due to its deep taproot, but is generally better adapted to the protected environment of the closed forest.
Ecology	Longer vegetative period. Pioneer species. Tolerates heavy, wet/moist lowlands, with nutrient-rich soils and periodic flooding. Continental climates. Thrives in open gaps and forest edges.	Prefers well-drained, sandy, or rocky acid soils, where it is more competitive. Often seen on slopes and hilltops. Drought-tolerant. Has a superior ability to regenerate within a closed forest (higher shade tolerance).

Materials and methods

Location and land use history of Tinnet Shrub and Kollemorten Shrub

Tinnet Shrub and Kollemorten Shrub are two protected, oak-dominated coppice forests found in central Jutland, Denmark (Figure 6). Back in 1944, these two oak shrubs were part of Denmark's biggest oak shrub system that stretched from Rørbæk Lake and four kilometres SSW. This included Skovbøl Krat, Sønderskov, Tinnet Krat, Lindet Krat, and Kollemorten Krat (Gram et al., 1944). Today, some of these areas have changed management and have been converted to agriculture and more intensive, modern silviculture. However, many of the old oak shrub systems are still standing today, including much of Tinnet Oak Shrub and Kollemorten Oak Shrub.

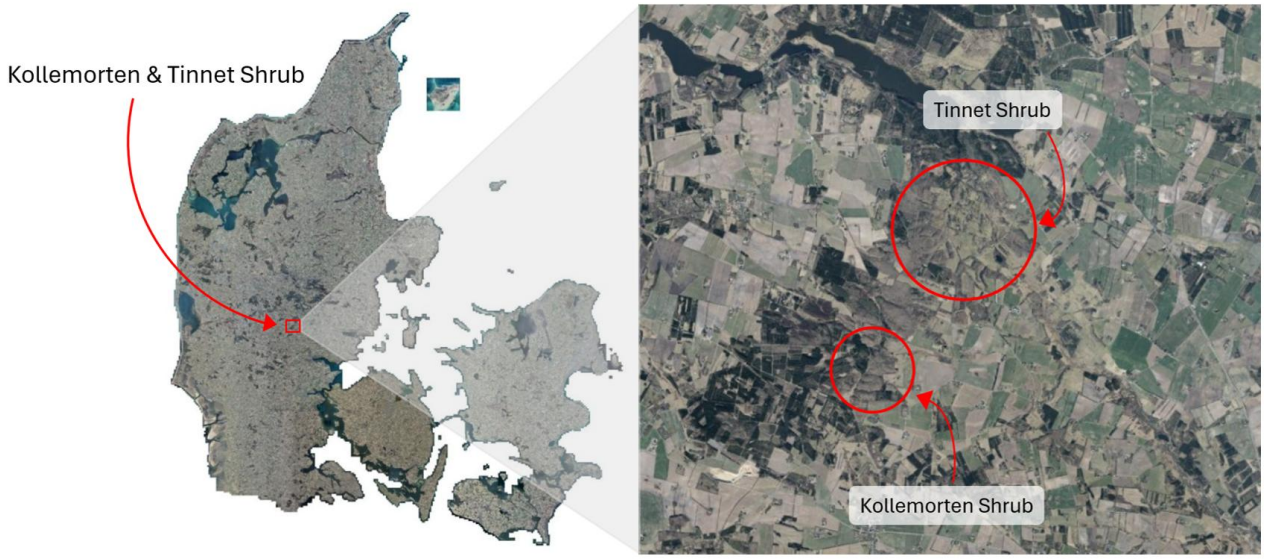


Figure 6 Location of Kollemorten Oak Shrub and Tinnet Oak Shrub in Denmark, central Jutland. Ortofoto Miljoegis.mim.dk (Miljøministeriet, 2026). *Adapted in Microsoft Power Point.*

Tinnet and Kollemorten Oak Shrub are located just east of the Weichselian glaciation's ice margin line (De Nationale Geologiske Undersøgelser for Danmark og Grønland (GEUS), 1998). This has played a role in the area's soil formation, as material was both displaced and deposited during the glacier's advance and retreat. The erosion that happened during the ice melting left the area sandy and nutrient-poor, with morainic sands as the dominant soil type. This soil type is ideal for the formation of oak shrubs (see Appendix 1.a) (Friis Møller et al., 2002; Gram et al., 1944).

Tinnet and Kollemorten shrubs are both potential continuity shrubs, with their origin possibly going back to the original oak shrubs and prehistoric forests (Friis Møller et al., 2002; NST Forvaltningsplaner, 2025). Today, Tinnet and Kollemorten Oak Shrubs are both owned by the Danish Nature Agency and located within the European Union's Natura 2000 network, area no. 76. This is referred to as habitat 9190 and described as "*Old acidophilous oak woods with Quercus robur on sandy plains"* (*Natura 2000 Viewer*, 2026). The area contains mapped sections of conservation-worthy oak shrubs (Danish: *bevaringsværdige egekrat*), which has been coppiced between 3 and 83 years ago (Hammer Holck, 2026).

The primary forest habitat types include pedunculate oak shrub (9190) and wooded peat bogs (91D0), with a significant portion of the oak shrub believed to be dominated by sessile oak (*Quercus petraea*). The light-open areas include protected habitat types such as dry heath (4030), acidic grassland (6230), and purple moor-grass meadows (6410) (*Natura 2000 Viewer*, 2026). Both areas are characterised by having coppiced oak as the dominant species. Secondary tree species, which are largely found in the understory, include aspen (*Populus tremula*), downy and silver birch (*Betula pubescens* and *Betula pendula*), buckthorn (*Rhamnus cathartica*), rowan (*Sorbus aucuparia*), and locally introduced norway spruce (*Picea abies*). The understorey shows signs of a historically semi-open coppice system, although increasing canopy closure has led to reduced light availability in many stands (Friis Møller et al., 2002). The presence of both *Quercus robur*, *Q. petraea* and admixed individuals is expected in both habitats, as the two habitats have been part of the same big oak shrub system, which has been coppiced and grazed throughout history (Gram et al., 1944).

Tinnet Oak Shrub

The structure of the landscape has undergone a major transition over the last several decades. Aerial photos from 1954 reveal that the area was almost entirely open heath and grassland with only scattered oak shrubs (Miljøministeriet, 2026). This was likely the result of intensive grazing and historical management practices like selective cutting and coppicing, which were particularly intense during World War II (Friis Møller et al., 2002). Though most of the plots in Tinnet Oak Shrub used to be heathland with scattered shrubs, some areas were planted. On maps from 1954, conifer forest covered all of plot T7 and parts of plot T5 (Figure 7). These were cut down between 1995 and 2002, and today the areas are open, dominated by grass- and heathland (Appendix 1.d). Today the formerly coppiced areas have grown into tall oak trees. Natural oak regeneration is limited, with few seedlings surviving beyond their first growing season. In some areas, regeneration is only recorded along the established paths if at all (Table 4).



Figure 7. Aerial photos of Tinnet Oak Shrub in 2025 and in 1954, including study areas (coloured) and reference areas (white).

Kollemorten Oak Shrub

Kollemorten Oak Shrub is a hilly area, with the vegetation characterised as being coppice-dominated oak woodland with sections of heathland on nutrient-poor, well drained soils. The overstory is dominated by oak, assumed to be pedunculate oak (*Quercus robur*) that shows signs of coppicing through crooked structure and clustering. This fits well with the site's long history of continuous coppicing combined with grazing by livestock, documented over several centuries up until 1960, and coppicing practices continued in smaller parts of the area until today (Friis Møller et al., 2002). Historical land use has created a mosaic of differently aged coppice plots. Since the stop or reduction of regular management, most of the site has progressed towards high forest structure across much of the site. Coppice management efforts have been carried out since 1999 by the Danish Nature Agency, in order to preserve oak shrub structure and the historical management type. The recorded coppice series therefore spanned from 1943 to 2023 (Figure 8). Since 1999, parts of the area have been experimentally managed and monitored to assess the effects of coppicing and grazing on biodiversity. Exclosure fencing was established in 2000 to exclude large herbivores in selected compartments. Red deer (*Cervus elaphus*) occur in the area and exert significant browsing pressure, particularly affecting regeneration and structural development during the first years following coppicing. Mature oak stands dominate the forest landscape today, where natural regeneration is very limited and with low survival beyond the first growing season. This is most likely because of reduced light availability under the closed canopy and the grazing pressure from both red deer and, in some areas, livestock grazing. (Friis Møller et al., 2002) As in Tinnet Oak Shrub, much of the former shrub has transitioned into high, closed-canopy oak forest today. Natural oak regeneration is limited, with only a few seedlings found at the edges of the plots.

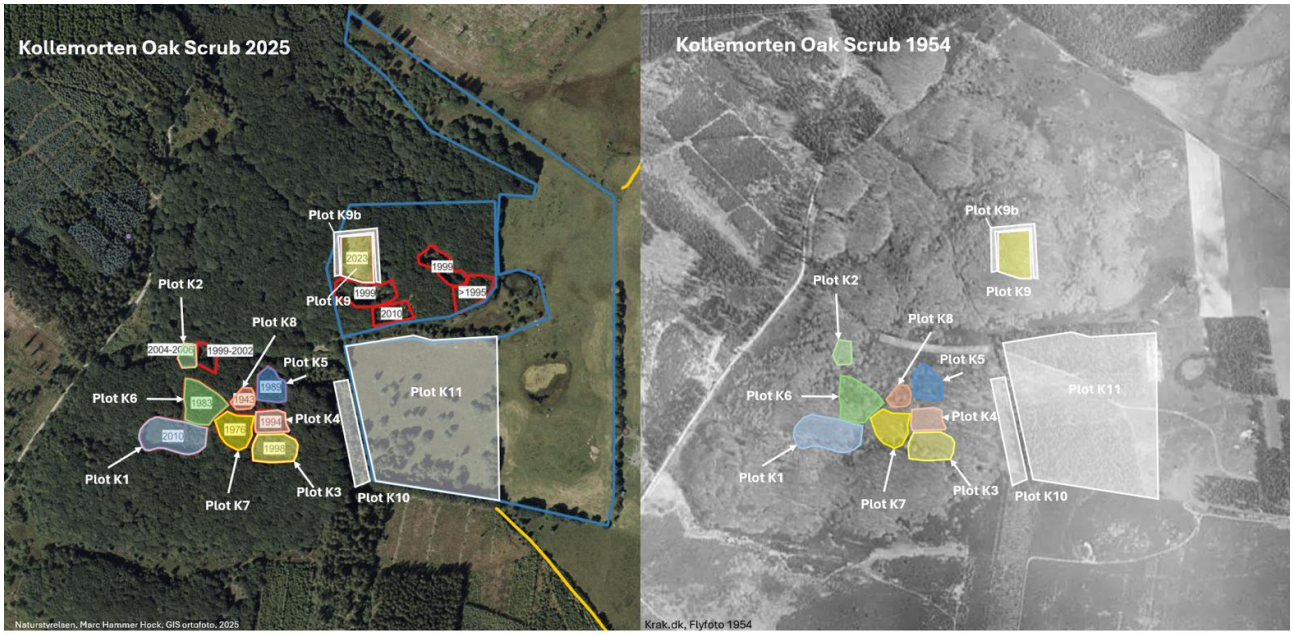


Figure 8. Aerial photos of Kollemorten Oak Shrub in 2025 and in 1954, including study areas (coloured) and reference areas (white).

Study areas and reference areas

Data were collected at two sites (also referred to as habitats) described above: Tinnet Oak Shrub and Kollemorten Oak Shrub, situated approximately 2 km apart in mid Jutland. These sites were chosen based on the documented management of coppicing, in intervals from 1943 to 2023 in well-defined plots (Gram et al., 1944). For the fieldwork, twenty plots were chosen: twelve plots in Kollemorten Oak Shrub and nine plots in Tinnet Oak Shrub. Twelve of the plots were study areas which had been coppiced over a period of 81 years (1943 to 2024). The remaining eight plots were reference areas that consisted of old coppiced forest, natural regrowth on open land and plots that historically had been coniferous forestry, but today stand as open, grazed areas.

These plots were chosen to create a chronological timeline, illustrating stand development in the years after coppicing. The graphs based on the measured parameters therefore represent a potential structural development of the stands over time. However, this timeline is based on data from different plots, not the same plot evolving. Therefore, the patterns should be seen as indications of how oak shrubs may develop after coppicing rather than a direct representation of stand development. Differences between plots could be influenced by locally differing ecological conditions in soil conditions, light availability, closeness to open areas, management history, *etc.*

The reference areas were chosen to provide a reference for comparison against the study areas and to examine what happens in the different categories of dispersion zones. The reference areas can be divided into three categories: 1. *old, coppiced stands*, 2. *open grazed areas* and 3. *edge of coppiced stands.*

1. The *old, coppiced stands* were expected to portray how the stands would have developed if not coppiced.

2. Within the category of open *grazed areas*, plots with old trees (100+ years) and plots with new regeneration (<10 years old) were chosen. Some of these plots had previously been coniferous silviculture but are today open, grazed areas with few, large oak trees present.
3. The *edge of coppiced stands* was chosen to further examine the special distribution in the area between the coppiced forests and the open land.

Figure 9 shows the spatial layout of both study areas (coloured plots) and reference areas (white plots) in Kollemorten and Tinnet Oak Shrub (see Figure 9 for spatial layout of the plots and Table 2 for plot notation and type).

Data collection and marking of analysed trees were done with permission from Marc Hammer Holck, biologist at The Danish Nature Agency (NST Trekantsområdet), who has also provided selected maps and management history of the two sites, as he has been a co-planner of the most recent coppicing efforts in both Tinnet and Kollemorten Oak Shrub.

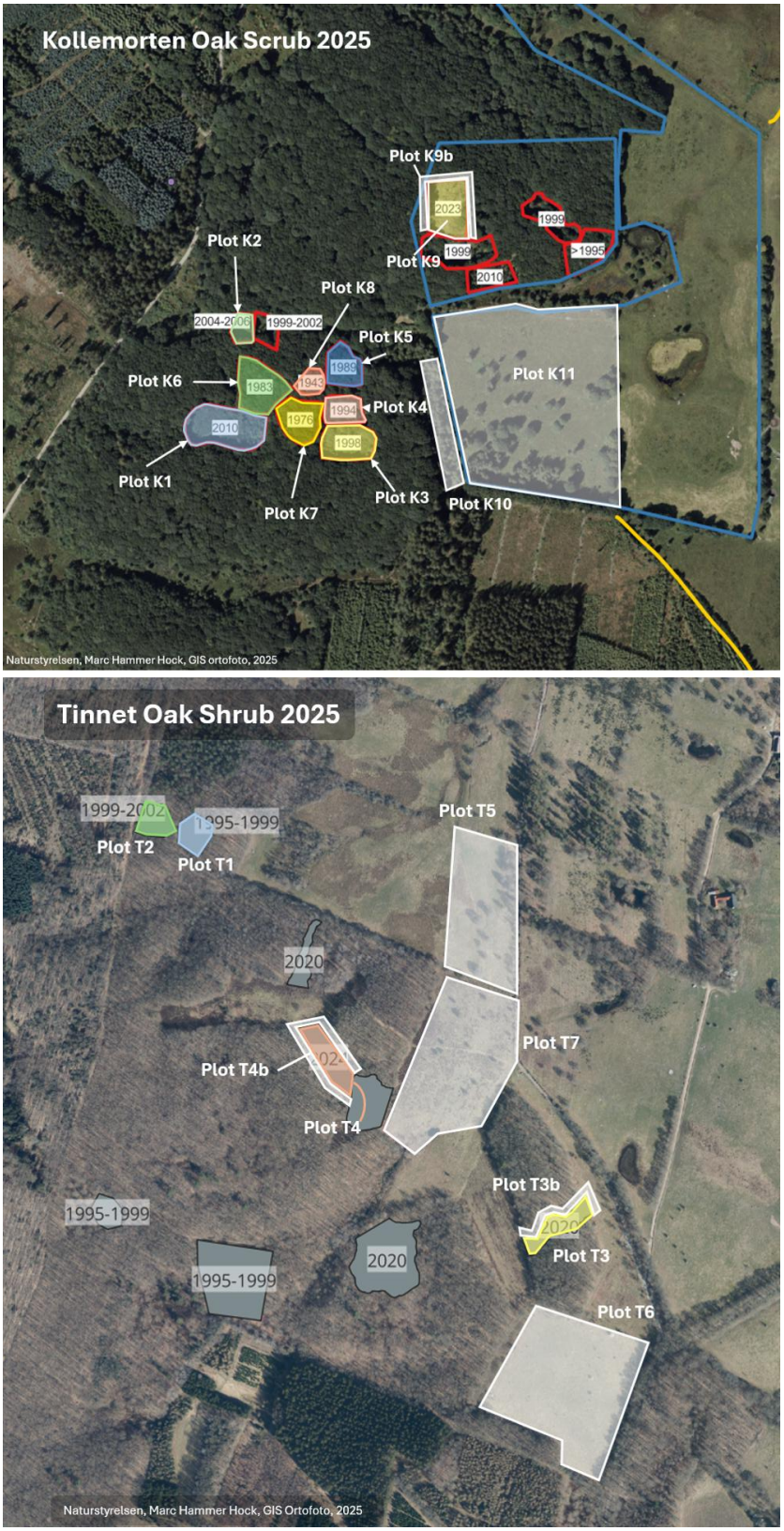


Figure 9. Spatial layout of plots K1 to K11 in Kollemorten Oak Shrub (55.888792, 9.365671) (top) and plots T1 to T7 in Tinnet Oak Shrub (55.908316, 9.383498) (bottom). The years indicate when the areas have been coppiced. Coloured plots = study areas, white plots = reference areas. Grey plots = other recently coppiced areas. The blue line indicates areas grazed by cattle. The yellow line indicates future grazing areas. Satellite images: Naturstyrelsen, Marc Hammer Hock, GIS Ortofoto 2025. Altered in Microsoft Power Point.

Fieldwork and data collection

Fieldwork was carried out during March and April 2026. The collected data included DBH (Diameter at Breast Height: 1.3m), height, DNA samples, plot descriptions and a score on the crookedness of the individual trees (shrub score). In each study and reference plot, 3-16 trees were chosen for sampling, depending on the available number of trees on the plot. These trees were, if the circumstances allowed, chosen in transects with length and width varying according to plot size and tree density/size. In this way, each individual tree was randomly chosen and GPS-marked with a *Garmin GPSmap 60CSx* GPS and could therefore be found again to re-measure if needed. In total, 170 trees were selected for analysis from 20 unique plots (Table 2).

Table 2. Plot names and their corresponding names (number) used in the results sections data analysis.

Plot name	Data analysis name	Habitat	Type
K1	**1**	Kollemorten	Study area
K2	**2**	Kollemorten	Study area
K3	**3**	Kollemorten	Study area
K4	**4**	Kollemorten	Study area
K5	**5**	Kollemorten	Study area
K6	**6**	Kollemorten	Study area
K7	**7**	Kollemorten	Study area
K8	**8**	Kollemorten	Study area
K9	**9**	Kollemorten	Study area
K9B	**10**	Kollemorten	Reference area, old coppiced
K10	**11**	Kollemorten	Reference area, edge
K11	**12**	Kollemorten	Reference area, open grazed
T1	**13**	Tinnet	Study area
T3	**14**	Tinnet	Study area
T4	**15**	Tinnet	Study area
T3B	**16**	Tinnet	Reference area, old coppiced
T4B	**17**	Tinnet	Reference area, old coppiced
T5	**18**	Tinnet	Reference area, open grazed
T6	**19**	Tinnet	Reference area, open grazed
T7	**20**	Tinnet	Reference area, open grazed

The following measurements and samples were taken from each individually selected tree: stem diameter (DBH), tree height, stem number, DNA samples and scrub score. The DBH (diameter at breast height) was measured with two perpendicular measurements on up to five stems per tree. These measurements were taken on the thickest stem, the thinnest stem, and three stems in sizes in between. Each DBH was measured using a club or a measuring band (Figure 10). If DBH was above 30 cm, a measuring band were used to find the circumferences that were then divided by π to get the diameter of the tree. For trees with multiple stems, mean DBH was used as the unit of analysis. Tree height was measured with a Vertex measuring device that determines height by combining distance and angle measurements (Figure 10). DNA samples were collected using a tree pruner to cut down branches that were then stripped from buds. Thirty to forty-five buds from each tree were placed in

three separate teabags and stored in a sealed plastic bag containing silica gel beads to prevent moisture accumulating until further analysis for species/hybrid identification (see below). The stem number was determined by counting all living stems emerging from the ground in each tree. Shrub score was determined with a nine-point shrub score scale based on the morphological traits of the trees (see section *Shrub Score data collection*). Aside from these recordings, also a general description of each analysed plot was performed including photos, management history, coppice year *etc.* (see Table 4). All collected data is available on request (Appendix 5.c).



Figure 10. Measurements of DBH (Diameter at Breast Height 1.3m) to the left. Height measurements taken with a Vertex measuring device to the right.

DNA samples and genetic analyses

For this study a total of 441 single nucleotide polymorphisms (SNPs) were genotyped using a pre-designed SNP panel previously used to analyse oaks in Europe (Pakull et al., 2025). Of the 441 SNPs, 29 were located in either the chloroplast or the mitochondria genome. Thus, in this study I only analysed the remaining 412 nuclear SNPs. A total of 2-4 buds per tree were isolated in 96-well plates and shipped to LGC Genomics Germany for further processing. DNA was extracted using standard procedures and then genotyped using a FlexSeq approach. Genotype calling was carried out by LGC genomics and supplied in an Excel format.

Samples and SNPs with more than 10% missing data were removed from the dataset, together with SNP markers with no variation between samples. For comparison and species assignment, a total of 210 samples from other ongoing projects on Danish oaks were included. In total, 374 samples were analysed (164 samples from this study) for 377 nuclear SNP markers. The genotypes were converted to STRUCTURE format and analyses of genetic admixture were carried out using fastSTRUCTURE

at K=2. The selection of K=2 was made as we expected two oak species in our dataset. A total of 10 runs at K=2 were performed and summarized in CLUMPK. The results of CLUMPK were then exported to Excel and visualized in a barplot in R v. 4.4.2. (J.K.Olofsson, pers. comm.).

The genomic assignment results were organised in Microsoft Excel for further analysis (Appendix 3.a). Each sampled tree was assigned an estimated proportion of *Q. petraea* and *Q. robur* ancestry, with the two values adding up to 1. These values therefore represent the proportional genetic assignment of each tree to the two species.

Individual trees were assigned to one of three categories based on their genetic composition. Trees with a *Q. petraea* DNA amount greater than 0.90 (*Q. petraea* > 0.90) were classified as *Q. petraea*, whereas trees with a *Q. petraea* DNA amount below 0.10 (*Q. petraea* < 0.10, equivalently *Q. robur* > 0.90) were classified as *Q. robur*. Individuals with intermediate genetic heritage (0.10 – 0.90) were classified as admixed. These results were then plotted into Google Earth Pro to visualise the special composition of the three different types: *Q. robur*, *Q. petraea* and admixed. These classifications were used in all analyses of species composition and hybrid occurrence.

Statistical analysis has been carried out with the dataset divided into two different groups. The first group is where the data is divided based on the percentage of *Q. petraea*, as described above, and therefore results in three separate groups with two pure (>90% either *Q. robur* or *Q. petraea*) and one admixed (10-90% *Q. robur* or *Q. petraea*). These two species naturally hybridise and produce fertile offspring. This can result in successful backcrossing over several generations leading to introgression and a mixing of the gene-pools (Olrik & Kjaer, 2007). Because of this, a formation of a genetic gradient rather than two isolated groups can appear. Therefore, the second grouping of the DNA data is based on genetic averages per plot, without the division of species.

Shrub Score data collection

For this study, a scoring system has been developed to quantify the specific shrub features of the individual trees found in oak shrubs. Each score parameter represents a morphological trait that is found in typical oak shrubs, with trees that show the characteristic traits of an oak shrub that have been exposed to coppicing, poor soil, grazing, early frost, heavy winds, *etc*. A scoring system to measure shrub features has not previously been developed; however, a system for measuring tree straightness exists and is used in forestry to define the quality of the tree's genetics. The straightness score system is based on a nine-point scale, and hence, the oak shrub score system is made in a similar way for the purpose of comparability. The shrub score rests on a binary system: if a feature is observed, a score of 1 is given; if the feature is absent, a score of 0 is given. The total shrub score is then calculated as the sum of all nine score points, with the lowest shrub score possible being 0 points and the highest being 9 points. Three of the score parameters describe branch architecture: 1. irregular branch arrangement, 2. a horizontal branch plane, and 3. the presence of low branches below breast height (1.3 m). The remaining six parameters describe stem morphology: 4. epicormic growth, 5. the presence of a clear monoaxial stem, 6. multiple stems, 7. stem angles exceeding 30°, 8. stem angles exceeding 60°, and 9. stems with more than ten bends. Table 3 describes each score parameter and

the connected ecological and morphological characteristics. A shrub score of 1-3 indicates a tree with very few shrub features, mostly associated with a typical high forest tree. A shrub score of 4-6 indicates an intermediate growth form, where the tree shows several shrub-like features but does not appear either as a classic high forest tree nor a fully developed shrub, but rather something in between.

Table 3. The nine shrub score parameters and their definitions used to obtain a single shrub score value characterizing the growth of trees in oak shrubs.

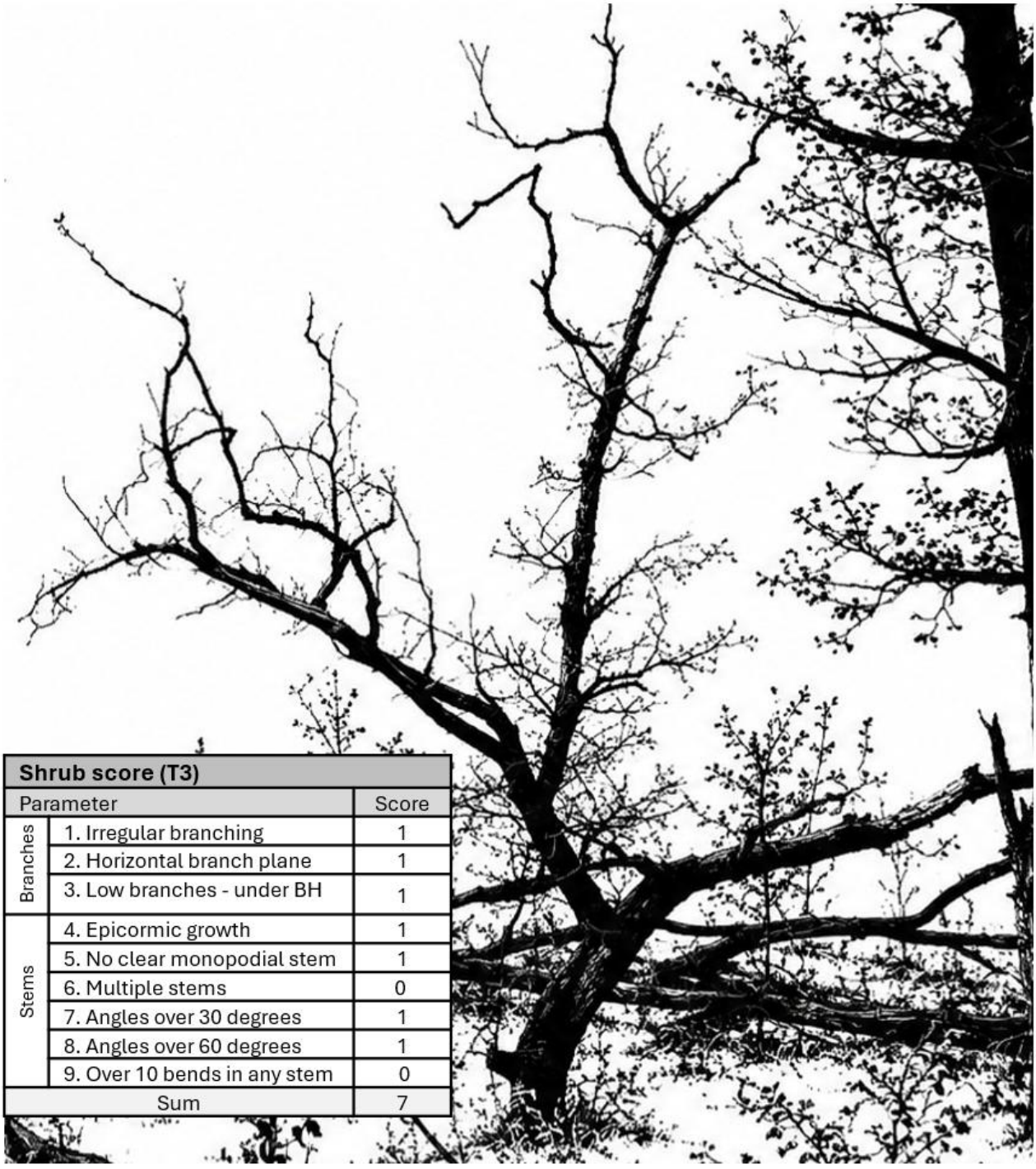
Shrub score		
Area	**Parameter**	**Description**
Branches	1. Irregular branching	Branch architecture is not symmetrical or regular, but with uneven spacing, thickness and frequency. This can be a sign of disturbance such as browsing, early frost damage (Kleinschmit, 1993b).
	2. Horizontal branch plane	Branches are almost the size of the mainstem, grow horizontally instead of vertically. The tree is as wide or wider than it is tall. This creates the possibility of several different types of microhabitats and can lead to bigger branches (Ø≥20cm) breaking off (Kraus et al., 2016).
	3. Low branches - under 1.3m	If any branches are present under 1.3m. This can be a sign of stress at the bottom of the tree, such as browsing damage, leading to a more shrub like expression (Friis Møller et al., 2002). It can also be because of high amounts of light reaching the bottom of the tree/the forest floor.
Stems	4. Epicormic growth	If there is any epicormic growth, it could indicate a stress factor or disturbance being present (Friis Møller et al., 2002; Vaupell, 1863).
	5. No clear monoaxial stem	The lack of a clear, single main axis. This can be caused by environmental stress such as repeated grazing and browsing, wind exposure or coppicing (Friis Møller et al., 2002; Vaupell, 1863).
	6. Multiple stems	More than one stem protruding from the ground. This is often the result of coppicing (Vaupell, 1863).
	7. Angles over 30 degrees	Branches with big bends add to the shrub-like characteristic of the tree and facilitate microhabitats (Kraus et al., 2016).
	8. Angles over 60 degrees	Branches with big bends add to the shrub-like characteristic of the tree and facilitate microhabitats (Kraus et al., 2016).
	9. Over 10 bends in any stem	The twisted snake stem form of many old oak shrubs is a result of repeated coppicing and browsing over centuries. This growth form is considered part of the cultural heritage associated with traditional coppice landscapes and resembles the gnarled "troll trees" ("troldetræer" in Danish) described from other historically coppiced woodlands.

Visualisation of oak shrubs and shrub score

To visualise the physical expression of the shrubs, AI image-generation has been used to obtain silhouettes of oak trees and coppiced oak plots. These images have been used to validate the shrub score by comparing the overall visual appearance and growth characteristics with their corresponding shrub scores. This was to assess whether changes in shrub score were consistent with the changes in structural development and vice versa. A clear difference in progression of the shrub score and the visual representation of the plots could indicate that the scoring system did not reflect the structural development. This was not the case, as comparisons show a general agreement between measured shrub scores and the AI-generated images, suggesting that the shrub score does indeed capture the structural development of the oak shrubs to a large extent (Figure 12).

In this thesis, AI-based tools such as NotebookLM, Grammarly and OpenAI have been used (see AI declaration in Appendix 4.c.). Grammarly was used for proofreading and language editing on selected sentences, including identifying grammatical errors and improving sentence structure. OpenAI has been used for AI image-generation (Appendix 2.a) as it would not have been possible within the timeframe of this thesis to use a manual vectorisation tool. AI image-generation models are not image-tracing tools. Even when you give a prompt that specifies "exactly the same as the picture" the AI tool interprets the image and redraws it. It will often thicken or thin stems, add or remove buds, simplify fine twigs, change branching angles slightly and invent details where the image is blurry. The images in this thesis have been generated using OpenAI (*OpenAI*, 2026). The images have been cross-checked against the originals. The cross-checking was based on the categories in the nine-point shrub score system. The silhouettes deemed appropriate for the purpose of visualising tree structures have been included in this thesis. For precise generation of future silhouettes of oak trees, a vectorization/tracing tool could be used, such as Photoshop or InDesign. The exact prompt used for the generation of silhouettes can be found in Appendix 4.c. The wording in this prompt has been chosen after several trials and is the one that led to the most precise images.

Figure 11 shows an example of a tree from Tinnet Oak Shrub (plot T3) scored according to the developed shrub score system. The tree has a total score of 7, which is at the high end of the scale. The tree was found at the edge of a plot that was coppiced in 2020 (6 years ago). The tree is located relatively low in the landscape compared to the surroundings, on the edge of an open grazed area, and there were many signs of browsing on the smaller trees and saplings surrounding it. It can therefore be assumed that this tree has been exposed to several disturbances, such as grazing, browsing, wind, sun and frost, likely explaining the relatively high shrub score of 7 for the area.



Shrub score (T3)		
Parameter		Score
Branches	1. Irregular branching	1
	2. Horizontal branch plane	1
	3. Low branches - under BH	1
Stems	4. Epicormic growth	1
	5. No clear monopodial stem	1
	6. Multiple stems	0
	7. Angles over 30 degrees	1
	8. Angles over 60 degrees	1
	9. Over 10 bends in any stem	0
Sum		7

*Figure 11. Example of shrub scoring on a tree from Tinnet Oak Shrub plot 3 (T3). Final shrub score: 7. Picture converted to a silhouette with OpenAI (*OpenAI*, 2026) and adapted in Microsoft Power Point.*

All 170 analysed trees have been scored according to this shrub score system and an average has been calculated for each plot in order to evaluate the link between shrub score and coppice history (see Results). To visualize the structural development, a photo of each plot has been converted into a silhouette and connected the year of coppicing and the plots average shrub score. Figure 12 shows a subset of four plots out of 20 plots in chronological order. The first plot is newly coppiced, with many

oak saplings emerging and one old tree left on the plot. Here the shrub score is 2.7, as the saplings have not yet been exposed to the elements in a way that has affected their growth. The second silhouette illustrates a plot that was coppiced 16 years ago. Here, both multi-stemmed oak trees and single-stemmed saplings occur in the same area, together with several other tree species that are characteristic of oak shrubs. This is the plot with the highest average shrub score of 5.9. In the fourth plot, we see that the trees have grown tall after 27 years, and a mix of single-stemmed and multi-stemmed trees is found. A high frequency of trees maintains the multi-stemmed characteristic, with the thin stems competing for light. The average shrub score has fallen to 5.3. Few saplings are emerging underneath, and only one other tree species (*Betula* sp.) is present on the plot. In the last plot, coppiced 37 years ago, the trees have grown even taller, and although the area still maintains the multi-stemmed trees, the number of stems has decreased while the thickness of each stem has increased. The forest floor is dark, and no emerging oak saplings nor saplings from other species were found. The trees have lost much of their shrub characteristics and have an average shrub score of only 4.6. The silhouettes of all eighteen plots and images of the average trees found on the plots can be seen in Appendix 2.a.

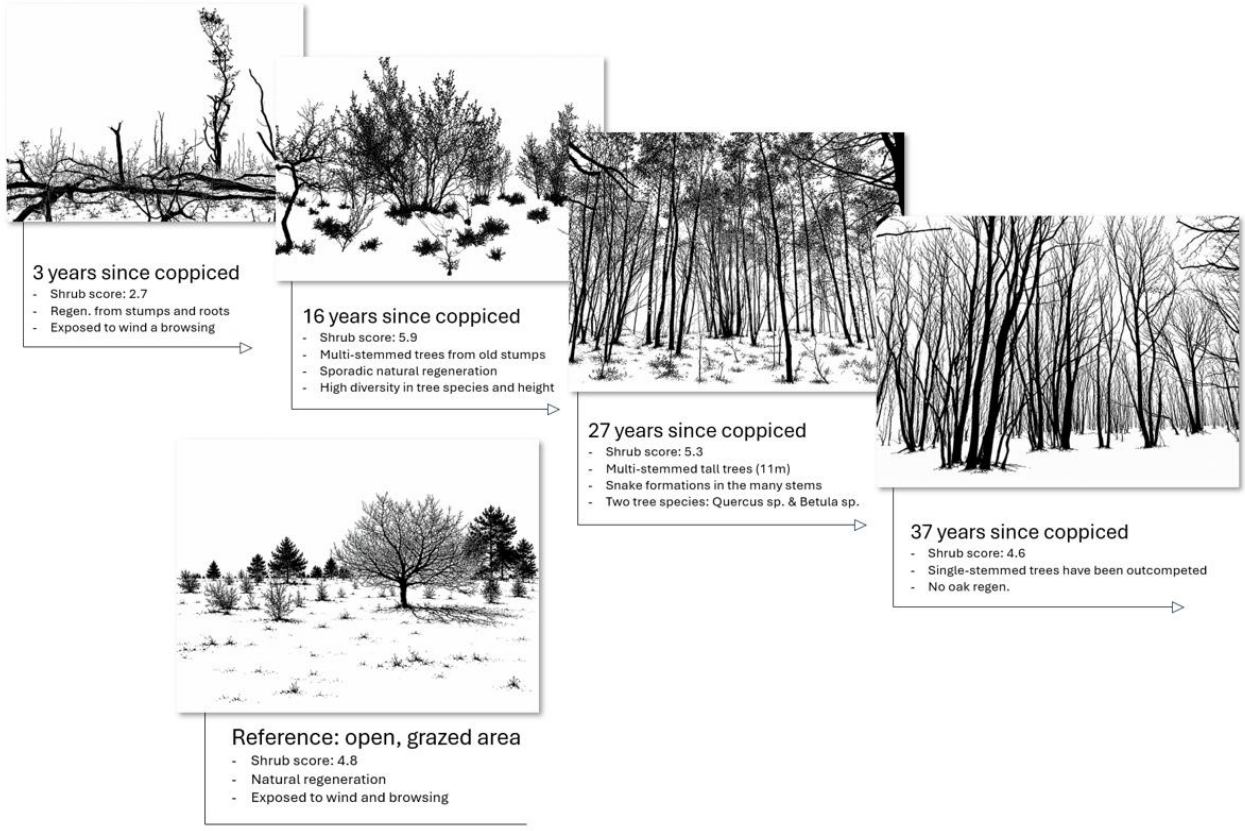


*Figure 12. Structural development in oak shrubs 3, 16, 27 and 37 years after coppicing, including one reference area.. Silhouettes generated by converting a photo of the plots with OpenAI (*OpenAI*, 2026) and adapted it in Microsoft Power Point.*

Data analyses

Data analysis was carried out using Excel and IBM SPSS (Statistical Package for the Social Sciences). Parametric tests (e.g. ANOVA) were preceded by tests of assumptions (normality, homogeneity of variance) and, if violated, data were either log- or rank-transformed to meet the requirements before statistical testing, or non-parametric statistics were used. Frequency data on *Q. petraea*/*Q. robur* genotypes were arcsine-transformed prior to parametric testing as the proportion of *Q. petraea* usually exceeded 85% or fell below 15%. All graphic presentations of data are, however, based on untransformed raw data if not stated otherwise. The two-way ANOVA's were carried out in two steps: a full model testing the presence of interaction between factors, followed by a reduced model excluding the (usually non-significant) interaction term. In these tests, the unit of analysis was the plot mean in order to stabilise variance. Although shrub score was measured as a categorical variable (0-9), it was mostly analysed as a continuous dependent variable. This was found justified (1) because most recorded shrub score values were intermediate (score 3-6, i.e. approx. normally distributed) and (2) because application of the obvious frequency analyses was statistically unsound due to a relatively low number of trees distributed across many score values (10).

This also allowed a multiple regression approach including shrub score as the dependent variable and the other measured variables (coppice age, percent *Q. petraea*, tree-height, stem number, stem diameter) as predictors. In the resulting analysis, however, stem number and stem diameter were excluded because stem number is integrated into the shrub score measurement, and because stem diameter caused violation of collinearity assumptions. To obtain sufficient statistical power for the multiple regression, the unit of analysis was individual trees (study plots only).

Results

Plot descriptions

Some of the sampled plots stood out, either in management history or development after coppicing. The newly coppiced plots (T4, K9 and T3) differed, as the trees that were coppiced had been left on the plots. According to Marc Hammer Holck from The Danish Nature Agency, this is due to biodiversity considerations and because of legislation regarding set aside forests, where The Danish Nature Agency is not allowed to sell the trees. They could have decided to move the trees within the coppiced forest, but decided against this (M. Hammer Holck, pers. comm., 31-07-26). Plot T2 also stood out, as there was no oak regeneration on the entire plot. All oak trees coppiced in 1999 had died off, leaving only dead stumps and a thick regeneration consisting of *Betula* sp. Furthermore, some plots in Kollemorten (K3-K5) coppiced between 1989 and 1998 had no visible oak saplings. On older plots, a few small saplings were observed, however, none seemed to survive more than a couple of years (Table 4).

Table 4. Plot descriptions and photos, including shrub score and year of coppicing. Sorted by youngest to oldest coppice age, in study areas followed by reference areas. Dark blue = Tinnet study areas. Light blue = Tinnet reference areas. Dark green = Kollemorten study areas. Light green = Kollemorten reference areas.

Plot	Description	Photo
T4	Coppiced in 2024. Years since last coppicing: 2. Shrub score: 4.0 Only saplings were sampled here as no living old trees were left on the plot. Plot with high forest (18-20m) on two sides and open heathland/coppiced area on the two other sides. Sporadic oak regeneration. The coppiced trees remain within the plot, likely functioning as protection against browsing pressure on emerging saplings. **Legislation:** Natura 2000, habitat 9190 **Timelines:** - 1954: heathland with scattered trees. - 1969: full forest cover, possibly under coppicing management. - 2005: full forest cover, coppicing management ceased. - 2024: one single coppicing event. **Percentage *petraea* ancestry:** 99	
K9	Coppiced in 2023. Years since last coppicing: 3. Shrub score: 2.7 Young saplings were sampled here as only one living old trees was left on the plot. Site located on an exposed hilltop, though partially sheltered by surrounding woodland (15-17m). The coppiced trees remain within the plot, likely functioning as protection against browsing pressure on emerging saplings. Oak regeneration was observed emerging from old stumps, with establishment primarily concentrated on the southern part of the plot. The area is currently grazed by cows, new sprouts are clearly bitten down, soiled disturbed. **Legislation:** Danish Forest Act, paragraph 25 **Timeline:**	

	- 1954: full forest cover, possibly under coppicing management - 200-2021: grazing with cattle was introduced. - 2023: one single coppicing event. **Percentage *petraea* ancestry:** 96	
T3	Coppiced 2020. Years since last coppicing: 6 Shrub score: 3.8 High forest on the two long sides of a coppiced area (15-17m). Some trees left on the plot. Heathland and meadow on the two short sides of the plot. **Legislation:** Natura 2000, habitat 9190 **Timeline:** - 1954: forest cover - 2020: grazing with cattle was introduced including one single coppicing event. **Percentage petraea ancestry:** 65	
K1	Coppiced in 2010 Years since coppice: 16 Shrub score: 6.0 Very open, mixed with many other species, diverse in age, much regeneration of oak. **Legislation:** Danish Forest Act, paragraph 25 **Timeline** - Has maintained canopy cover at least since 1954. - 2010: one single coppicing event. **Percentage petraea ancestry:** 89 (all trees), 90 (old trees), 88 (young trees)	
K2	Coppiced in 2006 Years since coppice: 20 Shrub score: 7.0 Very open, mixed with different species. Several oak saplings at different ages – successful regeneration. Only few of the coppiced oaks survived. Tall trees surrounding the area. **Legislation:** Danish Forest Act, paragraph 25 **Timeline:** - Has maintained canopy cover at least since 1954. - 2006: one single coppicing event. **Percentage petraea ancestry**: 88 (all trees), 84 (old trees), 89 (young trees)	

T2	Coppiced in 1999-2002. Years since coppice: 24 No oaks at all, not old nor young. Signs of coppicing as the stumps are still present. No oak regeneration. Dominated by *betula sp.*. Tall trees surrounding the area, quite dark. **Legislation:** Natura 2000, habitat 9190 **Timeline:** - Has maintained canopy cover at least since 1954. - 1999-2002: coppiced.	
T1	Coppiced in 1995-1999. Years since coppice: 27 Shrub score: 5.3 Coppiced oaks in groups and scattered individuals mixed with big Betula pendula (some look like they were also coppiced). **Legislation:** Natura 2000, habitat 9190 **Timeline:** - Has maintained canopy cover at least since 1954. - 1995-1999: coppiced. **Percentage petraea ancestry:** 94 (all trees), 94 (old trees), 94 (young trees)	
K3	Coppiced in 1998. Years since coppice: 28 Shrub score: 5.6 No oak Regeneration. Trees in scattered groups. Many self-dead trees, Scattered *Betula sp*. **Legislation:** Danish Forest Act, paragraph 25 **Timeline:** - Has maintained canopy cover at least since 1954. - 1998: one single coppicing event. **Percentage petraea ancestry:** 98	
K4	Coppiced in 1994. Years since coppice: 32 Shrub score: 4.6 No oak regeneration. **Legislation:** Danish Forest Act, paragraph 25 **Timeline:** - Has maintained canopy cover at least since 1954. - 1994: one single coppicing event. **Percentage petraea ancestry:** 92	

K5	Coppiced in 1989. Years since coppice: 37 Shrub score: 4.6 No solitary trees present and no natural regeneration. Trees occur in widely spaced, open clusters of oak. **Legislation:** Danish Forest Act, paragraph 25 **Timeline:** - Has maintained canopy cover at least since 1954. - 1989: one single coppicing event. **Percentage petraea ancestry:** 90	
K6	Coppiced in 1983. Years since coppice: 43 Shrub score: 5.2 Few solitary trees, plausible old oak regeneration, approx. the same age as the coppiced trees. Numerous seedlings were observed, but most appear unlikely to persist beyond one growing season, where lack of sunlight seems to be the reason. **Legislation:** Danish Forest Act, paragraph 25 **Timeline:** - Has maintained canopy cover at least since 1954. - 1983: one single coppicing event. **Percentage petraea ancestry:** 89 (all trees), 91 (old trees), 88 (young trees)	
K7	Coppiced in 1976. Years since coppice: 50 Shrub score: 5.8 Plausible old oak regeneration, approx. the same age as the coppiced trees. These were solitary trees, therefore they might represent plausible historic regeneration, although this remains uncertain. Other tree species recorded consisted primarily of rowan (Sorbus aucuparia) and honeysuckle (Lonicera spp.). **Legislation:** Danish Forest Act, paragraph 25 **Timeline:** - Has maintained canopy cover at least since 1954. - 1976: one single coppicing event. **Percentage petraea ancestry:** 94 (all trees), 95 (old trees), 93 (young trees)	
K8	Coppiced in 1943. Years since last coppicing: 83. Shrub score: 5.7 No natural regeneration was observed, apart from a single small sapling. A dead juniper (Juniperus communis) was found, suggesting that the site may previously have been more open. Several large trees are dead, likely suppressed and shaded out within dense groups. **Legislation:** Danish Forest Act, paragraph 25 **Timeline:** - Has maintained canopy cover at least since 1954. - 1943: one single coppicing event. **Percentage petraea ancestry:** 93 (all trees), 94 (old trees), 92 (young trees)	

K10	Reference area. Not coppiced. Shrub score: 1.7 This plot is the edge of the forest. Seemingly not coppiced. Mixed trees of ages up to approx. 30-60 years of age. Several other woody species present. **Legislation:** Natura 2000, habitat 4030 **Timeline:** - 1968: The area was under canopy cover (possibly *Quercus sp.*) - 1999: The area had been cleared – open grassland. - 2002: Natural regeneration occupies the area. - 2026: A mix of native forest species with individual oak trees scattered across the area. **Percentage petraea ancestry:** 57	
K11	Reference area. Grazed open field. Shrub score: 0.2 No oak regeneration. Several old oaks present (approx. 70-100 years old). **Timeline:** - 1954: Coniferous forest cover, with few solitary oaks. - 1968: Thinning of trees in southern area of the plot. - 1999: Coniferous forest, with open areas in the south end. - 2002: The area had been cleared, only few deciduous trees left on the southern end of the plot. - 2005: Scattered deciduous trees over the entire plot. - 2026: Few solitary oaks, beech and birch. **Percentage petraea ancestry**: 68	
T5	Reference area. Grazed since 2000. Shrub score: 2.3 Open grass land, grazed since EU-life project in 2000, where it was cleared from conifer trees. No oak regeneration. Six scattered oak trees, 100-200 years old. **Legislation:** Natura 2000, habitat 6230 **Timeline:** - 1954: Forestry in the southeast corner, agricultural fields in the remaining area. - 1969: Forestry in the southeast corner, meadow/grassland seemingly grazed in the remaining area. - 1995: Deciduous trees with gaps in the southeast corner. - 2002-5: Heavily thinned, only few trees left. - 2025: only six oaks left where the old forestry edge used to be, rest is grazed meadow and grassland. **Percentage petraea ancestry:** 4	

T6	Reference area. Open grass land. Shrub score: 6.2 Grazed since 2022. (Maybe previously grazed – looks like it). Oak regeneration heavily grazed by deer/cows. Oak regeneration from the surrounding oaks, being established closest to the edges with oak trees present. **Timeline:** - 1954: Agricultural field. - 1968: Agricultural field. - 2005: Open grassland, potentially grazed. - 2025: grazed with scattered *Crataegus* sp. and *Quercus* sp. saplings and seedlings **Percentage petraea ancestry:** 3	
T7	Reference area. Open area. Shrub score: 4.8 Grazed since EU-life project in 2000, where it was cleared from conifer trees. **Legislation:** Natura 2000, habitat 4030 **Timeline:** - 1954: Forestry covering the entire plot. - 1968: Forestry covering the entire plot. - 2005: Open grassland periodically grazed. - 2025: Periodically grazed with cattle. Scattered Crataegus sp. and Quercus sp. saplings and seedlings **Percentage petraea ancestry:** 62 (all trees), 32 (old trees), 92 (young trees)	
K9b	Reference area. Edge of coppiced plot K9. Shrub score: 4.6 Edge of coppiced area. Assumed to be how the coppiced area would have looked like, if it was never coppiced. **Legislation:** Danish Forest Act, paragraph 25 **Timeline** - Has maintained canopy cover at least since 1954. **Percentage petraea ancestry:** 97	
T3b	Reference area. Edge of coppiced plot T3. Shrub score: 3.2 Edge of coppiced area. Assumed to be how the coppiced area would have looked like, if it was never coppiced. **Legislation:** Natura 2000, habitat 9190 **Timeline:** - 1954: open heathland - 1998: under canopy cover (most probably *Quercus sp.)*. **Percentage petraea ancestry:** 72	

T4b	Reference area. Edge of coppiced plot T4 Shrub score: 1.8 **Legislation:** Natura 2000, habitat 9190 **Timeline – historical maps:** - 1954: heathland with scattered trees. - 1969: full forest cover, possibly under coppicing management. - 2005: full forest cover, coppicing management ceased. - 2024: full forest cover, coppicing management ceased. **Percentage petraea ancestry:** 72	

The two types of reference areas, *old coppiced* and *open areas*, were tested for differences in measured parameters (Table 5). It was found that only the percentage *Q. petraea* ancestry differed significantly, showing much higher values in old coppice areas than in open areas. Also, tree height was about 50% higher in old coppiced areas but this was formally non-significant (albeit close).

Table 5. Summary statistics and difference in mean values (±SD) between the two types of reference-plots (open areas and old coppiced areas, habitats combined) according to measured variables. N = 3-5 per mean value. Due to low sample size and heterogeneity of variance, non-parametric Mann-Whitney test was applied (T = Mann-Whitney test statistics).

Parameter	**Open areas**	**Old coppiced**	**T**	**p**
Shrub score (0-9)	3.0 (2.5)	3.2 (1.4)	8	1.000
Tree height (m)	9.9 (3.3)	15.9 (1.5)	12	0.057
Stem diameter (cm)	34.9 (21.7)	26.3 (0.2)	7	1.000
No. of stems	1.3 (0.4)	1.3 (0.5]	6	1.000
Quercus petraea (%)	38.7 (33.2)	91.8 (10.6)	15	**0.036**

Shrub score

To get an indication of whether the plots differ significantly in shrub score, a bar chart with ±95% confidence intervals were made (Figure 13). The large difference in confidence intervals between selected plots reflects, to a large extent, differences in sample size. For instance, plot 18(T5) includes only 3 sampled trees and hence shows a very wide confidence interval. In comparison, plot 1(T1) has 16 sampled trees and a narrow confidence interval. Several of the plots with the highest shrub scores (1, 2, 3 & 19) do not overlap with the plots with the lowest shrub scores (11, 12 & 17), indicating a statistically significant difference between the plots, which is analysed through further statistical testing (Figure 6).

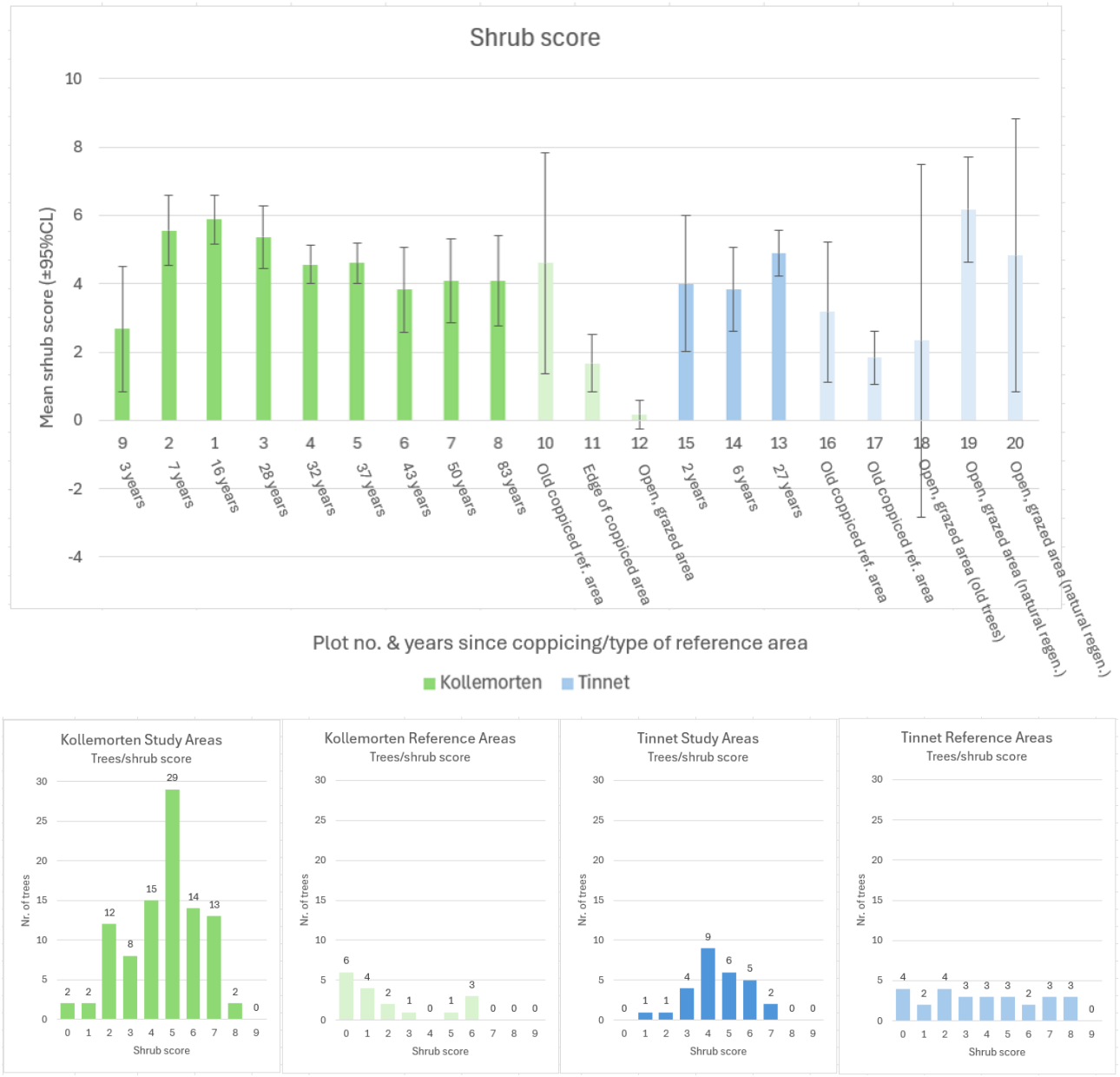


Figure 13. Bar chart of mean shrub score per plot (±95% confidence intervals) and number of trees with each shrub score per habitat and plot type. Dark green = Kollemorten study areas, light green = Kollemorten reference areas, dark blue = Tinnet analysis areas and light blue = Tinnet reference areas. Upper panel: n=3-16 per plot.

The average shrub score per plot ranges between 0.2 in plot 12(K11) to 7 in plot 2(K2). The average shrub score for all plots combined in Kollemorten was 4.2, while it was 4.1 in Tinnet. Excluding reference areas, the average shrub scores ranged marginally higher at 4.6 in Kollemorten and 4.5 in Tinnet, placing both sites in the lower end of the intermediate range on the 1-9 shrub score scale. The reference areas scored lower in both habitats, with an average of 2 in Kollemorten and 3.8 in Tinnet. The distribution of shrub scores across the scale showed a high number of intermediate values in both study areas and a more even distribution of shrub scores across the scale in the two reference areas (Figure 13).

A two-way ANOVA showed shrub scores that were significantly higher in the study plots compared to the reference plots (Figure 14). This pattern is statistically the same in both habitats (no interaction), however, study plots and reference areas in Tinnet Oak Shrub were numerically closer to each other than in Kollemorten (Figure 14).



Figure 14. Mean of mean shrub score in Kollemorten and Tinnet study areas and reference areas (±SD, N=3-9 plots). The adjacent table shows summary statistics of reduced model two-way ANOVA entering shrub score as dependent variable and habitat (Kollomorten vs. Tinnet) and plot type (study plots vs. reference plots) as fixed factors. Full model ANOVA showed no significant interaction between factors ($F_{1,16}$=1.661, p=0,216).

To evaluate the relative influence of the different measured variables on shrub score, a multiple regression analysis was carried out, entering shrub score as the dependent variable (old and young trees, study plots only) and coppice age, percent *Q. petraea* and tree height as predictors (see Data analysis for the exclusion of DBH and stem number in the analysis). The overall regression was highly significant ($F_{3,81}$=7.384, p<0.001), indicating that the three predictors together explain a significant proportion of the variance in shrub score. However, correcting each predictor for the influence of the others showed that only coppice age has an isolated statistically significant (and negative) impact on shrub score (Table 6).

Table 6. Summary statistics of multiple regression analysis with shrub score as dependent variable and tree height, log-transformed coppice age and arcsine-transformed percent Quercus petraea as predictors.

Predictor	t	p
Tree height (m)	1.335	0.186
Coppice age (years)	-3.454	**<0.001**
Q. petraea proportion (%)	1.147	0.255

Accordingly, relating shrub score of both old and young trees to the log-transformed number of years since a plot was coppiced (here based on plot means for simplicity), we see a marked decrease in shrub score the more time has passed (Figure 15). The relationship between shrub score and log-

transformed coppice age was statistically significant, and coppice age explains more than 75% of the variation in shrub score (r^2=0.776, p=0.002) (Figure 15).

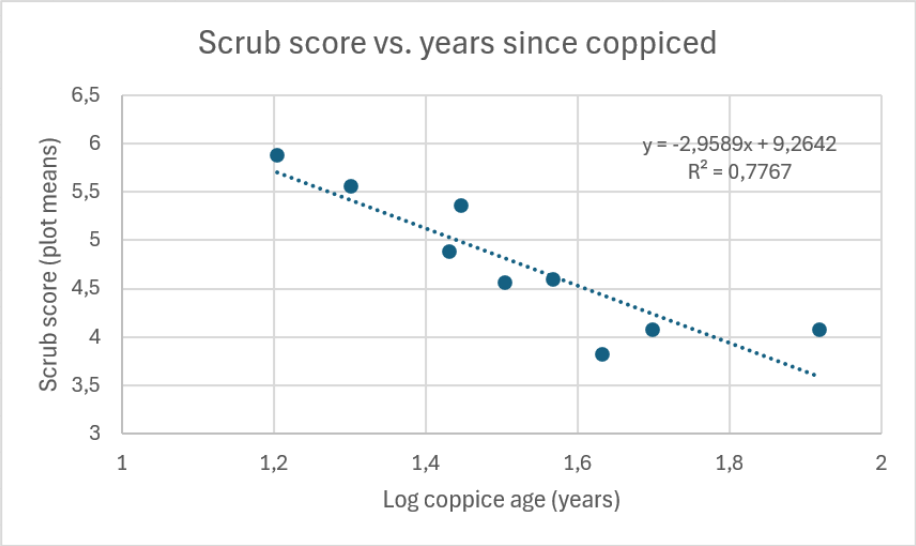


Figure 15. Linear regression between mean shrub score per plot of old & young trees and log-transformed coppice age (years since coppiced): $F_{1,7} = 24.041$, $r^2 = 0.776$, $p = 0.002$. Coppice age range between 16 years since coppiced to 83 years since coppiced.

Although the multiple regression analysis did not suggest any link between *Q. petraea*-proportion and shrub score (see above), this issue was further analysed using a different approach by testing differences in median shrub score between the three defined genotypes (admixed, *Q. petraea* and *Q. rubor*). This different analysis confirmed the results from the multiple regression analysis, as median shrub score was statistically similar across genotypes (Independent-samples Kruskal-Wallis test, K = 1.981, df = 2, p = 0.371, n = 163; medians for respectively admixed, *Q. petraea* and *Q. robur* = 4, 5 and 5).

Focusing solely on old trees, the relationship between shrub score and years since coppicing results in a somewhat different pattern (Figure 16). First a moderate increase in shrub score until twenty years after coppicing, followed by a drop until between 30 and 40 years after coppicing. Hereafter, the shrub score increases slowly from 4-5 to about 6 during the following 40-50 years. Shrub score decreased significantly as a function of coppice age during the first time period (16-37 years since coppice; r^2 = 0.706, p = 0.038 [one-tailed significance]). Note that the unit of analysis is plot means. Therefore, a drop from 7 to 4.6 can represent a considerable change (Figure 16).

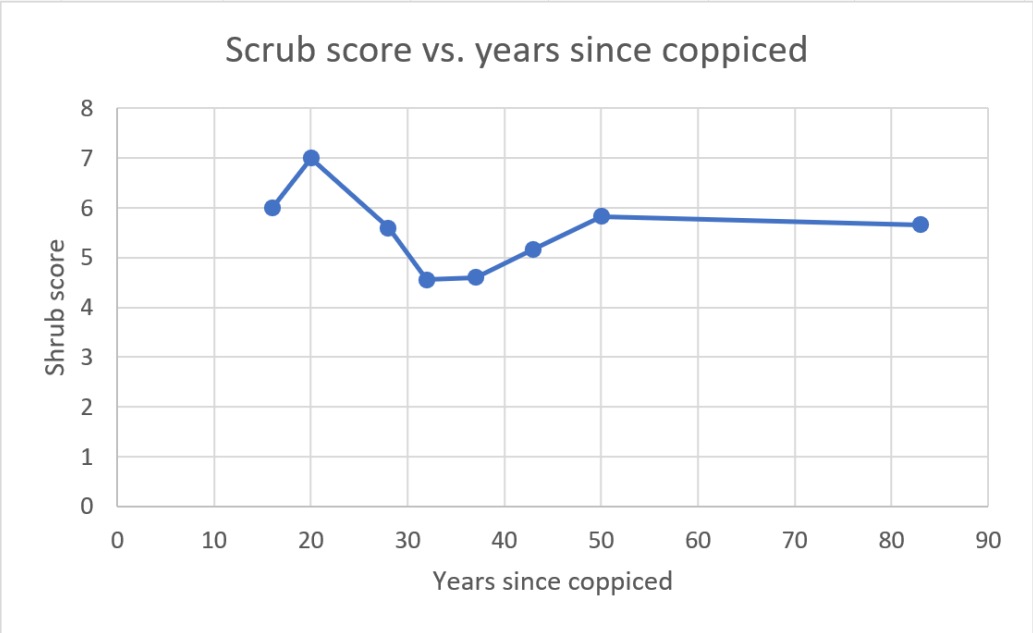


Figure 16. Mean shrub score per plot of coppiced old trees as a function of years since coppicing.

To obtain an indication of what lies behind the changes in shrub score over time, the nine different parameters of the shrub score have been divided into separate graphs (Figure 17). These graphs show different patterns in the years after coppicing. Some characteristics are more common in plots coppiced within the last decade, whereas others become rare in older plots (Figure 17).

1. *Irregular branching* increases slightly with time since coppicing. The average rises from 0.7 in the youngest plots to around 0.9 after 10-30 years and remains high in the oldest plots. This suggests that once irregular branching has developed, it is a relatively persistent structural characteristic.
2. *Horizontal branch planes* show a different pattern. They are rare in the younger stands, and most common 15-30 years after coppicing, but disappear almost completely after approximately 30 years.
3. *Branches below 1.3m* have a clear tendency. They are very common in plots coppiced 5-20 years ago but decline rapidly after 20 years to become almost absent from stands older than 35-40 years. This could be due to increased competition and canopy closure as the trees grow taller.
4. *Epicormic growth* is common throughout all the plots. Although the values fluctuate considerably, there is a tendency towards an increase with stand age, as some of the highest values occur after 40-50 years. Therefore, epicormic growth appears to be a persistent feature.
5. *No clear monoaxial stem* has approximately the same development over time as multiple stems. There is an overlap in these two parameters, as the multi-stemmed trees rarely have a clear monoaxial stem.
6. *Multiple stems* increase during the first decades after coppicing (although with substantial variation), obtaining the highest values 25-35 years after coppicing. The loss of stems with increasing stand age is a sign of competition between stems within individual coppiced trees.

The presence of multi-stemmed trees, even in older stands, indicates that coppicing can leave a structural mark for many decades.

7. *Angles greater than 30º* peak 15-30 years after coppicing followed by a gradual decline.
8. *Angles greater than 60º* show more variation, with the highest occurrence around 20-25 years followed by low values in most older stands.
9. *More than 10 bends in a stem* shows almost the opposite pattern to low branches and horizontal branching. This feature is uncommon during the first decades following coppicing but becomes more common in older stands, reaching its highest value in the oldest plots. This suggests that this type of stem crookedness, in Danish known as "slangetræer" or "troldetræer" may be a structural feature that develops over long periods rather than immediately following coppicing.

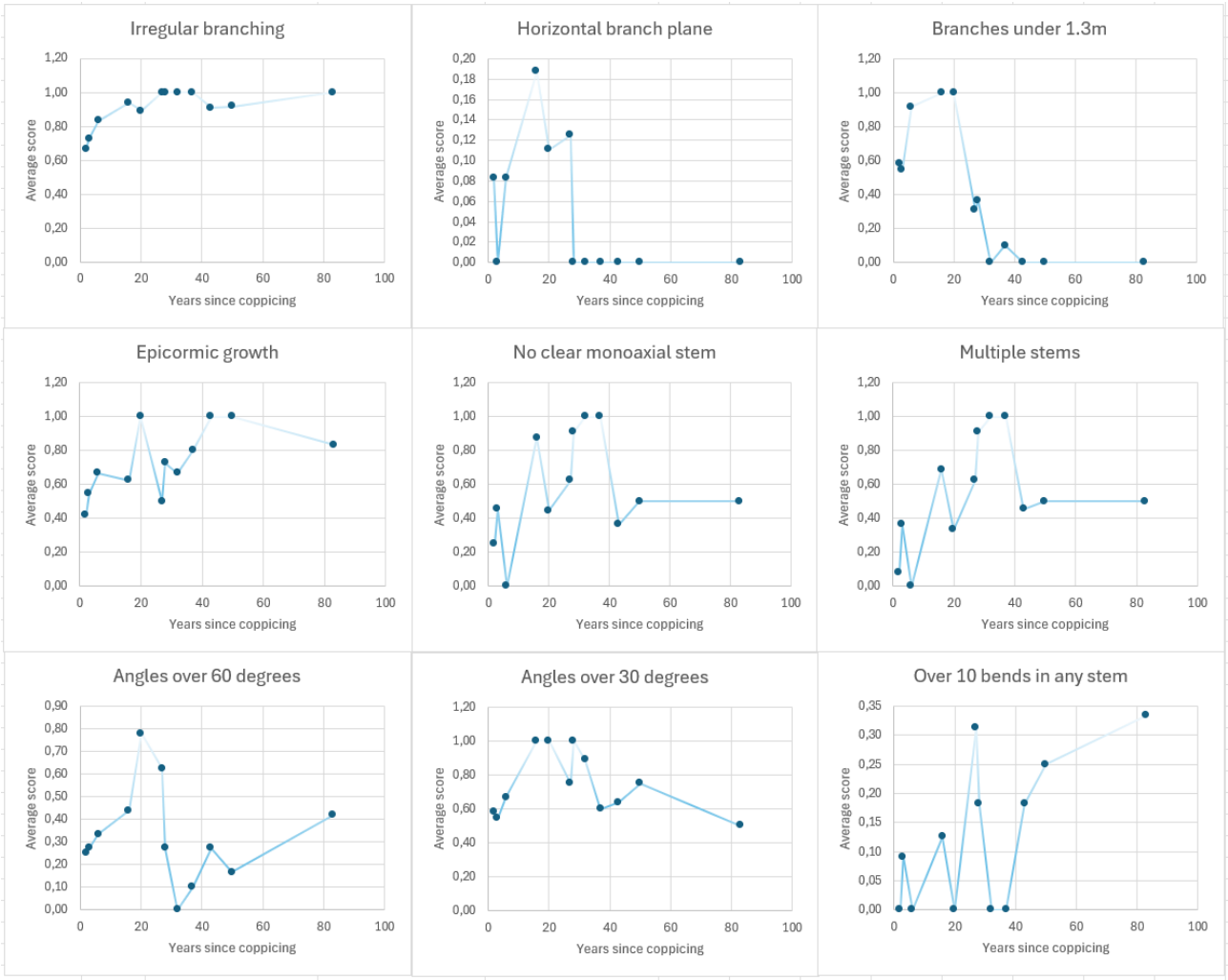


Figure 17. Shrub score parameters as a function of years since coppiced (N=126).

Tree height and DBH

The relationship between tree height across habitats and plot type was analysed by two-way ANOVA (Figure 18). No significant differences were found in tree height across habitats (Kollemorten vs. Tinnet) nor plot types (study vs. reference area), and no interaction. Therefore, the data from the two habitats were combined in further analysis.

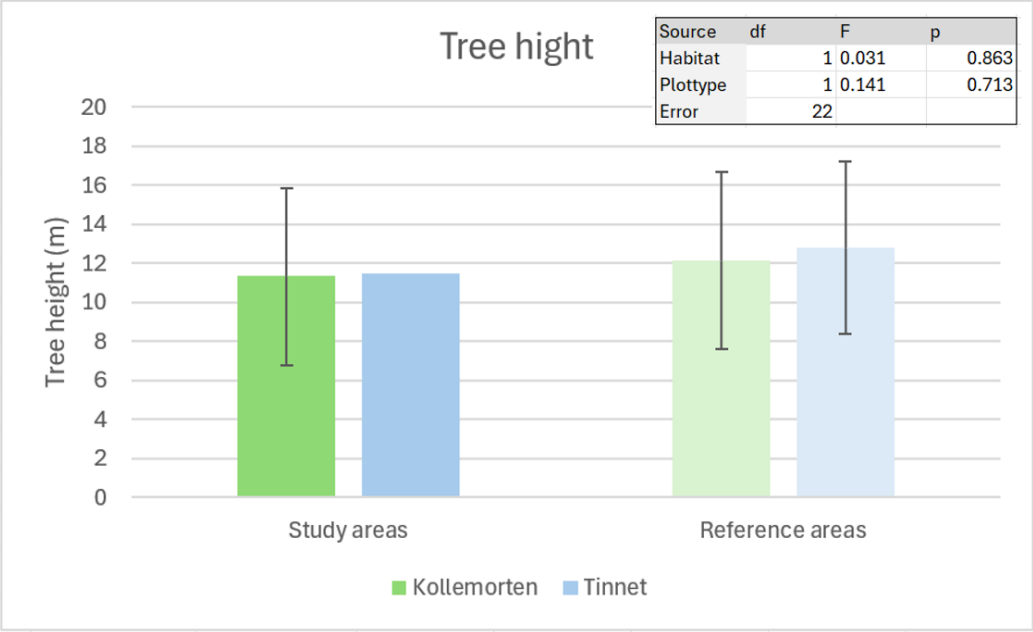


Figure 18. Mean of mean tree height (m) in Kollemorten and Tinnet study areas and reference areas (±SD, N=1-8 plots). Adjacent table shows summary statistics of reduced model two-way ANOVA entering tree height as dependent variable and habitat (Kollomorten vs. Tinnet) and plot type (study areas vs. reference areas) as fixed factors. Full model ANOVA showed no significant interaction between factors ($F_{1,12}$=0.007, p=0,935). Standard deviation missing in Tinnet study areas, as only one study area in Tinnet had tall oak trees present.

Mean tree height increased rapidly in the first approximately 35 years after coppicing, reaching around 14 to 15 m. Thereafter, the rate of height increase slows, and tree height appears to level off between 14 to 17m. This suggests that trees at these two locations may have approached their maximum height (Figure 19).



Figure 19. Mean tree height per plot (m) as the function of years since coppiced, showing also 3-order polynomial trendline. Data points include plot K1, K2, T1, K3-K8 (N=3-18). Plot T4, K9, T3 had no trees taller than DBH and were therefore excluded from this graph (n = 71).

The stem diameter at breast height (DBH) steadily increased with years since coppicing, showing the same trend as the height increase (Figure 20).

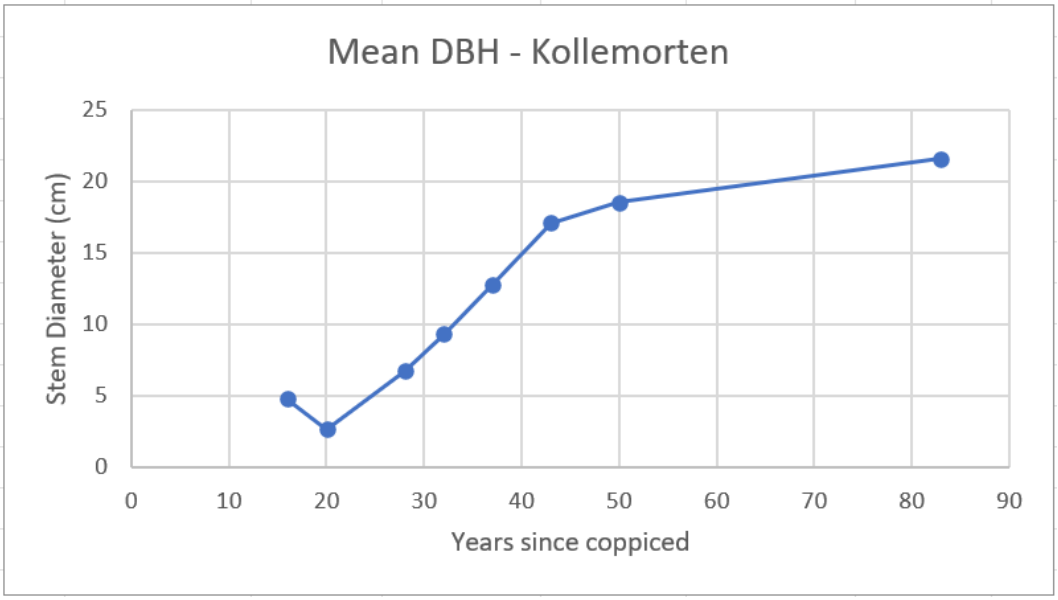


Figure 20. Mean stem diameter (cm) at breast height (1.3 m, DBH) per plot as a function of years since coppiced. Plots included: K1-K8 (n=61).

Stem number

Stem number shows no significant difference between habitats (Figure 21). Trees from reference areas, however, have overall fewer stems than those from study areas. This is the case for both Kollemorten and Tinnet Oak Shrub (no interaction).

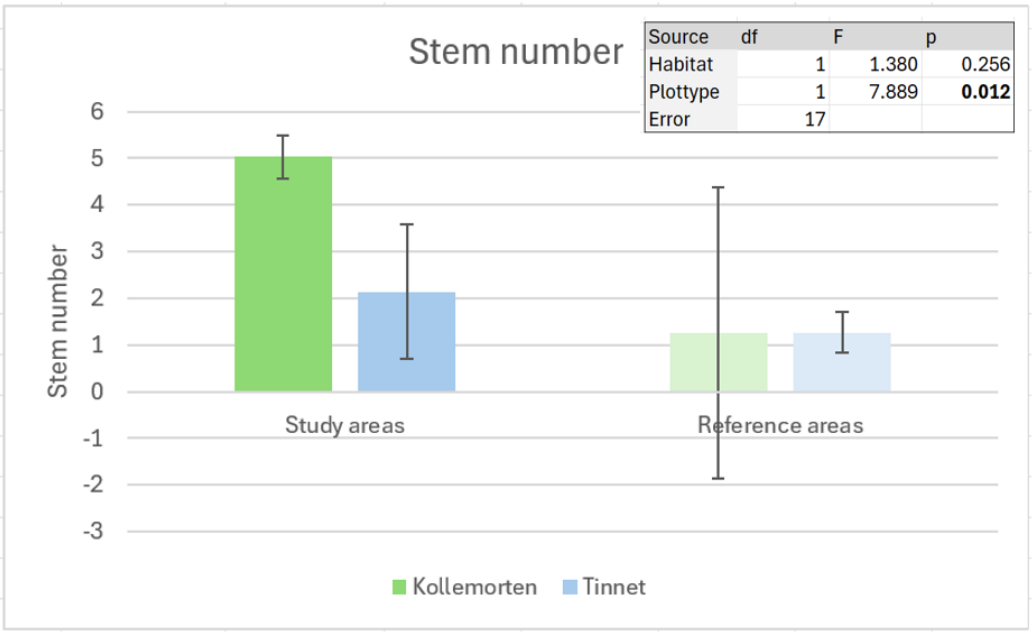


Figure 21. Mean of mean stem number in Kollemorten and Tinnet study areas and reference areas (±SD, N=8-12 plots). Adjacent table shows summary statistics of reduced model two-way ANOVA entering shrub stem number dependent variable and habitat (Kollomorten vs. Tinnet) and plot type (study plots vs. reference plots) as fixed factors. Full model ANOVA showed no significant interaction between factors ($F_{1,16}$=1.661, p=0,216).

The development in mean stem number in the years after coppicing in Kollemorten Oak Shrub (Figure 22), shows a steep increase during the first 5-10 years after coppicing. After approximately 15 years, the number of stems stabilises between 8 and 10 per tree. When the trees reach an age of 35-40 years, the stem number drops to around 4 per tree, where it more or less stabilises (Figure 22).

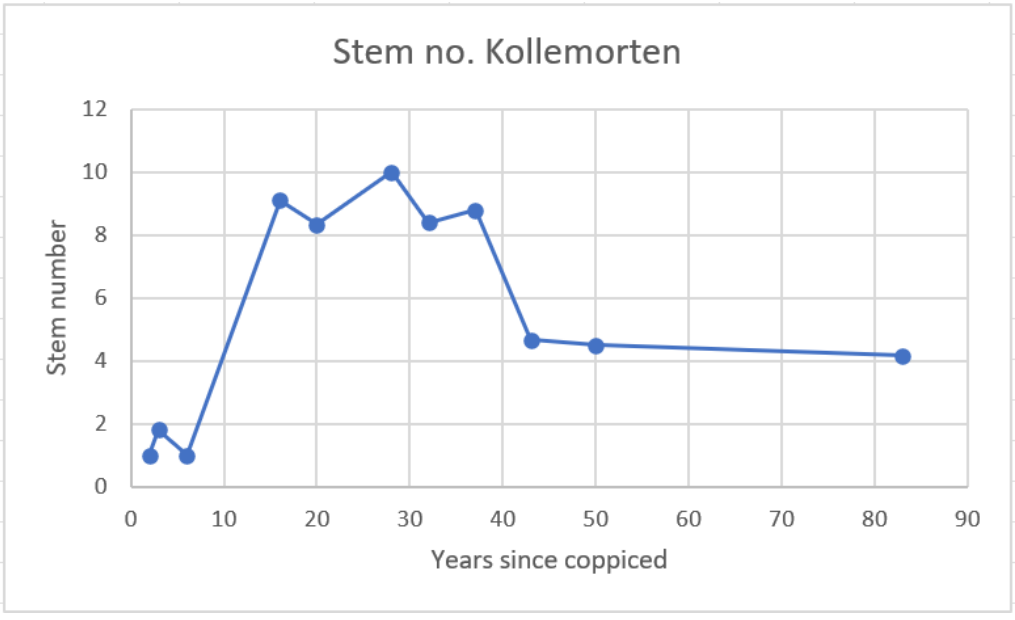


Figure 22. Mean stem number in the years after coppicing in Kollemorten Oak Shrub study areas. Each average is based on stem-number of n=9-16 trees per plot.

DNA results – genetic composition of sampled oak shrubs

A genetic analysis was performed to determine the ancestry of each individual tree in both Kollemorten and Tinnet habitats. Each tree was assigned a percentage representing its contribution from *Q. robur* and *Q. petraea* (Figure 23). Trees were then assigned either *Q. petraea*, *Q. robur,* or admixed based on their estimated ancestry proportions. If a tree had >0.90 (90%) *Q. petraea* it was considered a *Q. petraea*. If it had <0.10 (10%) it is defined as a *Q. robur*. Intermediate values of 0.10-0.90 (10%-90%) are considered admixed/hybrids.

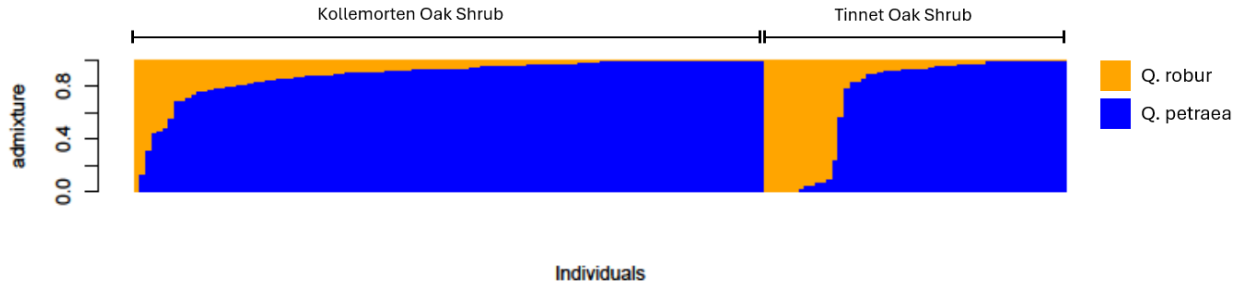


Figure 23. Barplot showing percentage Quercus petraea *(blue) and* Q. robur *(orange). Each bar represents one tree (n=164). Data based on DNA samples from Kollemorten (left) and Tinnet (right) Oak Shrub.*

The genomic analysis showed a marked variation in the proportion of *Q. petraea* vs. *Q. robur* ancestry among the sampled oak trees. Across all sampled plots, *Q. petraea* was the dominant species in most of the coppiced oak shrub stands (Figure 23). Considering the two habitats combined, the total number of admixed trees sampled was 42 individuals (26%), the total number of *Q. petraea* individuals sampled was 108 individuals (66%), and the total number of *Q. robur* individuals sampled was 13 individuals (8%), which is hence comparatively rare to the admixed and pure *Q. petraea* individuals.

The plots in Kollemorten were dominated by *Q. petraea* trees. The average proportion of *Q. petraea* ancestry ranged from 84% to 95% in study areas, with most plots exceeding 90%, while the reference areas in Kollemorten ranged from 57% to 98% (Figure 24). Combining study areas and reference areas, Kollemorten had 88% *Q. petraea* ancestry overall, while Tinnet had 62%.

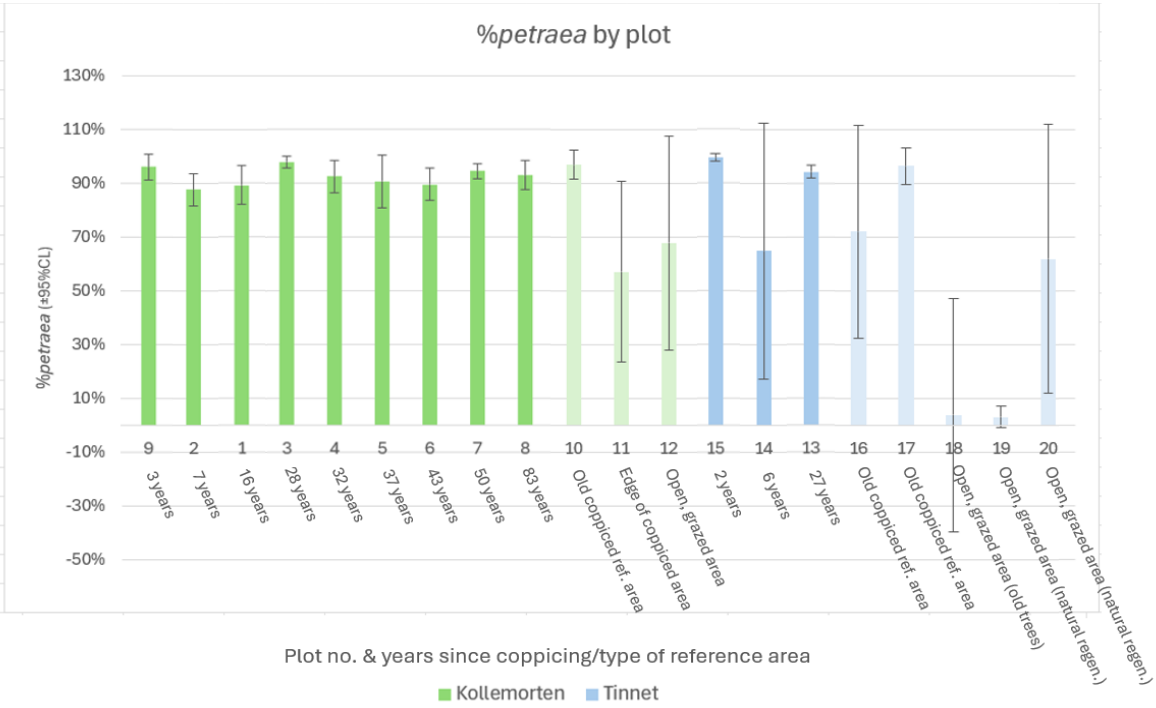


Figure 24. Bar chart: average percentage Quercus petraea per plot with ±95% confidence intervals. n=3-16 per plot. Dark green = Kollemorten study areas. Light green = Kollemorten reference areas. Dark blue = Tinnet study areas. Light blue = Tinnet reference areas.

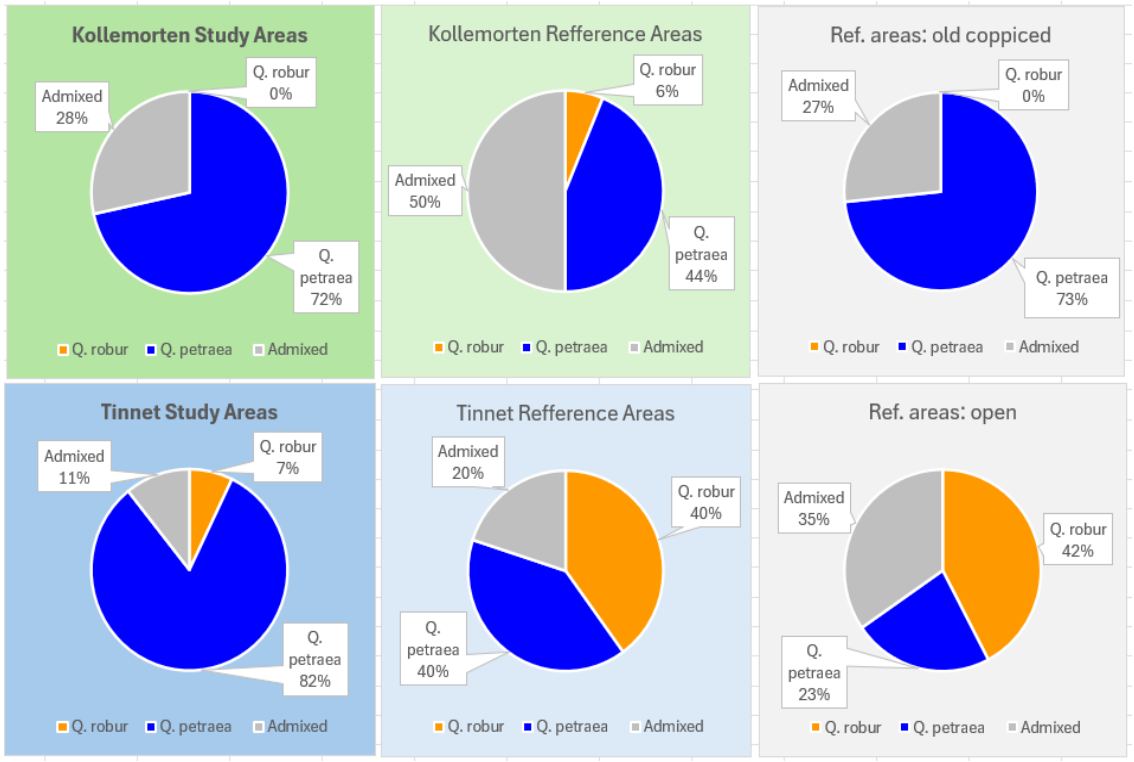


Figure 25. Cake charts based on number of pure species and admixed species: n=164. Blue = percentage of individuals with >90% Quercus petraea *ancestry. Orange = percentage of individuals with >90%* Q. robur *ancestry. Grey = percentage of admixed individuals.*

Admixed individuals were common throughout both habitats and occurred in nearly all plots. Pure *Q. robur* individuals were comparatively rare and primarily found in Tinnet plots, with only one pure individual found in Kollemorten (plot K11). Several plots showed intermediate average values (approximately 57-72% *Q. petraea* ancestry). A mixture of *Q. petraea*, *Q. robur* and admixed individuals was most common within plots, rather than pure populations composed of a single species. While most plots were genetically dominated by *Q. petraea*, hybridisation between *Q. petraea* and *Q. robur* was common, and only a small number of plots contained a substantial amount of *Q. robur* ancestry (Figure 25). The data analysis showed that the overall distribution of genotypes was significantly different between habitats (plot types combined; 2-way chi-square test $X^2_2 = 25.239$, $p < 0.001$, $n = 164$), as *Q. robur* tended to be more frequent in Tinnet, whereas the admixed was relatively more frequent in Kollemorten (Figure 26). *Q. petraea*, on the other hand, appears more or less evenly frequent in the two habitats. Similarly, the distribution of genotypes was significantly different between plot types (2-way chi-square test, $X^2_2 = 30.207$, $p > 0.001$, $n = 164$), in that *Q. rubor* was relatively more frequent in reference plots whereas *Q. petraea* was particularly dominant in study plots (Figure 26).

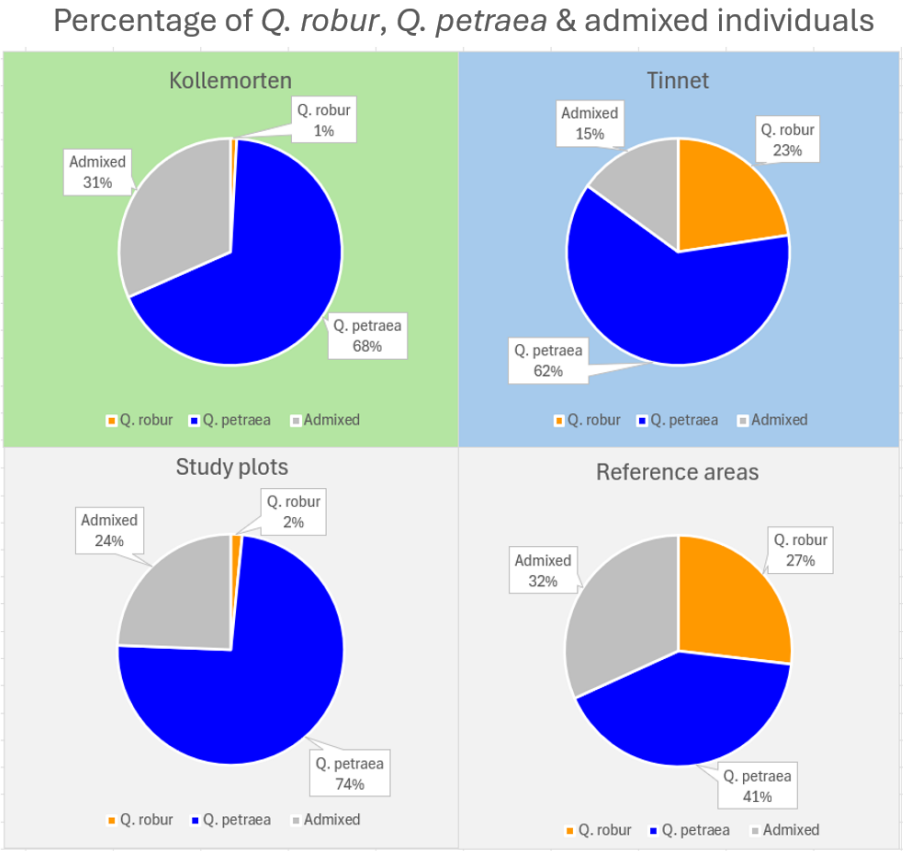


Figure 26. Percentage of tree ancestry per individual tree across habitat (plot type combined, upper panels) and across plot types (habitats combined, lower panels). Tree ancestry is categorized as either Quercus robur *(>90%*Q. robur *ancestry),* Q. petraea *(>90%*Q. petraea *ancestry) or admixed individuals (10-90%* Q. petraea *or* Q. robur *ancestry). There was significant difference between the two habitats (upper panels) regarding ancestry (2-way chi-square test $X^2_2 = 25.239$, $p < 0.001$, $n = 163$).*

The apparently evenly frequent occurrence of *Q. petraea* in both habitats is supported by the 2-way ANOVA analysing plot means of percent *Q. petraea* (Figure 27). Here there was an overall tendency for higher values in study areas than in reference areas, though this is not formally statistically significant (p = 0.082, Figure 27). This pattern is statistically the same in both Kollemorten and Tinnet Oak Shrub (Figure 27).

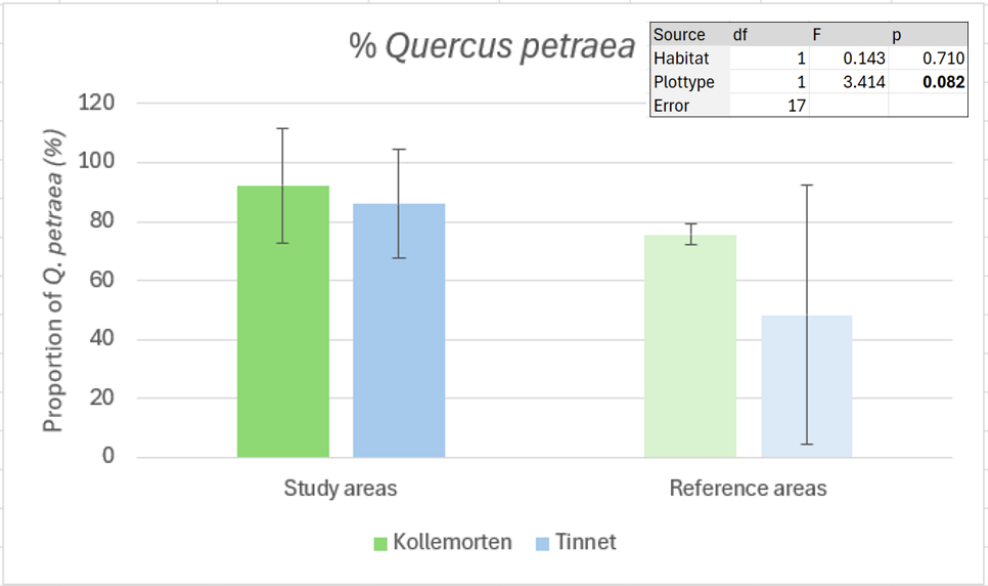


Figure 27. Mean of mean percentage Quercus petraea *in Kollemorten and Tinnet study areas and reference areas (±SD, N=3-9 plots). Adjacent table shows summary statistics of reduced model two-way ANOVA entering percentage* Quercus petraea *as dependent variable and habitat (Kollomorten vs. Tinnet) and plot type (study areas vs. reference areas) as fixed factors. Full model ANOVA showed no significant interaction between factors ($F_{1,16}$=0.844, p=0,372).*

To determine whether coppicing affects the genetic composition of the oak trees, an age-structured analysis was carried out. In Kollemorten study areas, old, coppiced trees (16+ years since coppicing) have 2 percent-point more *Q. petraea* ancestry on average than the young saplings (Figure 28). This difference was greater in Tinnet, as the old trees had 8 percent-point more *Q. petraea* ancestry on average than the young saplings. This difference becomes even bigger when comparing the ancestry of the old trees in study areas with the old trees in the reference areas. In Kollemorten, old trees in the study areas have 18 percent-point more *Q. petraea* ancestry than old trees in reference areas. Tinnet had an even higher divergence of 43 percent-point more *Q. petraea* ancestry in the old trees when comparing reference and study areas (Figure 28). There is no data for young saplings in Kollemorten reference areas, as there was no oak regeneration in these areas.

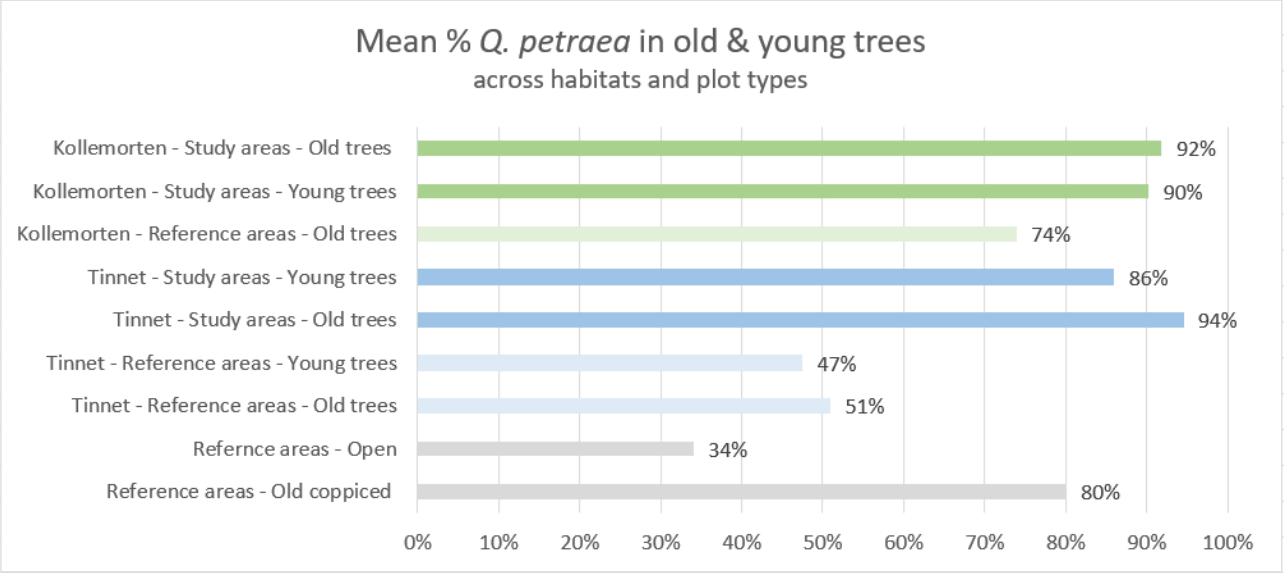


Figure 28. Average percentage of Quercus petraea *ancestry in young & old trees in Kollemorten & Tinnet Oak Shrub and test plots. n=164. Dark blue = Kollemorten Oak Shrub, light blue = Kollemorten reference areas. Dark green = Tinnet Oak Shrub, light green = Tinnet reference areas. Grey = reference areas divided into open grassland and old coppiced areas.*

When plotting the oak trees by ancestry in Google Earth, a non-random distribution appears in both habitats. Oak individuals with ≥90% *Q. petraea* ancestry is primarily found within the protected forest landscapes, while individuals with ≥90% *Q. robur* ancestry is primarily found in the open landscapes (plot K11, T5 and T6 on Figure 29), with only a few exceptions in plot T3 (Figure 29). The genomic assignments showed that Tinnet had fewer admixed individuals and a higher frequency of pure species than Kollemorten (Figure 26).

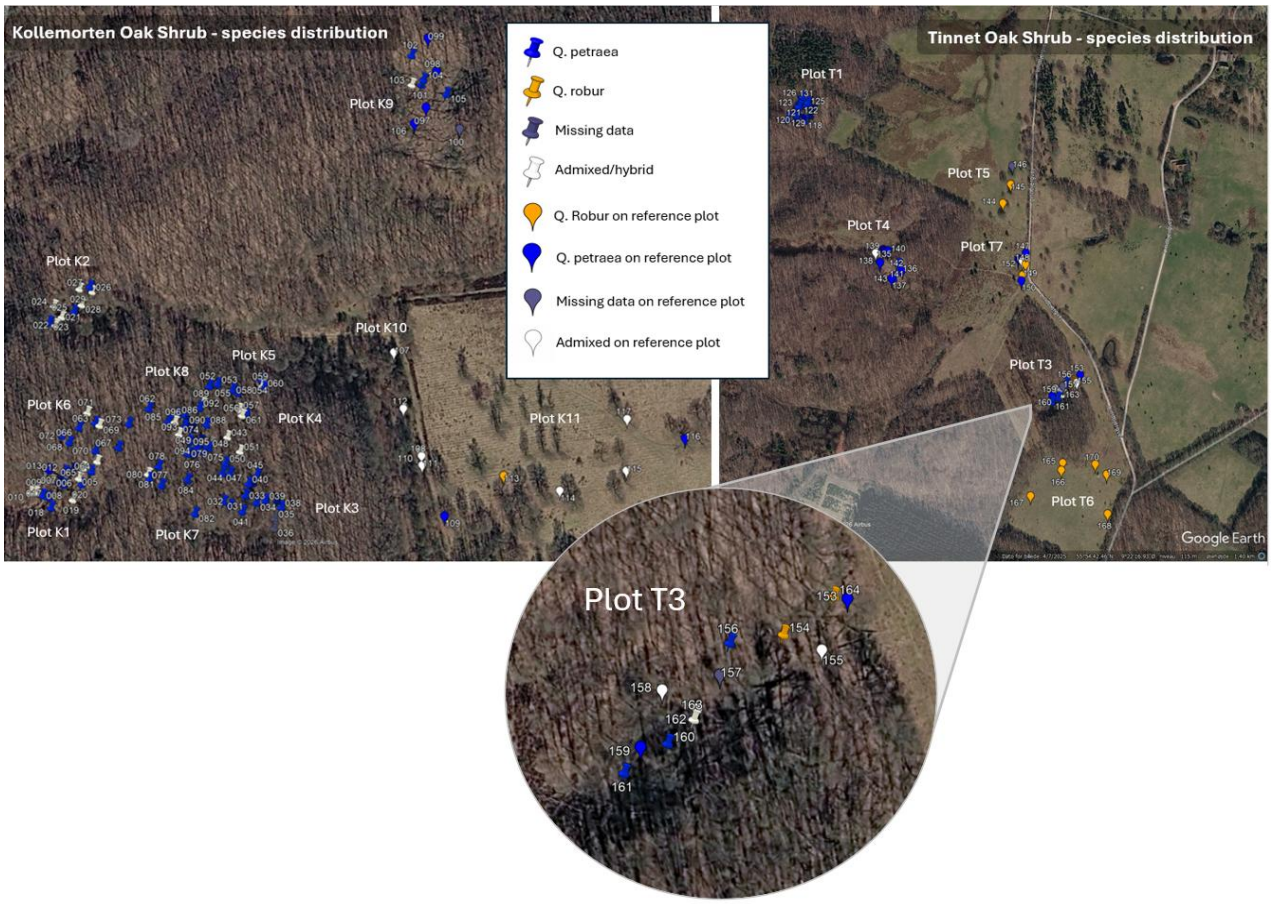


Figure 29. Species distribution of Quercus petraea, Q. robur *and admixed individuals in Kollemorten and Tinnet Oak Shrub. Blue marks =* Q. petraea, *orange marks =* Q. robur, *white marks = admixed/hybrids, Dark grey = data missing. Thumbtack = trees on coppiced plots, map markers = trees on reference plots. (n = 170).*

The genotype distribution differed significantly between grazed and ungrazed plots. Across all plot types and tree ages, *Q. robur* only occurs as a pure species (>90% *Q. robur* ancestry) in grazed areas (Figure 30).

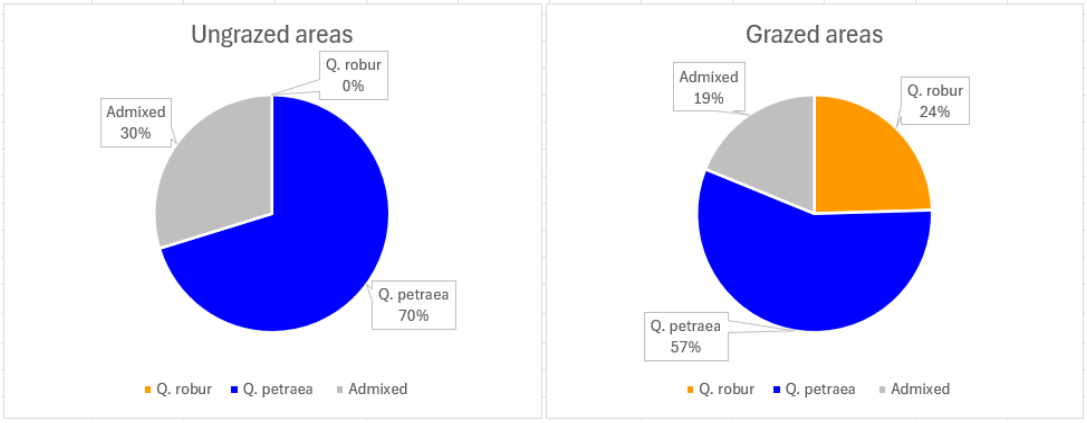


Figure 30. Ancestry based on whether an area has been grazed or left ungrazed. Data from all plot types and all tree ages combined. 2-way chi-square test, $X^2_2 = 26.799$, $p < 0.001$. Grazed areas: n=53. Ungrazed areas: n=111 Blue = individuals with >90% Quercus petraea *ancestry. Orange = individuals with >90%* Q. robur *ancestry. Grey = admixed individuals.*

Analysis & discussion

Transition from oak shrub to high forest

The average shrub score across all plots was 4.2 in Kollemorten and 4.1 in Tinnet, placing both sites in the lower end of the intermediate range on the 1-9 shrub score scale (Figure 14).

The relationship between shrub score and years since coppicing supports the interpretation that coppicing leads to more shrub-like characteristics in the oak trees. The relationship between shrub score and log-transformed coppice age was statistically significant and explained a considerable proportion of the variation in shrub score (R^2=0.776, p=0.002). The graph based on these data showed a declining linear regression. This indicates that shrub characteristics decline with time gone since coppicing. However, it does not disappear immediately. Even the oldest coppiced stands had some individuals with intermediate shrub characteristics.

When analysing the raw data of the coppiced trees, the highest shrub scores are found around 20 years after coppicing, decreasing from 7 to 4.6 ten years later. Here it would be expected that the shrub score keeps decreasing, however, after 40-50 years after coppicing, the data show a small increase in shrub score (Figure 16).

This aligns with the overall impression of the two areas, where many stands still contain visible shrub characteristics, but have developed considerably towards high forest. This development is seen across several of the parameters investigated in this thesis, including shrub score, tree height and stem number. These variables show that the longer time has passed since coppicing, the more the structure changes towards high forest, however, this is not the whole story. The nine different shrub scores analysed together and separately suggest that development after coppicing is not just a linear development from a high shrub score in the years after coppicing to a progressively lower shrub score (Figure 16+17). The different parameters of the shrub score emerge and disappear at different stages. Right after coppicing, the new saplings have not had time to develop many of the structural features associated with mature oak shrubs. In the 10-30 years after coppicing, several shrub characteristics increase, such as low branches, multiple stems, large stem angles and the absence of a clear monoaxial stem. This is the time period with the highest shrub scores. After approximately 30-40 years, low branches and horizontal branch planes disappear, and multiple stems become less frequent (Figure 17). These changes are a sign of the transition toward a high forest structure with taller, denser trees, where the competition for light plays a role in the tree's development. However, the shrub score in the older stands shows a slight increase, showing that they do not lose all of their previous shrub structure (Figure 16). Irregular branching and epicormic growth stay common, and stems with many bends (Danish: slangetræer or troldetræer) become more pronounced. The succession toward high forest appears to remove some oak shrub characteristics while preserving or accumulating others. Therefore, the shrub characteristics of an old, formerly coppiced oak stand still show signs of its previous management, even 83 years after coppicing.

The shrub score was significantly higher in the coppiced study areas than in the uncoppiced reference areas in both Kollemorten and Tinnet Oak Shrub. The study areas in Kollemorten and Tinnet had

average shrub scores of 4.6 and 4.5, while reference areas had average scores of 2.0 in Kollemorten and 3.8 in Tinnet. In Tinnet Oak Shrub, the coppiced areas and reference areas were numerically closer to each other than in Kollemorten. This could be explained by the higher percentage of *Q. robur* in Tinnet shrub (12% *Q. robur* in Kollemorten, 38% *Q. robur* in Tinnet). *Q. robur* naturally portrays several of the shrub-like characteristics, even without coppicing management, such as lacking monoaxiality and irregular branching. The low scores in the reference areas could be an indication that coppicing management does lead to a higher shrub score, where the trees show crooked stems, multiple stems, low branches, irregular branching and other structural characteristics found in traditional oak shrub systems. However, the reference areas on open land, with strong signs of browsing (T6, T7) showed relatively high shrub scores (T6=s6.2, T7=s4.8), which are comparable with the coppiced plots on Kollemorten.

Tree height showed the opposite pattern. The height data showed an average height of 4-6 meters within the first ten years. This is within the average height growth of oak trees in Denmark (Appendix 4.b). Average tree height then increased rapidly during the first approximately 35 years after coppicing, reaching around 14- 15 m. Thereafter, the growth rate slowed, and tree height appeared to level off between 14 and 17m. This indicates that much of the vertical growth happens within the first three to four decades after coppicing. The stands become relatively tall within a short period, even though their morphological transition towards a regular high forest structure continues beyond this point. The levelling of height should not necessarily be interpreted as the maximum height of oak trees in these two sites, since the data represent a snapshot of the different plots rather than repeated measurements of the same trees. However, it suggests that the trees in these two habitats have approached their site-dependent maximum height after 35-50 years. The oldest plot (83 years since coppicing management) has an average height of 16.7m, which supports this interpretation. The increase in height does not alone mean that the stands have become high forest, but rather that the area is developing towards a high forest structure, as the trees in the study areas still exhibit shrub-like characteristics and predominantly originate from coppiced shoots. Structurally, Danish oak shrubs can range from low shrub-like stands to taller forests that almost resemble high forest, and the boundary between the two is more gradual rather than fixed.

Stem number also shows evidence of development towards high forest, as the reference areas generally contained fewer stems than the coppiced study areas in both Kollemorten and Tinnet Oak Shrub. Looking at the development in coppiced areas, we see a sudden increase in stem number in the first ten years. This is due to the coppicing management, but also likely due to the high browsing pressure from the red deer and roe deer in the area. The trees reach 8-10 stems per tree 20 years after coppicing. This number is relatively stable until 30-40 years after coppicing. As the stand develops, competition between the stems increases. Some stems are shaded out, while a smaller number of stems dominate the canopy. The data show a drop in stem number from 8-10 to 4-5. This number seems to be stable, as the data show approximately the same average stem number in the plot that was coppiced 83 years ago. This self-thinning leads to fewer and larger stems as time passes, however, it does not lead to a more open canopy, as the canopy of the other stems gradually takes over, while others are being shaded out. To achieve a more open oak shrub that supports the light-demanding species connected to this nature type, a thinning regime or selective cutting may be necessary.

When shrub score, tree height and stem number are considered together, the transition appears to begin within the first decades after coppicing. Height increases rapidly, while the number of surviving stems and the number of shrub-like characteristics gradually decline. The results show a continuous transition towards high forest, rather than a single point, where the oak shrub suddenly becomes high forest. Looking at the data from Kollemorten and Tinnet, the rapid change in height appears to occur during the first 35 years, while the reduction in shrub score is continuous from 16 all the way to 83 years after coppicing. After around 40 years, the stands are relatively tall, but they may still contain old coppice structures with multiple, crooked stems. In plots that have not been managed for a longer time (30+ years), these characteristics are mainly found in the old trees, while the general stand becomes taller, closed and more forest-like.

Several sources (Friis Møller et al., 2002, 2002; Gram et al., 1944; Worsøe, 1982a), and the hypothesis of this thesis, state that the preservation of Danish oak shrubs requires historical management types such as grazing and coppicing, and that oak shrubs left unmanaged will develop from shrubs towards high forest. The results in this analysis support this hypothesis, with data showing that Kollemorten and Tinnet Oak Shrub are examples of this transition. However, the result also shows that single coppicing events only preserve selected components of the shrub structure permanently, while others disappear around 20 years after coppicing. Findings in Tinnet oak shrub plot T1 show that coppicing on its own, in some cases, can cause oaks in the area to disappear completely. In this particular case, the oak death could be due to the tall surrounding stands and high browsing pressure. Other studies have found that oak shrubs have a finite number of times that the oaks can survive being coppiced. Therefore, another reason for the dead oaks on plot T1 could be that the plot historically has been coppiced too many times (Worsøe, 1982a).

Historical oak shrub management did not consist of only one isolated coppicing, but consisted of several coppicing rounds, with thinning, grazing and selective cutting in between. This creates multiple stems and increases light availability to the forest floor, where grazing and browsing is necessary to maintain the light forest floor and create low branches, irregular architecture and an open stand structure over longer periods of time (Jensen, 2000). The importance of grazing and browsing is seen in the data, as the highest individual shrub scores are found outside the coppiced plots. The uncoppiced reference areas T6 and T7, both situated on open land with clear signs of browsing and with a history of cattle grazing, exhibit shrub scores comparable to the highest shrub scores found in the coppiced plots. This suggests that extensive browsing alone may maintain several shrub-like characteristics, even without coppicing management, as the browsing repeatedly removes shoots, suppresses apical dominance and starts growth of new branches from dormant buds. Therefore, to maintain the structural elements of these systems, we must manage not only with solitary coppicing events, but with management that more closely resembles the historical management practices, involving repeated interventions combined with grazing and browsing.

Today, historical management types may not be enough to maintain the shrub-like characteristics anymore, due to nitrogen deposition. Tybirk and Strandberg (1999) found that the cessation of management, combined with historical nitrogen deposition, led to a decrease in biodiversity (Tybirk & Strandberg, 1999). This increase in nutrients could give an advantage to species such as *Fagus*

sylvatica and *Picea abies*, which can pose a threat to oak shrubs. The development of Hald Ege represents a later stage of the same successional direction observed in Kollemorten and Tinnet. The stands become taller, denser and darker when traditional management ceases. The results from Kollemorten and Tinnet Oak Shrub indicate that this transition is already very advanced. The coppicing characteristics are still visible in individual trees, but the overall structure of many plots is increasingly characterised by tall trees, fewer stems and relatively low shrub scores. However, with the knowledge that we have today, to preserve the open, crooked and multi-stemmed character of the oak shrub in Kollemorten and Tinnet, rather than merely maintaining oak-dominated forest with selected shrub characteristics, a continuous coppicing management regime, possibly every 40 years, depending on site conditions, combined with selective cutting and grazing.

Genetic Composition & Spatial Distribution of *Q. robur* and *Q. petraea*

Historical records mention *Q. petraea* as being rare in Denmark, apart from Bornholm and a few places on the west coast (Fritzbørger, 1992). The findings in Kollemorten and Tinnet Oak Shrub point to something different. The data revealed that a mixture of pure species of *Q. petraea* and *Q. robur* and admixed individuals are present in both habitats. This mixture was genetically dominated by *Q. petraea* dominating across study areas, habitats and most reference areas, with 66% of the trees having >90% *Q. petraea* ancestry. The mix. between *Q. petraea* individuals, *Q. robur* individuals and numerous admixed individuals shows that the stands consist of an oak species complex rather than populations of two separate species. Although both species are present in both habitats, their distribution has shown a non-random spatial pattern, with a higher percentage of *Q. petraea* ancestry in Kollemorten compared to Tinnet (Figure 26). Furthermore, there is a tendency towards a higher percentage of *Q. robur* individuals in the newly coppiced study areas and on the open, wind-exposed, and browsed reference areas. In comparison, individuals with higher *Q. petraea* ancestry show a strong tendency to occur in plots that have remained under forest cover for several decades, where the trees are less exposed.

A thesis made by Mathilde Lundt Larsen (Lundt Larsen, 2025) showed that the two species occupy different ecological niches in Kaas Skov, with *Q. robur* showing a preference for forest edges and wind-exposed areas, while *Q. petraea* is more dominant in the denser forest interior. This conclusion aligns with the spatial distribution found in Kollemorten and Tinnet Oak Shrub, as the distribution of the trees was reflected in the genetic composition. When testing the genetic composition of trees standing on plots that show high forest characteristics; closed canopies and a darker forest floor, a significantly higher percentage of the trees were categorised as *Q. petraea* individuals. This tendency could also be detected on plots that were newly coppiced but had been under closed canopy for several decades before coppicing. This could indicate that trees with a higher percentage *Q. petraea* ancestry have an ecological advantage the more the area develops towards high forest. Trees with a relatively high amount of *Q. robur* ancestry were primarily found on the open, wind-exposed areas.

When comparing the genetic composition of old trees (16+ y/o) and young saplings a tendency towards a higher percentage of *Q. petraea* ancestry in the old trees versus the young saplings emerged.

Only two plots (T5 & T6) showed a dominating *Q. robur* population, and both of these plots are open, grazed areas.

As *Q. robur* has stronger pioneer characteristics than *Q. petraea*, with a bigger acorn and higher tolerance towards drought in the early years, it could be expected to see a higher frequency of *Q. robur* in the young saplings found on recently coppiced plots. However, this was only partly the case. When looking at the data from the newly coppiced plots (T4, K9, T3 and K1) the plots in Kollemorten had saplings with 89-96% *Q. petraea* ancestry, while the saplings in Tinnet had a bigger range of 65-99% *Q. petraea* ancestry (Figure 28). These results show a slightly higher percentage of *Q. robur* saplings in the newly coppiced plots. However, *Q. petraea* individuals still dominated, which may reflect the genetic composition of the surrounding mature trees, in the older coppiced stands, where *Q. petraea* individuals were most common.

The only mature trees with >90% *Q. robur* ancestry were found standing in the open, wind-exposed, grazed areas (T5 & K11), while older coppiced stands (≥16 years since coppicing) contain almost exclusively individuals with >90 percentage *Q. petraea* ancestry or admixed individuals with dominating *Q. petraea* ancestry. This indicates that the individuals with the most *Q. robur* ancestry are disappearing with time. In the plot descriptions, we see a pattern of saplings being absent in the older coppiced plots. On plots coppiced between 3 and 20 years ago, an abundance of oak saplings was observed. In the plot coppiced 27 years ago, few saplings were observed, primarily at the edge of the plot. On the plots coppiced between 28 and 83 years ago, either no saplings were found, or merely one to two were found at the very edge of the plot (Table 4). This could indicate that the saplings are being shaded out as the stand develops towards a high forest system or succumb to browsing before they grow to a size that can compete with the coppiced trees. Coppiced trees may have a competitive advantage over seed-derived saplings, as the already well-developed root system allows them to regenerate quickly and potentially outgrow and shade out the smaller saplings. In contrast, the open, grazed reference areas contained a higher proportion of *Q. robur*, suggesting that environmental conditions in these areas favour *Q. robur*. Traits such as larger acorns and higher frost and wind tolerance during early growth may give *Q. robur* a competitive advantage in the open areas.

The higher percentage *Q. robur* ancestry in Tinnet Oak Shrub could be due to the history of Tinnet, with much of the area being open heathland, as seen on historical maps from 1954. This is seen specifically on plot T3, which has a shorter history of being under forest cover (*Krak.dk*, 1954). The overall data in Tinnet Oak Shrub show a higher percentage of individuals with >90% *Q. robur* ancestry and a higher percentage of *Q. robur* genes on average. Based on these data, it could be hypothesized that the higher amount of *Q. robur* ancestry is a result of the historical management on a landscape scale, going back 100 years. The history of the area could be the reason why *Q. robur* is seen in higher numbers. The opposite is the case in Kollemorten Oak Shrub, where most of the area has been under forest cover for centuries (Appendix 1.d).

When adding the second component: grazing, we see that pure *Q. robur* individuals were exclusively located in grazed areas such as study area T3 and reference areas T5-T7 and K11. This could indicate that grazing as management plays a considerable role in shaping the genetic composition of the oak populations. The driving factors that lie behind this could be a combination of the open conditions

created by grazing, which favour *Q. robur*, and the competitive advantage of *Q. robur* under browsing pressure.

When the average genetic composition of each plot was compared between grazed and ungrazed areas (Figure 28), the difference between the two groups was only 4.9%, with grazed areas having an average of 83.5% *Q. petraea* ancestry, compared with 88.4% in ungrazed areas. Based on the spatial distribution of the two species, a larger difference was expected, with grazed areas containing more *Q. robur* and less *Q. petraea* ancestry. When analysing the data, two plots stood out, as they contributed particularly high *Q. petraea* values to the average of the grazed area. These were the newly coppiced plots where felled trees had been left as deadwood (T4 = 99% *Q. petraea* and K9=96% *Q. petraea*). One possible explanation could be that the deadwood provides shelter and protects the oak saplings from browsing and drought, potentially removing the competitive advantage that the *Q. robur* saplings had over the *Q. petraea* saplings. However, when comparing the ancestry in plots coppiced 20 or fewer years ago with whether deadwood had been left in the area, no apparent pattern appeared (Appendix 5.b). The apparent effect of deadwood should therefore be interpreted with caution and cannot be confirmed with the present data.

A gradient can be detected, with 80-99% *Q. petraea* ancestry within the closed canopy coppiced systems, 57% *Q. petraea* ancestry on the edge of the systems and 3-68% *Q. petraea* ancestry on the open grassland surrounding the oak shrubs. This indicates a high selection pressure, as the two oaks are found in markedly different niches. This could be the reason why we still see a mixture of *Q. robur*, *Q petraea* and admixed individuals, as the trees occupy prominently different areas in the landscape. The landscape in Tinnet Oak Shrub is more diverse, with larger, open areas between the coppiced oaks combined with a larger area being grazed. The genomic assignments showed that Tinnet had fewer admixed individuals and a higher frequency of pure species than Kollemorten (Figure 26). Overall, there was an almost even amount of *Q. robur, Q. petraea* and admixed individuals in Tinnet Oak Shrub, which could be due to the more diverse landscape and the two species' tendency to occupy different niches. This diversity in the landscape was also reflected in the shrub score, where the shrub score values were evenly distributed across the scale (Figure 13).

Perspectives

Legislation and protection of the oak shrubs

The legislation that affects Kollemorten and Tinnet Oak Shrub is an example of the gap between conservation policy and ecological reality. The two areas are partly protected under the EU's Natura 2000 network, as habitat 9190 ("*Old acidophilous oak woods with Quercus robur on sandy plains*")(*Natura 2000 Viewer*, 2026). This definition assumes that the areas are dominated by *Q. robur*, however, the findings of this research reveal that it is quite the opposite, with a composition dominated by *Q. petraea*. Danish oak shrubs could represent a unique species complex that does not fit into existing European legislation.

Danish oak shrubs are uniquely dynamic ecosystems because their existence is defined not just by natural succession, but by centuries of integrated cultural and historical management types. Furthermore, the recent designation of these areas as set aside (Danish: urørt skov) in 2021 introduces new management difficulties (NST Forvaltningsplaner, 2025). Under these regulations, the Danish Nature Agency is prohibited from removing the majority of the harvested wood, requiring it to be left on-site as deadwood. The results of the genomic analysis on plots T4 and K9, show that this deadwood could play a role as a protective microhabitat that shields the saplings from browsing, drought and frost, effectively removing the competitive advantage *Q. robur* saplings had as a pioneer species. Therefore, current protection laws may accelerate a genetic shift toward *Q. petraea*, and the structural elements caused by disturbances in the early years of the tree's lifespan. This could go against what both the Natura 2000 legislation and the Danish Oak Shrub protection aims for. To ensure the intended protection of Danish oak shrubs, new legislation is needed, both on a European level and a national level.

A challenge in the conservation of Danish oak shrubs is the unclear definition of what it is that we are protecting. Although the Danish Forest Act aims to preserve certain characteristics (low, multi-stemmed, crooked growth), the legislation does not specify how low or how crooked a tree must be to qualify and there is no clear definition of exactly what should be maintained (Appendix 4.d, (1995 LSF 151 ÆNDRING AF SKOVLOVEN, 1996; Skovloven, 2009)). This raises the question of whether the conservation aim is to preserve the structural characteristics of the trees, the historical management that created these structures, or the biodiversity connected to the open conditions of traditionally managed oak shrubs.

Future research

The findings on genetic and structural development in Kollemorten and Tinnet Oak Shrub highlight several areas for more potential research. Examples of these areas are effects of light availability on the forest floor, the effect of deadwood on genetic composition in saplings and the effect of grazing on height increase in oak shrubs. These topics are further described below.

Light availability on the forest floor

Future research could investigate how light availability changes as oak shrubs develop after coppicing. The data in this thesis show that the stands become taller and more closed with increasing

time since coppicing, while shrub characteristics gradually decline. It could be interesting to measure canopy openness or light levels at the forest floor across plots of different ages to identify when conditions become too shaded to maintain the characteristic open oak shrub vegetation. These studies could include botanical observations of understory species composition, as changes in light availability is reflected in the loss of light-demanding species and an increase in more shade-tolerant vegetation. This could work as an ecological measurement of when management such as coppicing, selective cutting or grazing should be repeated. Measuring light availability together with DNA sampling of seedlings and mature trees could help determine if the darker overstory creates a selection pressure towards the more shade-tolerant *Q. petraea*.

Genetic composition in oak shrubs

The results of this thesis indicate the genetic composition of oak shrubs may change as the stands develop towards high forest. *Q. petraea* ancestry becomes increasingly dominant in older, closed canopy stands, whereas *Q. robur* was more often found in open areas and in newly coppiced areas. This is interesting when compared with the historical observations of Gram et al. Their survey found *Q. robur* in almost all investigated oak shrubs, while *Q. petraea* occurred less frequently. *Q. petraea* was recorded in only 53% of the "forest oak shrubs", which, according to their descriptions, is comparable to the old, coppiced areas in Kollemorten and Tinnet Oak Shrub. Comparatively, *Q. robur* was found in 100% of the forest oak shrubs (Appendix 4.e, (Gram et al., 1944)). This difference between the historical observations and the dominance of *Q. petraea* found in the closed stands raises several questions. Has the species composition of Danish oak shrubs changed as traditional management disappeared? Is the historical data incorrect, as the species identification was purely based on morphological characteristics, while the data in this study are based on genetic analysis? Or are the results in Kollemorten and Tinnet Oak Shrub not representative of the species composition in other oak shrubs that are developing into high forest?

Conclusion

The Danish oak shrubs are developing into high forest. This gives an advantage to *Q. petraea,* leading to this species being dominant, and *Q. petraea* is much more common than we thought. If we want to manage for *Q. robur* we need measures that secure more light and disturbance in the shrubs. Coppicing helps but is not enough – grazing and browsing plus maybe selective cutting should be added to the management regime.

This study investigated the structural development and genetic composition of Kollemorten and Tinnet Oak Shrub in the decades after coppicing. A chronosequence of oak shrubs, coppiced 2-83 years ago, was investigated as an indication of the development over time. The results show that, when left without repeated management, the stands gradually develop from the characteristic open oak shrub structure towards a taller and more closed high forest structure.

This structural development was visible across several of the investigated parameters. Tree height increased during the first approximately 35 years after coppicing, after which it levelled off around 14-17 m. Stem number increased after a coppicing event, reaching an average of 8-10 stems per tree but declined again around 35 years after coppicing and then levelled off, staying at an average of 4 stems per tree.

The shrub score was measured using a nine-point shrub scale, developed for this purpose. Many of the characteristic shrub features, including multiple stems, low branches, large stem angles and horizontal branching, were most frequent 10-30 years after coppicing and then declined as the canopy closed. However, other characteristics, such as irregular branching, epicormic growth and strongly crooked stems, remained or became more pronounced with age. According to these results, coppicing management therefore leaves structural traces that can remain visible for many decades, while the overall stand develops towards high forest. These results show that coppicing does contribute to maintaining the characteristic structure of Danish oak shrubs, as the coppiced study areas had significantly higher shrub scores and a higher stem-number than the reference areas.

However, a single coppicing event is not sufficient to maintain the characteristic low, open shrub structure over longer periods of time. The high shrub scores observed in open, browsed reference areas also indicate that grazing and browsing play an important role in creating and maintaining shrub-like growth.

Depending on the management goals, preservation of the characteristic oak shrub structure should therefore not rely on isolated coppicing events, but rather on repeated interventions combined with grazing, browsing and potentially selective cutting, resembling the historical management that created these systems.

The genetic analyses showed that Kollemorten and Tinnet Oak Shrubs contain both *Q. petraea*, *Q. robur,* and genetically admixed individuals. However, the two species were not randomly distributed across the landscape. *Q. petraea* ancestry strongly dominated the older, closed coppiced stands, whereas individuals with a higher proportion of *Q. robur* ancestry were more frequently associated with open and grazed areas. The only mature individuals classified as *Q. robur* were found in open

grassland. This suggests that the ecological conditions created by management may not only influence the physical structure of the oak shrubs but also their genetic composition.

The development towards high forest may therefore favour *Q. petraea*, while open, grazed areas appear to provide more favourable conditions for *Q. robur*. Consequently, the disappearance of historical management may result in two parallel changes: a structural transition from oak shrub towards high forest and a genetic shift towards increasing dominance of *Q. petraea*. The unexpectedly high proportion of *Q. petraea* found in this study also raises questions about whether this species has historically been underestimated in Danish oak shrubs, or whether the genetic composition has changed as traditional management has declined.

Overall, the findings demonstrate that Danish oak shrubs are dynamic systems whose characteristic structure and genetic composition are closely connected to disturbance and management. If the aim is to preserve the low, crooked, multi-stemmed and open character associated with traditional Danish oak shrubs, active management is necessary. Coppicing remains an important tool, but should be considered as part of a continuous management regime rather than as a solitary intervention. Maintaining a mosaic of coppiced stands of different ages together with open, grazed areas may preserve both the structural variation and the ecological conditions that have characterised these oak shrubs historically. Without such continued disturbance, Kollemorten and Tinnet Oak Shrub are likely to continue their development towards high forest, gradually changing both the physical expression and genetic composition of this culturally and ecologically distinctive forest type.

References

Bekendtgørelse af lov om skove, LBK nr 945 af 24/09/2009 (2009). https://www.retsinformation.dk/eli/lta/2009/945

Bertness, M., & Ragan, C. (1994). *The stress gradient hypothesis (SGH)*. ResearchGate. https://www.researchgate.net/figure/The-stress-gradient-hypothesis-SGH-Bertness-Callaway-1994-applied-to-the-case-of_fig1_369235277

Brander, P. (2017). *Træer og Buske i By og Land*. Grønt Miljø.

Buttenschøn, R. M., Gottlieb, L., & Bille, D. (2018). *Naturplejeportalen—Rapportudgave* (s. 255). Københavns Universitet. chrome-extension://efaidnbmnnnibpcajpcglclefindmkaj/https://curis.ku.dk/ws/portalfiles/portal/201047207/Naturplejeportalen_Samlet_rapport_web.pdf?pure=da%2Fpublications%2Fnaturplejeportalen--rapportudgave(1494f6f9-79cb-45de-9759-c285790d3806).html

Dalgas, E. (1883). Fortids- og Fremtidsskovene i Jyllands Hedeegne (D. 8). *Hedeselskabets Tidsskrift*, *4*, 218–224.

De Nationale Geologiske Undersøgelser for Danmark og Grønland (GEUS). (1998). *Israndslinjer og isafsmeltning*. Danmarksarealinformation. https://data.geus.dk/arcgis/services/Denmark/Israndskort/MapServer/WMSServer?

Den Danske Rødliste. (2026, januar 9). [Text/html]. https://ecos.au.dk/forskningraadgivning/temasider/redlist

Eaton, E., Caudullo, G., Oliverira, S., & De Rigo, D. (2016). *Quercus robur and Quercus petraea in Europe: Distribution, habitat, usage and threats* [E01c6df+]. Off. EU, Luxemburg.

EUFORGEN. (2025). European Forest Genetic Resources Programme. https://www.euforgen.org/species

Frederiksen, S., Seberg, O., & Rasmussen, F. (2019). *Dansk Flora*. Munksgaard.

Friis Møller, P., M. Buttenschøn, R., & Tybirk, K. (2002). *Forvaltning af Egekrat. Værdier, problemer, muligheder og fremtidig drift.* (No. 105; GEUS, s. 102). Geological Survey of Denmark and Greenland (GEUS). https://data.geus.dk/gpub-landingpage/?id=18511

Friis Møller, P., & Staun, H. (2017). *Danmarks Træer og Buske* (2.). Koustrup & Co.

Fritzbørger, B. (1992). *Danske skove 1500-1800. En landskabshistorisk undersøgelse*. Landbohistorisk Selskab.

Gram K, Køie M, & Jørgensen C A. (1944). *De jydske Egekrat og deres Flora*. i Kommission hos Ejnar Munksgaard.

Hammer Holck, M. (2026, december 13). *Ansøgning om tilladelse til etablering af ekstensiv græsning i skovene Lindbjerg og Tinnet Krat*. Miljø- og Fødevareministeriet, Naturstyrelsen.

Høeg, E. (1992). *Om Mellemformerne mellem Quercus robur L. og Q. sessiliflora Martyn.* (Bd. 40).

Jensen, J. S. (2000). Provenance Variation in Phenotypic Traits in Quercus robur and Quercus petraea in Danish Provenance Trials. *Scandinavian Journal of Forest Research*, *15*(3), 297–308. (3990924). https://doi.org/10.1080/028275800447922

Kleinschmit, j., & Svolba, j. (1995). *Intraspezifische Variation von Wachstum und Stammform bei Quercus robur und Q. petraea. 34*, 202–208.

Kleinschmit, J. (1993). Intraspecific variation of growth and adaptive traits in European oak species. *annales des sciences forestières*, *50*(Supplement), 166s–185s. https://doi.org/10.1051/forest:19930716

Krak.dk. (1954). Flyfoto 1954. https://www.krak.dk/kort

Kraus, D., Bütler, R., Krumm, F., Lachat, T., Larrieu, L., Mergner, U., Paillet, Y., Rydkvist, T., Schuck, A., & Winter, S. (2016). *Catalogue of tree microhabitats—Reference Field List*.

Lundt Larsen, M. (2025). *The oak shrub forest Kaas Skov* (s. 122). Københavns Universitet.

Miljøministeriet. (2026, maj 1). *Miljøgis*. Miljoegis.mim.dk. https://miljoegis.mim.dk/spatialmap?mapheight=856.903&mapwidth=1750.45&label=&ignorefavorite=true&profile=miljoegis-skovdrift&selectorgroups=grundkort+gst_hist+admgraens+pubreg+natbeskyt+skovudv+nst_skovdrift&layers=theme-dtk_skaermkort_daempet_daf+theme-saba_arealanvendelse+theme-skovkort-vand+theme-skovkort-vand_tekst+theme-skovkort-vejnavn_skov+theme-skovkort-publikum_tekst+theme-skovkort-diger+userpoint+userline+userpolygon+bufferzone+smalluserpointsearch+smalluserlinesearch+smalluserpolygonsearch+smalluserpointfound+smalluserlinefound+smalluserpolygonfound+selectorpoint+selectorline+selectorpolygon+selectorbufferzone+redline-line+redline-point+redline-polygon+redline-circle+spatialanalyze-line+spatialanalyze-point+spatialanalyze-polygon+fr-dl-line+fr-dl-point+fn-dl-line+fn-dl-point&opacities=1+1+1+

NST Forvaltningsplaner. (2025). [Planlag: Gudenå Kilderne]. Naturstyrelsen. https://gis.nst.dk/difo/gaeldende/?data_id=dataSource_78-SamletUroert18og20og21ogNnp_668%3A1703%2CdataSource_79-DAIdb_582_9931%3A219&page=page_0&views=view_215%2Cview_3%2Cview_96%2Cview_221

Olrik, D. C., & Kjaer, E. D. (2007). The reproductive success of a Quercus petraea × Q. robur F1-hybrid in back-crossing situations. *Annals of Forest Science*, *64*(1), 37–45.

OpenAI (Version ChatGPT (GPT -5.5). (2026). [Large language model]. http://chatgpt.com

Oppermann, A. (1932). *Egens Træformer og Racer* (12. udg.). Det Forstlige Forsøgsvæsen i Danmark.

Skovlovens § 26-28, LOV nr 453. (2004). Styrelsen for Grøn Arealomlægning og Vandmiljø. https://sgavmst.dk/skovbrug-og-landbrug/skovbrug/lovgivning-om-skovbrug/vejledning-om-skovloven/skovlovens-26-28

Strandberg, B., Kristiansen, S. M., & Tybirk, K. (2005). Dynamic oak-scrub to forest succession: Effects of management on understorey vegetation, humus forms and soils. *Forest Ecology and Management*, *211*(3), 318–328. https://doi.org/10.1016/j.foreco.2005.02.051

Tybirk, K., & Strandberg, B. (1999). Oak forest development as a result of historical land-use patterns and present nitrogen deposition. *Forest Ecology and Management*, *114*(1), 97–106. https://doi.org/10.1016/S0378-1127(98)00384-3

Vaupell, Chr. (1863). *De Danske Skove*. P.G. Philipsens Forlag.

Vedel, H., & Møller, J. D. (2017). *Træer og buske i landskabet* ((første udgave 1958, senere reviderede udgaver bl.a. 2002)). Politikens Forlag.

Willkomm, M. (1887). *Forstliche Flora von Deutschland und Oesterreich; oder, Forstbotanische und pflanzengeographische Beschreibung aller im Deutschen Reich und Oesterreichischen Kaiserstaat heimischen und im Freien angebauten oder anbauungswürdigen Holzgewächse*. C.F. Winter. https://doi.org/10.5962/bhl.title.30016

Worsøe, E. (1982a). De Jyske Egekrat. *Urt 9, no.1*, *9*.

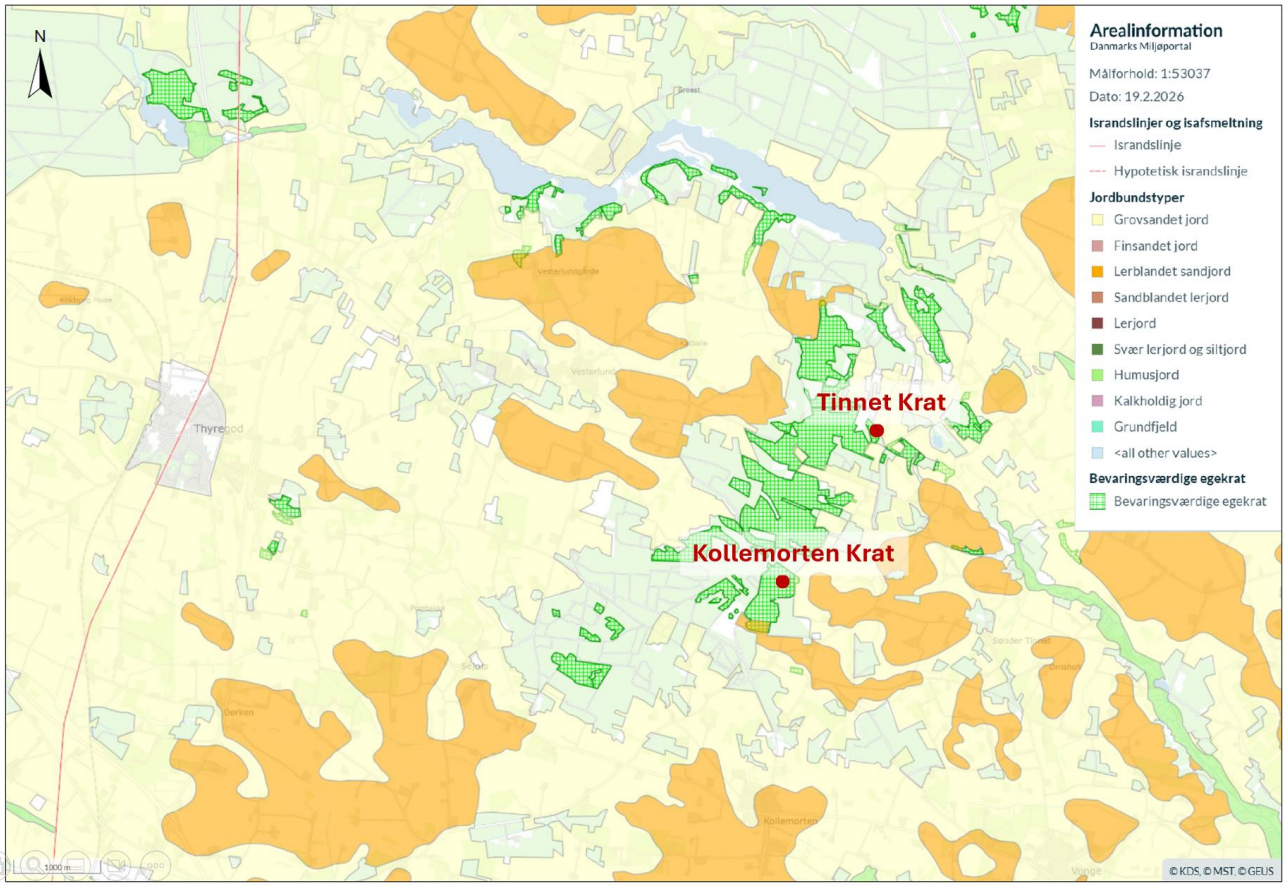
Worsøe, E. (1982b). Kan egen danne rodskud? *Urt*, *1*, 18–25.

Appendix

1. Maps

1.a) Soil types and glacial margin in Tinnet Krat and Kollemorten Krat.

Arealinformation.dk, lag: *Jordbundstyper*, Det Jordbrugsvidenskabelige Fakultet (DJF) (1975-79), *Israndslinjer og isafsmeltning*, De Nationale Geologiske Undersøgelser for Danmark og Grønland (GEUS) (1998), *Bevaringsværdige egekrat*, Miljøstyrelsen (MST).



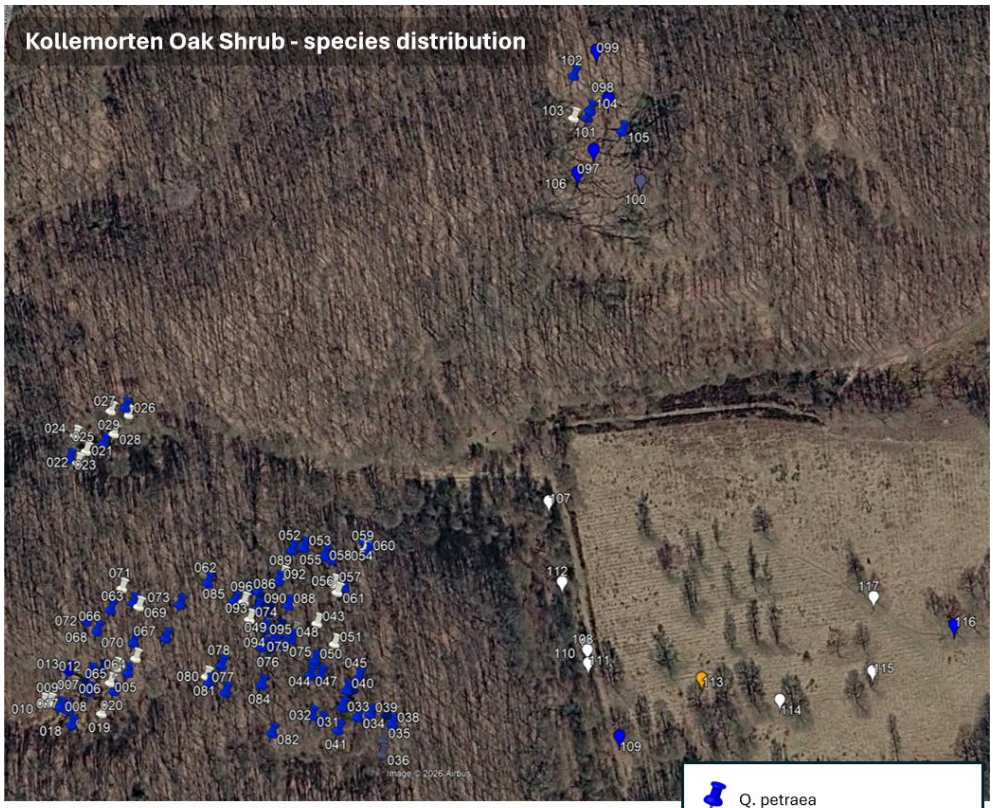
1.b) Google Earth satellite image (2025) of Kollemorten Oak Shrub, with plots 1-11.

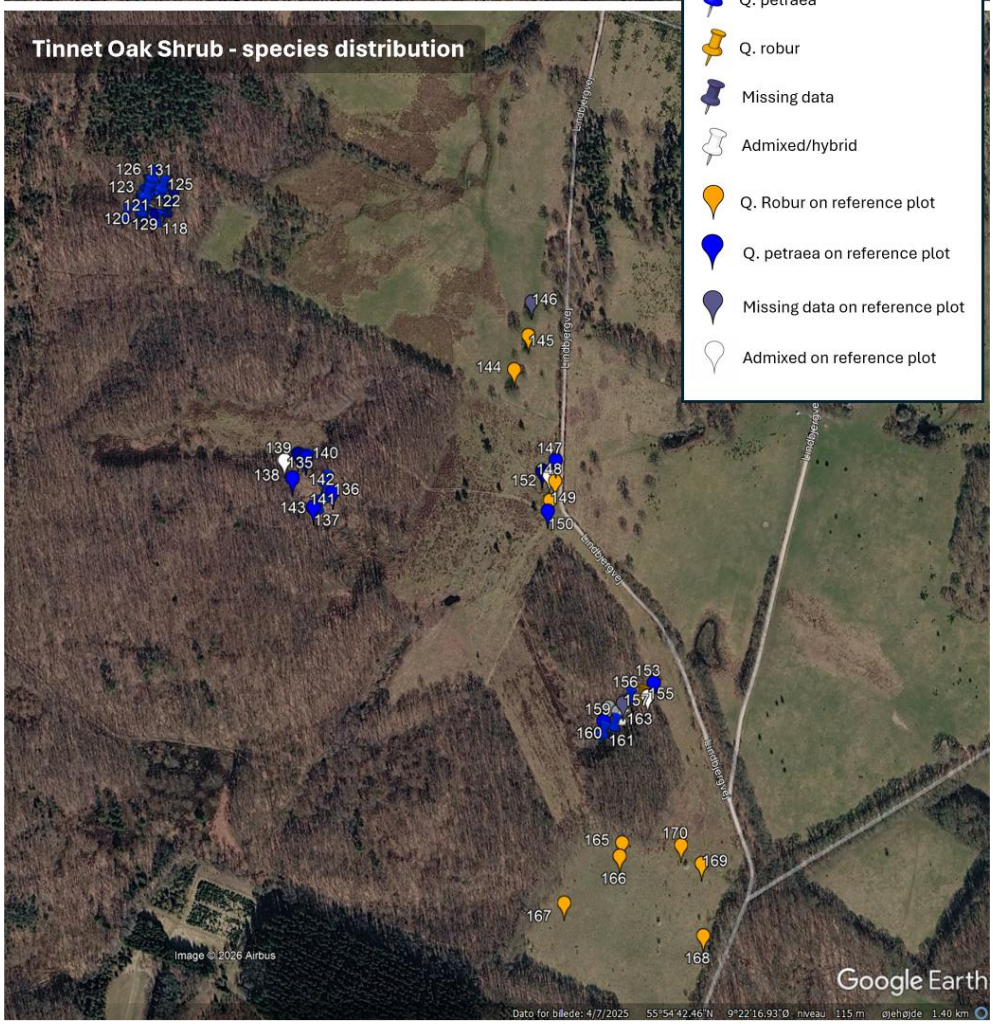
Green marks are trees coppiced between 1943 and 2023. White plots are reference plots and white marks are reference trees. GPS marks may be imprecise with up to 10 meters.

Google Earth Pro (2025). Satellite image of Kollemorten Oak Shrub, Denmark (V 7.3.7.1155 (64-bit)), Microsoft Windows (6.2.9200.0). Retrieved: 18-06-2026.

GPS coordinates collected on device: GARMIN GPSmap 60CSx. Retrieved between March and April 2026. Uploaded to Google Earth as a KML file.


Plot K9b
Plot K9
Plot K11
Plot K2
Plot K10
Plot K8
Plot K5
Plot K6
Plot K4
Plot K1
Plot K7
Plot K3
Google Earth


Kollemorten Oak Shrub - species distribution


Tinnet Oak Shrub - species distribution
Q. petraea
Q. robur
Missing data
Admixed/hybrid
Q. Robur on reference plot
Q. petraea on reference plot
Missing data on reference plot
Admixed on reference plot
Image © 2026 Airbus
Google Earth

1.c) Distribution maps of Quercus robur and Quercus petraea in Denmark

Distribution maps of Quercus robur and Quercus petraea in Denmark, including description of distribution markers.

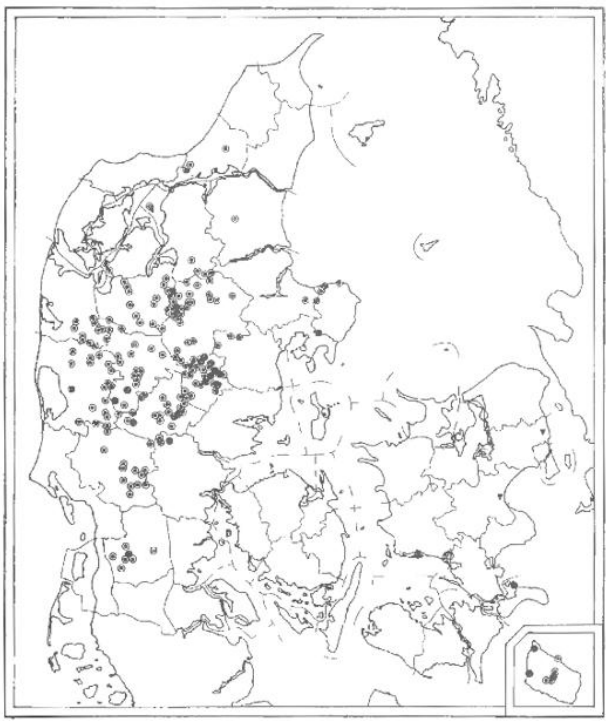


Fig. 17. *Quercus petraea* (MATTUSCHKA) LIEBL.
▼: oprindelig plantet. (Originally planted).

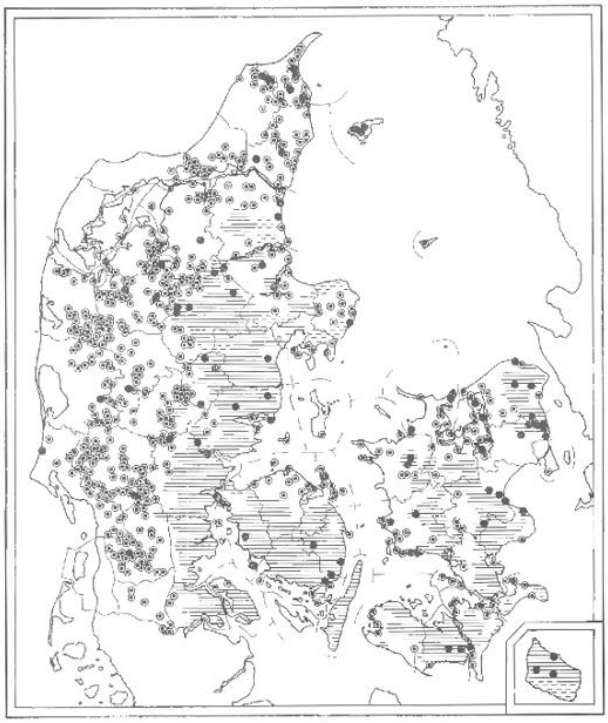
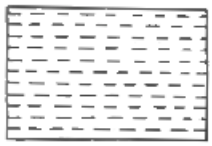


Fig. 18. *Quercus robur* L.

Forklaring til udbredelseskortene –
Explanation of the Maps of Distribution



Plantens hyppighed i det pågældende område karakteriseres som »temmelig almindelig« eller »almindelig«.
The frequency of the species in the particular area is characterized as "fairly common" or "common".



Plantens hyppighed i det pågældende område karakteriseres som »hist og her«.
The frequency of the species in the particular area is characterized as "here and there".



Lokaliteter.
Localities.

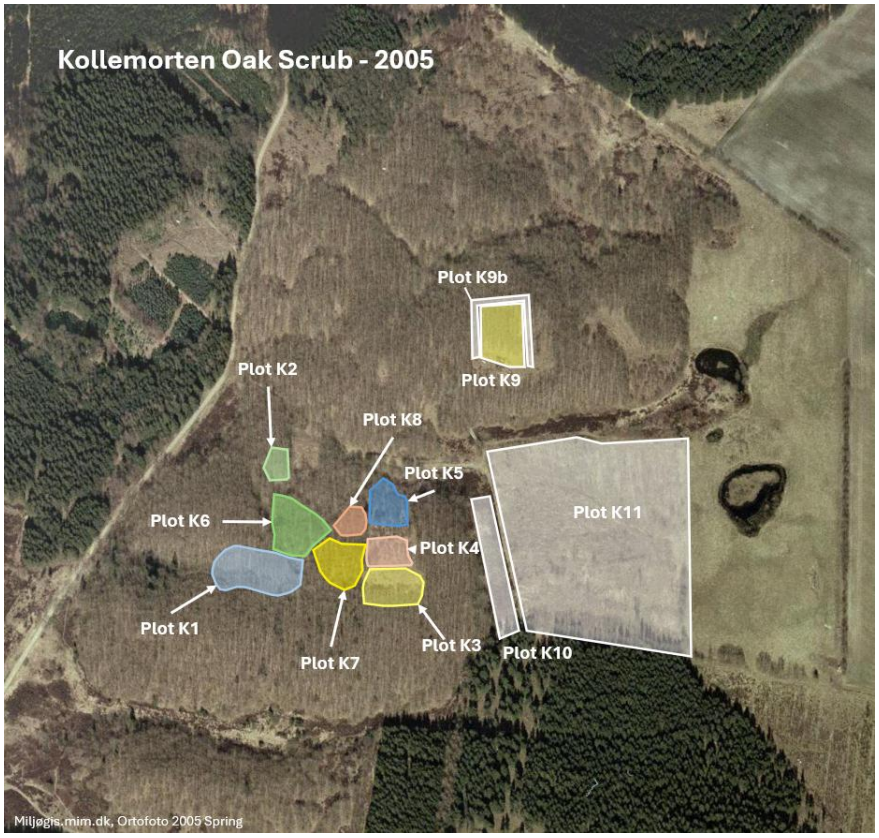
● Findested, hvorfra planten er repræsenteret i et af herbarierne på Botanisk Museum eller Landbohøjskolen, København, eller på Botanisk Institut, Århus.
A habitat from which the plant is represented by herbarium specimen in the Copenhagen Botanical Museum, or at the Agricultural College, Copenhagen, or in the Museum of Natural History, Århus.

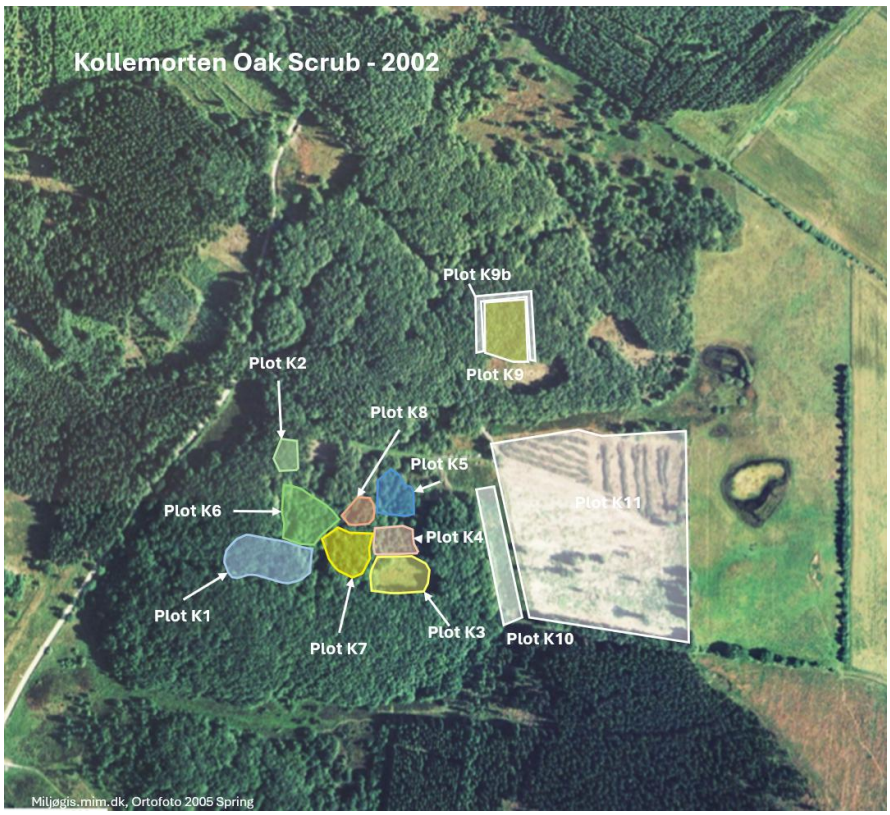
⊙ Findested, hvorfra planten ikke er repræsenteret i museernes herbarier, men enten publiceret i litteraturen, angivet i en af de til T.B.U. indsendte floralister, meddelt af botanikere eller registreret af forfatteren under karteringen 1964–66. I de skraverede områder er disse findesteder udeladt.
A habitat from which the plant is not represented in one of the herbaria but either published in the literature, indicated in one of the flora lists sent to the Topographic-Botanical Investigation, reported to the author by botanists or found by the author during the field work 1964–66. In the shaded areas these habitats are omitted.

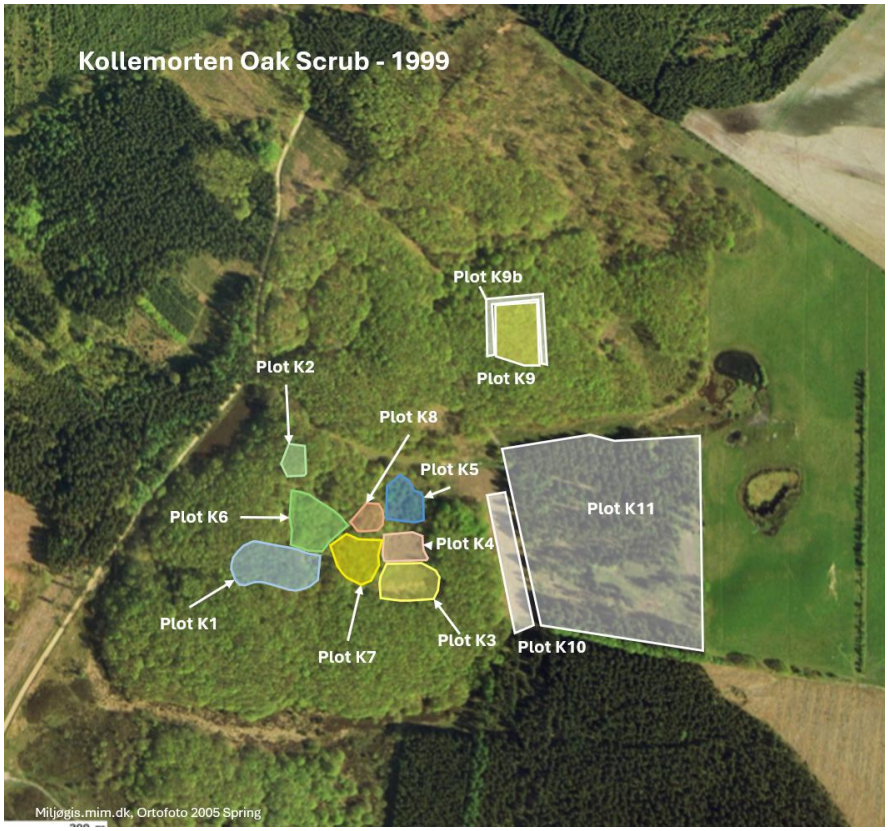
1.d) Historical maps of Kollemorten and Tinnet Oak shrub

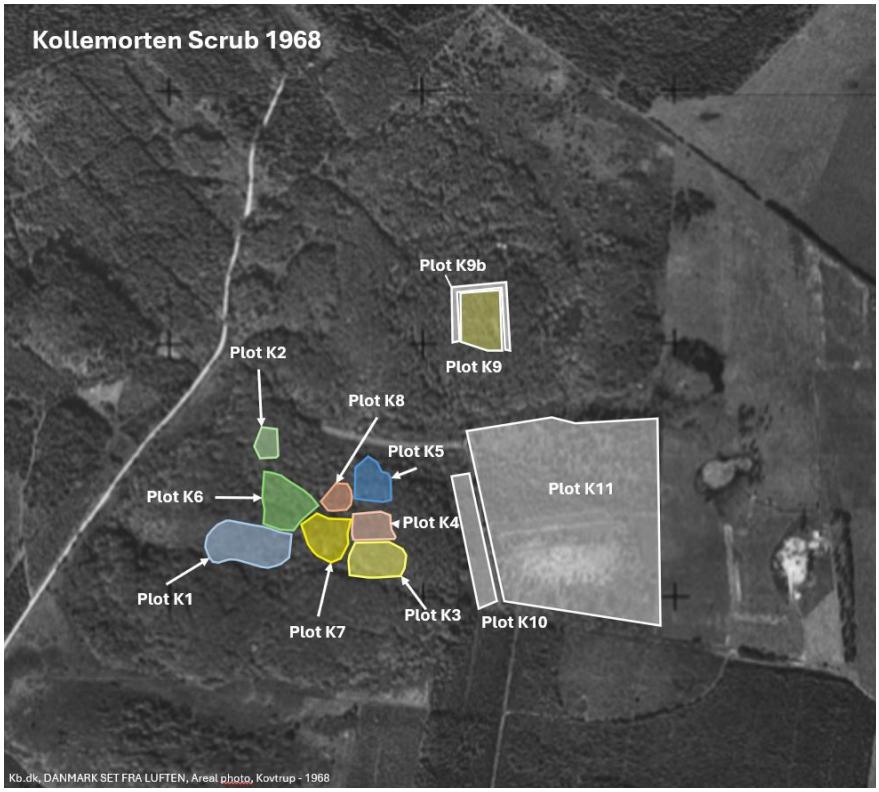
Aerial Photos from 1954 to 2025. (*DANMARK SET FRA LUFTEN*.; *Krak.dk*, 1954; Miljøministeriet, 2026)

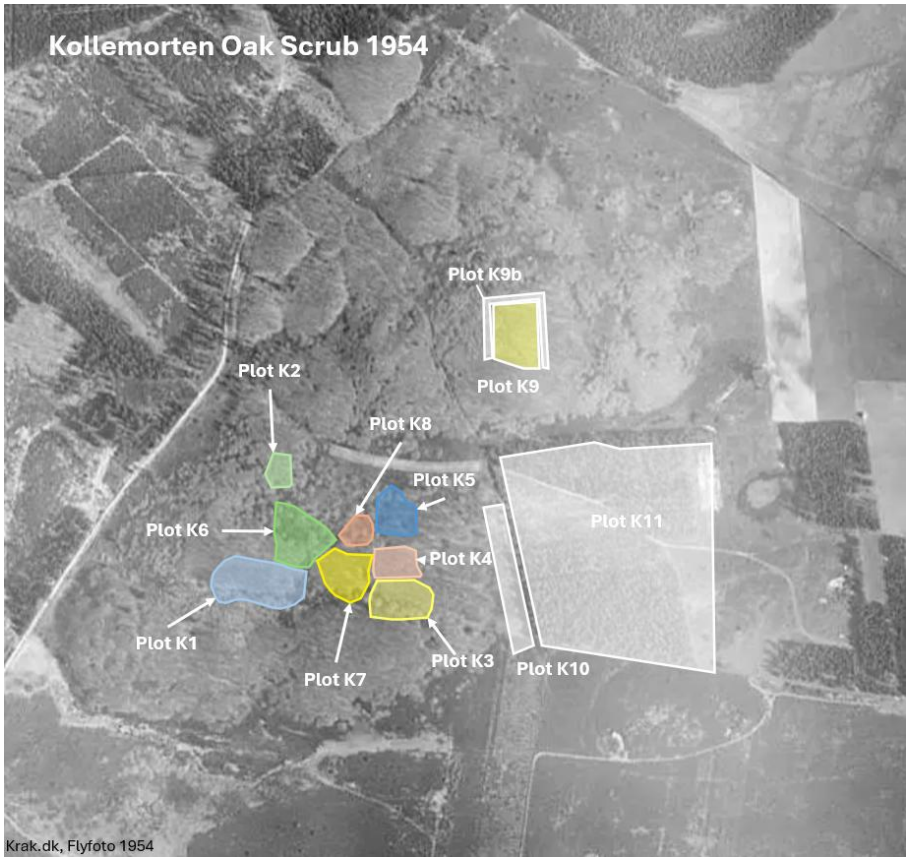
Kollemorten Oak Shrub:


Kollemorten Oak Scrub - 2005
Plot K9b
Plot K9
Plot K2
Plot K8
Plot K5
Plot K6
Plot K4
Plot K11
Plot K1
Plot K7
Plot K3
Plot K10
Miljøgis.mim.dk, Ortofoto 2005 Spring


Kollemorten Oak Scrub - 2002
Plot K9b
Plot K9
Plot K2
Plot K8
Plot K5
Plot K6
Plot K4
Plot K11
Plot K1
Plot K7
Plot K3
Plot K10
Miljøgis.mim.dk, Ortofoto 2005 Spring


Kollemorten Oak Scrub - 1999
Plot K9b
Plot K9
Plot K2
Plot K8
Plot K5
Plot K6
Plot K4
Plot K11
Plot K1
Plot K7
Plot K3
Plot K10
Miljøgis.mim.dk, Ortofoto 2005 Spring


Kollemorten Scrub 1968
Plot K9b
Plot K9
Plot K2
Plot K8
Plot K5
Plot K6
Plot K4
Plot K11
Plot K1
Plot K7
Plot K3
Plot K10
Kb.dk, DANMARK SET FRA LUFTEN, Areal photo, Kovtrup - 1968



Tinnet Oak Shrub:




Tinnet Oak Scrub 2002
Plot T2
Plot T1
Plot T5
Plot T7
Plot T4b
Plot T4
Plot T3b
Plot T3
Plot T6
400 m
Miljøgis.mim.dk, Ortofoto 2005 Forår
Miljøministeriet
Naturstyrelsen
Tinnet Krat 2002
Målforhold 1:6000
Dato 13-08-2026


Tinnet Oak Scrub 1995
Plot T2
Plot T1
Plot T5
Plot T7
Plot T4b
Plot T4
Plot T3b
Plot T3
Plot T6
400 m
Miljøgis.mim.dk, Ortofoto 2005 Forår
Miljøministeriet
Naturstyrelsen
Tinnet Krat
Målforhold 1:6000
Dato 13-08-2026
Signaturforklaring
DDOland 1995 (Hexagon)
DDOland 1995
Arealoversigt
Arealer


Tinnet Oak Scrub 1968
Plot T2
Plot T1
Plot T5
Plot T7
Plot T4b
Plot T4
Plot T3b
Plot T3
Plot T6
Kb.dk, DANMARK SET FRA LUFTEN, Areal photo, Kovtrup - 1968


Tinnet Oak Shrub 1954
Plot T2
Plot T1
Plot T5
Plot T7
Plot T4b
Plot T4
Plot T3b
Plot T3
Plot T6
Krak.dk, Areal Photo 1954

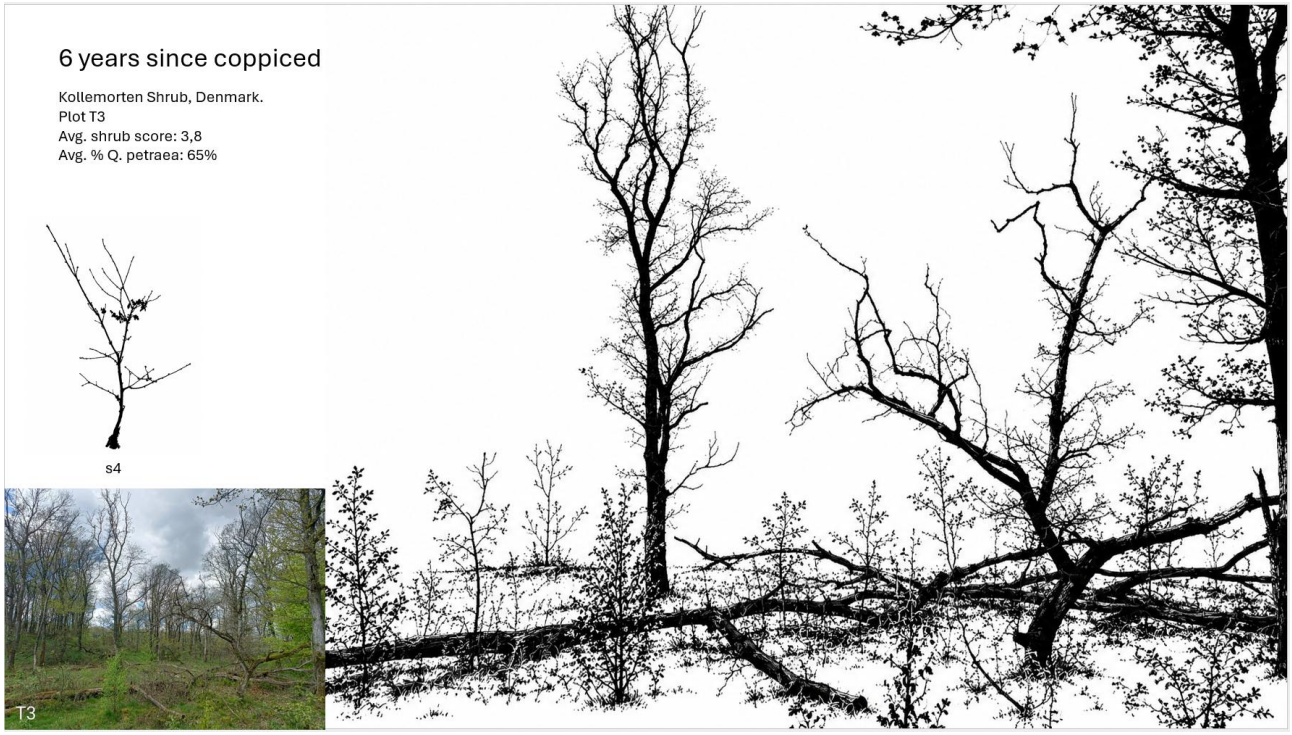
2. Plots

2.a) Coppiced forests – silhouettes

Silhouettes of each plot and examples of trees found on the plot.






6 years since coppiced
Kollemorten Shrub, Denmark.
Plot T3
Avg. shrub score: 3,8
Avg. % Q. petraea: 65%
s4
T3


16 years since coppiced
Kollemorten Shrub, Denmark.
Plot K1
Avg. shrub score: 5,9
Avg. % Q. petraea: 89%
s6
s7
K1

20 years since coppiced

Kollemorten Shrub, Denmark.
Plot K2
Avg. shrub score: 5,6
Avg. % Q. petraea: 88%



s8



s5



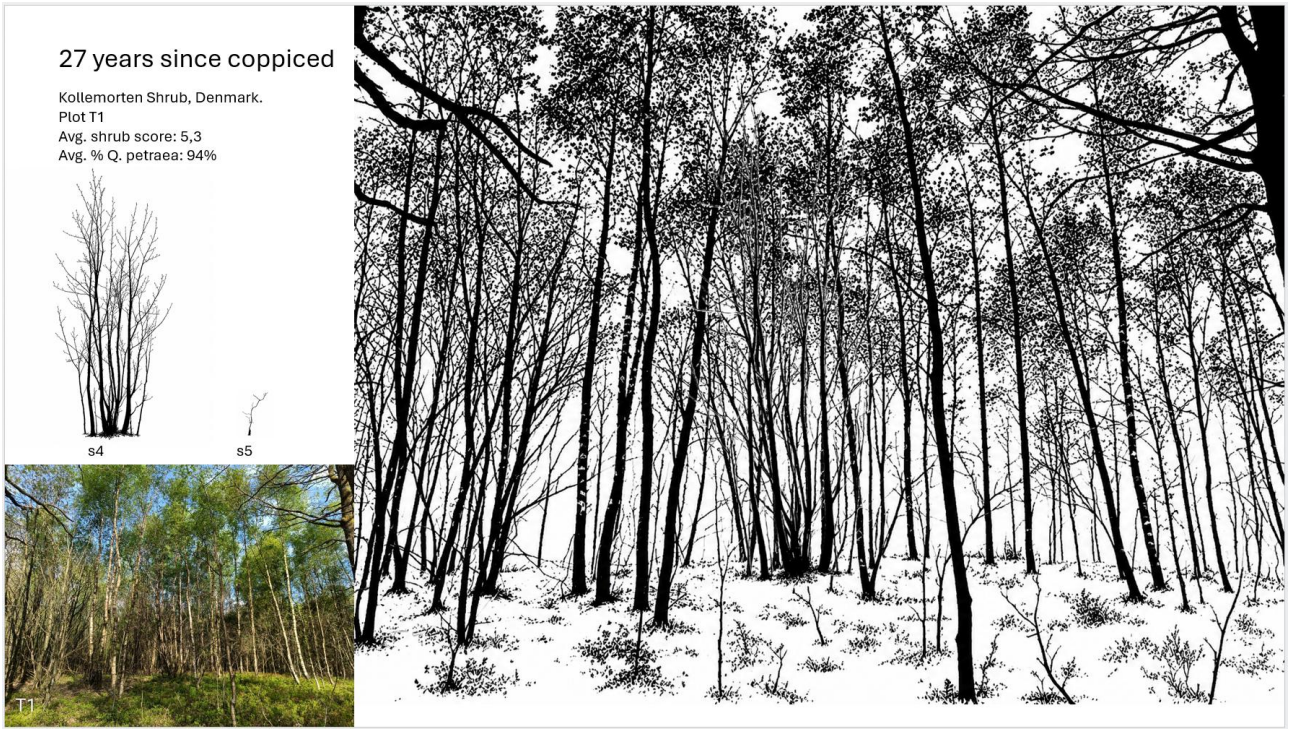


24 years since coppiced

Kollemorten Shrub, Denmark.
Plot T2
Avg. shrub score: N/A
Avg. % Q. petraea: 0%






27 years since coppiced
Kollemorten Shrub, Denmark.
Plot T1
Avg. shrub score: 5,3
Avg. % Q. petraea: 94%
s4
s5
T1


28 years since coppiced
Kollemorten Shrub, Denmark.
Plot K3
Avg. shrub score: 5,6
Avg. % Q. petraea: 98%
s5
s3
K3


32 years since coppiced
Kollemorten Shrub, Denmark.
Plot K4
Avg. shrub score: 4,6
Avg. % Q. petraea: 92%
s5
K4


37 years since coppiced
Kollemorten Shrub, Denmark.
Plot K5
Avg. shrub score: 4,6
Avg. % Q. petraea: 90%
s5
K5

43 years since coppiced

Kollemorten Shrub, Denmark.
Plot K6
Avg. shrub score: 5,2
Avg. % Q. petraea: 89%



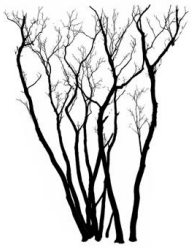
s6



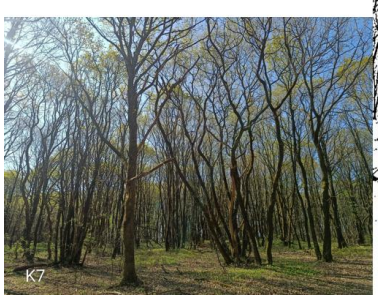


50 years since coppiced

Kollemorten Shrub, Denmark.
Plot K7
Avg. shrub score: 5,8
Avg. % Q. petraea: 94%



s6





83 years since coppiced

Kollemorten Shrub, Denmark.
Plot K8
Avg. shrub score: 5,7
Avg. % Q. petraea: 93%



s5





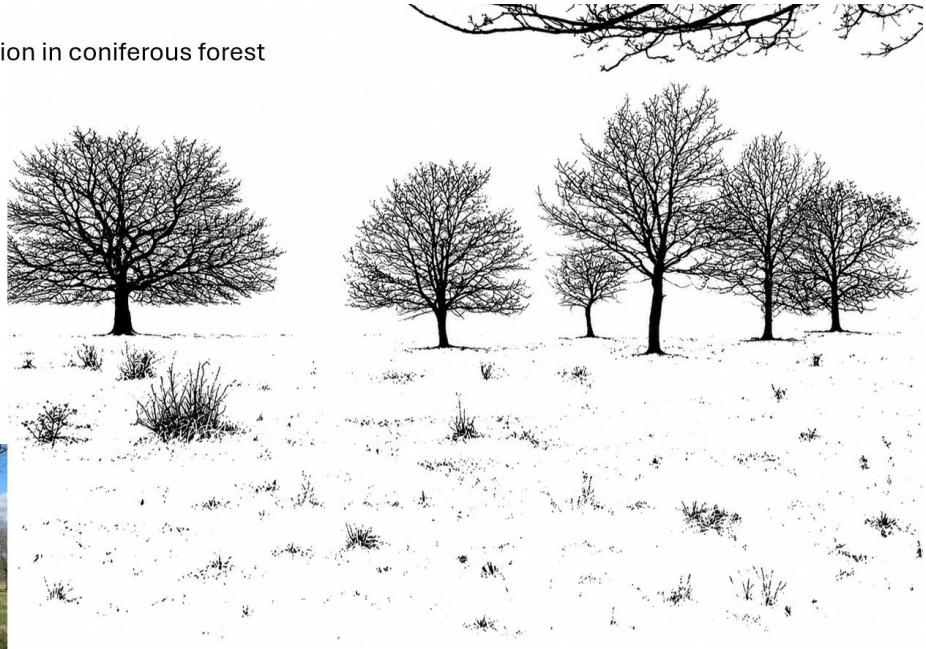
Assumed natural regeneration in coniferous forest

Kollemorten Shrub, Denmark.
Plot T5
Avg. shrub score: 2,3
Avg. % Q. petraea: 4%



s0





Assumed natural regeneration in coniferous forest

Kollemorten Shrub, Denmark.
Plot K11
Avg. shrub score: 0,2
Avg. % Q. petraea: 68%



s0





Natural regeneration on open land

Kollemorten Shrub, Denmark.
Plot T7
Avg. shrub score: 4,8
Avg. % Q. petraea: 62%


s6


s8


T7



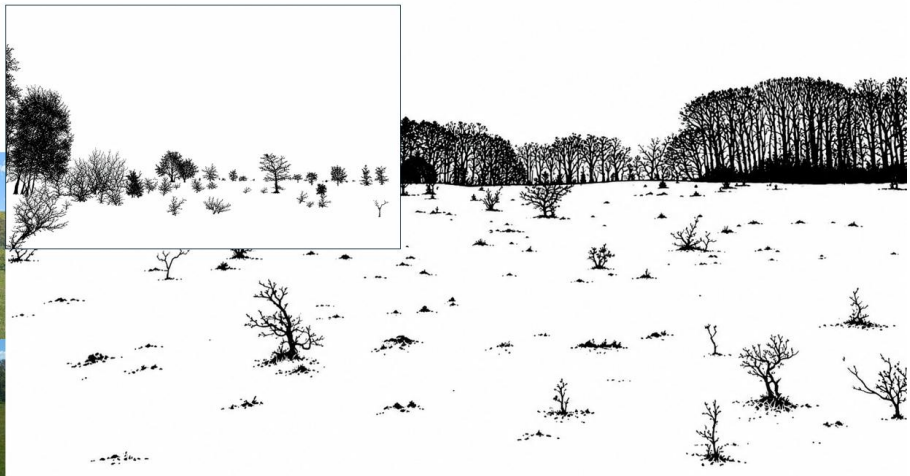
Natural regeneration on open land

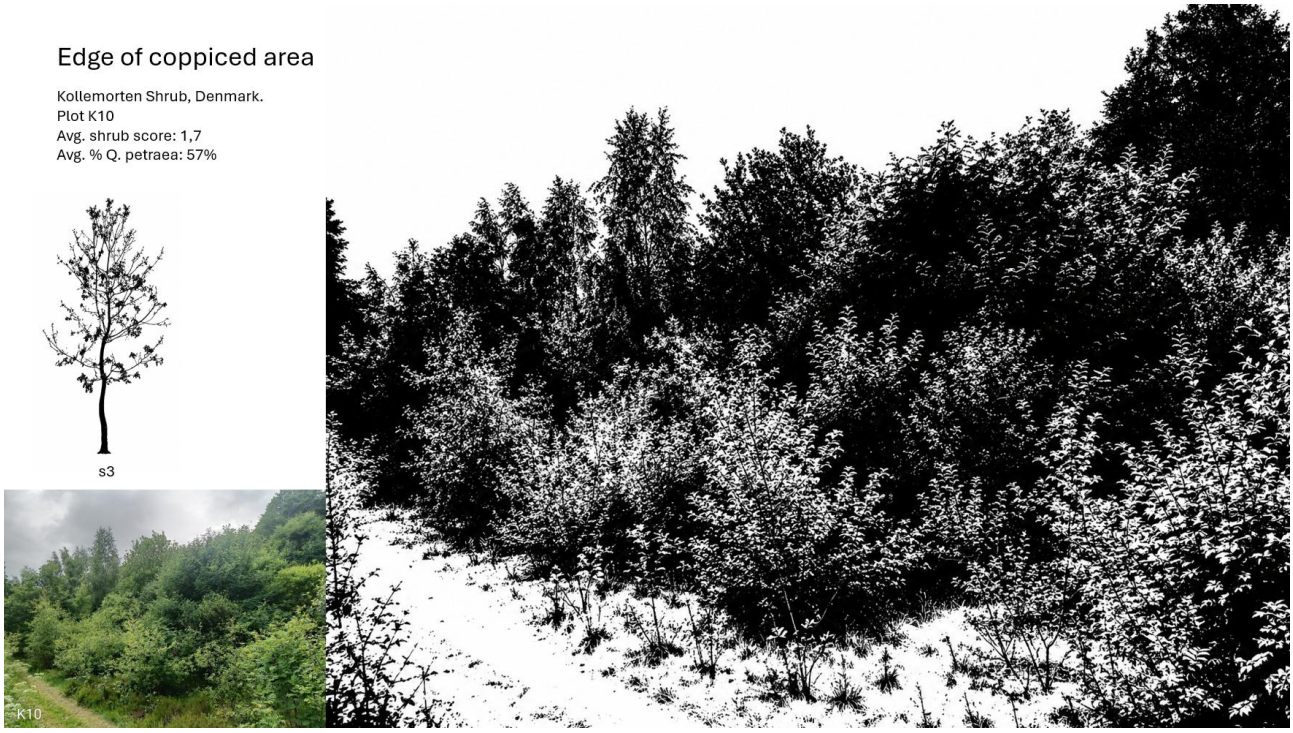
Kollemorten Shrub, Denmark.
Plot T6
Avg. shrub score: 6,2
Avg. % Q. petraea: 3%


s6




T6





3. Genomic assignments of sampled trees

3.a Genomic assignment of sampled trees in Kollemorten and Tinnet Oak Shrub

Genomic assignment of sampled trees in Kollemorten and Tinnet Oak Shrub. Orange = Q. robur. Blue = Q. petraea. Grey = Admixed. Dark green = Kollemorten study area. Light green = Kollemorten reference area. Dark blue = Tinnet study area. Light blue = Tinnet reference area. K = Kollemorten. T = Tinnet.

Genomic assignment of sampled trees - Kollemorten & Tinne Oak Shrub

Colour assignment
Q. robur
Q. petraea
Admixed
Kollemorten study area
Kollemorten reference area
Tinnet study area
Tinnet reference area

sample	pop1=pet	pop2=rob	species
K-1-1	0,9746	0,0254	petraea
K-1-2	0,8428	0,1572	admixed
K-1-3	0,9708	0,0292	petraea
K-1-4	0,9197	0,0803	petraea
K-1-5	0,6863	0,3137	admixed
K-1-6	0,871	0,129	admixed
K-1-7	0,9563	0,0437	petraea
K-1-8	0,9966	0,0034	petraea
K-1-9	0,9388	0,0612	petraea
K-1-10	0,8437	0,1563	admixed
K-1-11	0,4897	0,5103	admixed
K-1-12	0,9983	0,0017	petraea
K-1-13	0,991	0,009	petraea
K-1-14	0,9854	0,0146	petraea
K-1-15	0,8594	0,1406	admixed
K-1-16	0,9268	0,0732	petraea
K-2-1	0,8129	0,1871	admixed
K-2-2	0,7881	0,2119	admixed
K-2-3	0,9621	0,0379	petraea
K-2-4	0,8706	0,1294	admixed
K-2-5	0,9983	0,0017	petraea
K-2-6	0,9336	0,0664	petraea
K-2-7	0,8869	0,1131	admixed
K-2-8	0,8512	0,1488	admixed
K-2-9	0,7766	0,2234	admixed
K-3-1	0,9341	0,0659	petraea
K-3-2	0,9946	0,0054	petraea
K-3-3	0,9976	0,0024	petraea
K-3-4	0,9395	0,0605	petraea
K-3-7	0,9968	0,0032	petraea
K-3-8	0,939	0,061	petraea
K-3-9	0,9977	0,0023	petraea
K-3-10	0,9976	0,0024	petraea
K-3-11	0,9971	0,0029	petraea
K-4-1	0,8058	0,1942	admixed

K-4-2	0,8883	0,1117	admixed
K-4-3	0,9982	0,0018	petraea
K-4-4	0,9982	0,0018	petraea
K-4-5	0,9655	0,0345	petraea
K-4-6	0,9983	0,0017	petraea
K-4-7	0,9124	0,0876	petraea
K-4-8	0,9115	0,0885	petraea
K-4-9	0,9973	0,0027	petraea
K-4-10	0,77	0,23	admixed
K-5-1	0,9125	0,0875	petraea
K-5-2	0,9968	0,0032	petraea
K-5-3	0,9479	0,0521	petraea
K-5-4	0,9654	0,0346	petraea
K-5-5	0,9889	0,0111	petraea
K-5-6	0,5576	0,4424	admixed
K-5-7	0,9953	0,0047	petraea
K-5-8	0,8284	0,1716	admixed
K-5-9	0,998	0,002	petraea
K-5-10	0,8589	0,1411	admixed
K-6-1	0,9853	0,0147	petraea
K-6-2	0,9398	0,0602	petraea
K-6-3	0,8661	0,1339	admixed
K-6-4	0,7918	0,2082	admixed
K-6-5	0,9154	0,0846	petraea
K-6-6	0,9598	0,0402	petraea
K-6-7	0,9122	0,0878	petraea
K-6-9	0,8139	0,1861	admixed
K-6-10	0,7127	0,2873	admixed
K-6-11	0,9536	0,0464	petraea
K-6-12	0,9918	0,0082	petraea
K-7-1	0,9266	0,0734	petraea
K-7-2	0,8796	0,1204	admixed
K-7-3	0,9967	0,0033	petraea
K-7-4	0,9547	0,0453	petraea
K-7-5	0,998	0,002	petraea
K-7-6	0,9545	0,0455	petraea
K-7-7	0,9107	0,0893	petraea
K-7-8	0,9974	0,0026	petraea
K-7-9	0,9704	0,0296	petraea
K-7-10	0,9017	0,0983	petraea
K-7-11	0,8881	0,1119	admixed
K-7-12	0,9366	0,0634	petraea
K-8-1	0,9686	0,0314	petraea
K-8-11	0,9848	0,0152	petraea
K-8-12	0,7687	0,2313	admixed
K-8-2	0,9925	0,0075	petraea
K-8-3	0,9983	0,0017	petraea
K-8-4	0,9721	0,0279	petraea

K-8-5	0,7402	0,2598	admixed
K-8-6	0,9564	0,0436	petraea
K-8-7	0,964	0,036	petraea
K-8-8	0,9205	0,0795	petraea
K-8-9	0,9319	0,0681	petraea
K-8-10	0,9287	0,0713	petraea
K-9-1	0,945	0,055	petraea
K-9-11	0,9722	0,0278	petraea
K-9-2	0,9345	0,0655	petraea
K-9-3	0,9978	0,0022	petraea
K-9-5	0,9967	0,0033	petraea
K-9-6	0,9976	0,0024	petraea
K-9-7	0,9158	0,0842	petraea
K-9-8	0,9883	0,0117	petraea
K-9-9	0,9951	0,0049	petraea
K-9-10	0,885	0,115	admixed
K-10-1	0,8017	0,1983	admixed
K-10-2	0,6978	0,3022	admixed
K-10-3	0,4623	0,5377	admixed
K-10-4	0,1413	0,8587	admixed
K-10-5	0,3231	0,6769	admixed
K-10-6	0,9979	0,0021	petraea
K-11-1	0,0026	0,9974	robur
K-11-2	0,4518	0,5482	admixed
K-11-3	0,8938	0,1062	admixed
K-11-4	0,9722	0,0278	petraea
K-11-5	0,8353	0,1647	admixed
K-11-6	0,9063	0,0937	petraea
T-1-1	0,9308	0,0692	petraea
T-1-2	0,8399	0,1601	admixed
T-1-3	0,9394	0,0606	petraea
T-1-4	0,9577	0,0423	petraea
T-1-5	0,9384	0,0616	petraea
T-1-6	0,9171	0,0829	petraea
T-1-7	0,9982	0,0018	petraea
T-1-8	0,9664	0,0336	petraea
T-1-9	0,9598	0,0402	petraea
T-1-10	0,9979	0,0021	petraea
T-1-11	0,9275	0,0725	petraea
T-1-12	0,9969	0,0031	petraea
T-1-13	0,9631	0,0369	petraea
T-1-14	0,912	0,088	petraea
T-1-15	0,8638	0,1362	admixed
T-1-16	0,967	0,033	petraea
T-3-1	0,9976	0,0024	petraea
T-3-2	0,5737	0,4263	admixed
T-3-3	0,7856	0,2144	admixed
T-3-5	0,2442	0,7558	admixed

T-3-6	0,9978	0,0022	petraea
T-3-7	0,0544	0,9456	robur
T-3-8	0,0731	0,9269	robur
T-3-9	0,9642	0,0358	petraea
T-3-10	0,8946	0,1054	admixed
T-3-11	0,9325	0,0675	petraea
T-3-12	0,9717	0,0283	petraea
T-4-1	0,998	0,002	petraea
T-4-2	0,998	0,002	petraea
T-4-3	0,9954	0,0046	petraea
T-4-4	0,9973	0,0027	petraea
T-4-5	0,9578	0,0422	petraea
T-4-6	0,8319	0,1681	admixed
T-4-7	0,9649	0,0351	petraea
T-4-8	0,9974	0,0026	petraea
T-4-9	0,997	0,003	petraea
T-4-10	0,9979	0,0021	petraea
T-4-11	0,9971	0,0029	petraea
T-4-12	0,9937	0,0063	petraea
T-5-2	0,0717	0,9283	robur
T-5-3	0,0033	0,9967	robur
T-6-1	0,0531	0,9469	robur
T-6-2	0,0031	0,9969	robur
T-6-3	0,0956	0,9044	robur
T-6-4	0,0222	0,9778	robur
T-6-5	0,0058	0,9942	robur
T-6-6	0,0031	0,9969	robur
T-7-1	0,0027	0,9973	robur
T-7-2	0,0015	0,9985	robur
T-7-3	0,9444	0,0556	petraea
T-7-4	0,9383	0,0617	petraea
T-7-5	0,8987	0,1013	admixed
T-7-6	0,9185	0,0815	petraea

Genomic assignments of sampled trees summed up by plot and plot type.

Plot	Q. robur	Q. petraea	Admixed
K9	0	5	1
K1	0	10	6
K2	0	3	6
K3	0	9	0
K4	0	7	3
K5	0	7	3
K6	0	7	4
K7	0	10	2
K8	0	10	2
Sum	0	68	27
T1	0	14	2
T3	2	3	1
T4	0	6	0
Sum	2	23	3
K10	0	1	5
K11	1	2	3
K9b	0	4	0
Sum	1	7	8
T5	2	0	0
T6	6	0	0
T7	2	3	1
T3b	0	2	3
T4b	0	5	1
Sum	10	10	5
Sum	13	108	43

	Q. robur	Q. petraea	Admixed
Ref. Areas	11	17	13
Study plots	2	91	30

4. Others

4.a) Catalogue of tree microhabitats, Reference Field List

List of microhabitats from the *Catalogue of tree microhabitats – Reference Field List* (Kraus et al., 2016), found in Tinnet Oak Shrub and Kollemorten Oak Shrub. 27 out 64 microhabitats were located.

List of microhabitats found in Tinnet & Kollemorten Oak Shrub (27/64)
Cavaties
CV11
CV12
CV13
CV15
CV21
CV31
CV41
CV43
Injuries and wounds

IN11 IN12 IN21 IN22 IN23 IN31
Bark BA11 BA21
Deadwood DE11 DE12 DE13
Deformation/growth form GR11 GR12 GR22
Epiphytes EP11 EP31 EP33
Nests NE11 NE12
Other OT21

4.b) Site-specific height growth curves for European trees.

Site-specific height growth models for six common tree species in Denmark. THOMAS NORD-LARSEN, HENRIK MEILBY & JENS PETER SKOVSGAARD. Forest and Landscape Denmark, University of Copenhagen, 11 Hørsholm Kongevej, DK-2970Hørsholm, Denmark. (Nord-Larsen et al., 2009).

"*The models were derived based on base-age invariant methods to fitthe three-dimensional surface of stand age, stand top height and site index in a manner that directly estimated site indices as parameters from the fitting procedure*" (Nord-Larsen et al., 2009)

"*Comparedto historical site index curves, the growth patterns expressed by the site-specific height growth models were considerably different, indicating that the historical site index curves were*

biased. The pattern of deviation depended on tree species and site conditions."(Nord-Larsen et al., 2009).

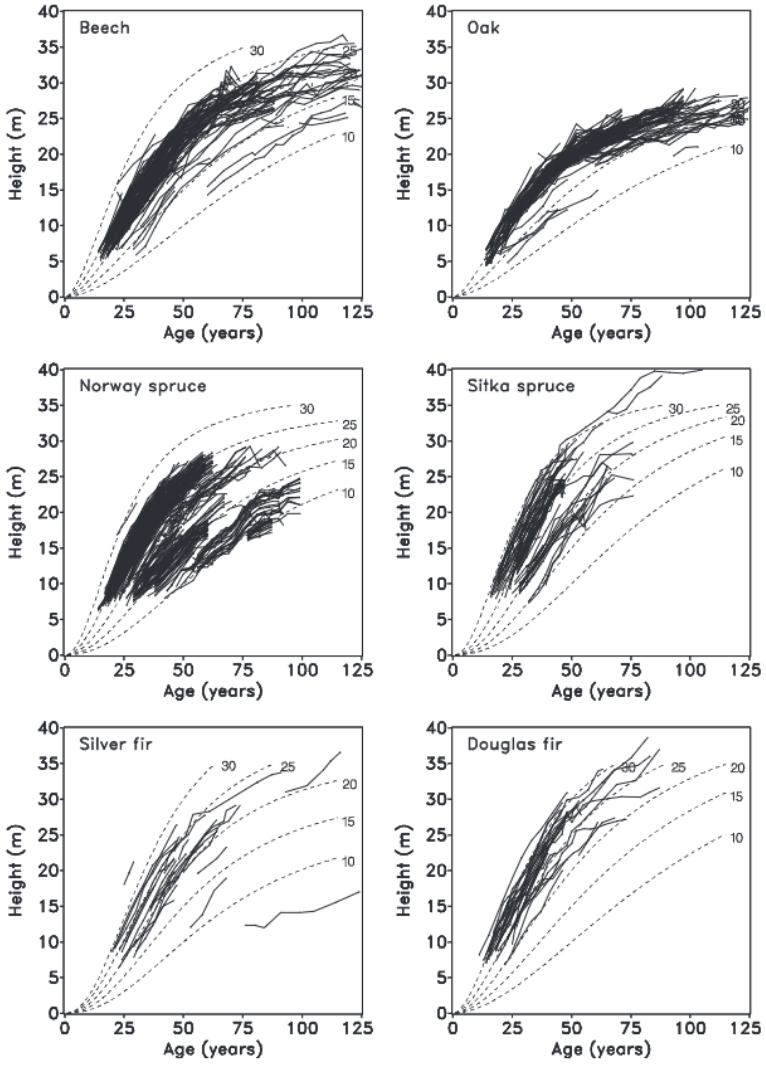


Figure 2. Site-specific height growth curves for European beech, oak, Norway spruce, Sitka spruce, European silver fir and Douglas fir along with observed age–height developments. Numbers refer to stand top height at base age 50 years.

4.c) Declaration of using generative AI tools

Declaration of using generative AI tools (for students)
☒ **I/we have used generative AI as an aid/tool** *(please tick)*
☐ **I/we have <u>NOT</u> used generative AI as an aid/tool** *(please tick)*

List which GAI tools you have used and include the link to the platform (if possible):

OpenAI (2026). ChatGPT Plus (GPT-5.6 Sol), Large language model, *https://chatgpt.com/*

Grammarly (2026). Grammarly, AI writing assistant. *Grammarly, Inc., https://app.grammarly.com/*

Google (2026). NotebookLM (Gemini Notebook), AI-powered research and writing assistant, https://notebook.google.com/?original_referer=https:%2F%2Fblog.google%23&pli=1

Describe how generative AI has been used in the exam paper:

1) Purpose (what did you use the tool for?).

- *OpenAI image-generation has been used to make the silhouettes in this thesis, as it would not have been possible within the timeframe, using a manual vectorization tool. AI image-generation models are not image-tracing tools. Even when you give a prompt that specifies "exactly the same as the picture" the AI interprets the image and redraws it. It will often thicken or thin stems, add or remove buds, simplify fine twigs, change branching angles slightly and invent details where the image is blurry. These images have been cross checked with the original images. The crosschecking was based on the categories in the nine point shrub score system. The silhouettes deemed appropriate for the purpose of visualising the tree structures have been including in this thesis. For precise generation of future silhouettes of oak trees, a vectorization/tracing tool could be used, such as Photoshop or InDesign, not AI image generation.*

Prompt used for silhouette generation:

- *"Generate a black and white silhouette of this tree/sapling. Make sure to include all of the tree and all its stems. Place it as it is in the picture, with exactly the same angles, buds and thickness - a true copy of the tree but just as a silhouette. It is very important that all angles are exactly as they are in the picture. Preserve every visible stem, twig, bud, fork, break, and irregularity, as if you were a vectorization/tracing tool, such as Photoshop or InDesign. Do not redraw, interpret, simplify, or stylize the sapling. Preserve the exact position, angle, curvature, thickness, and length of all stems. Preserve the exact size and position of all visible buds. Do not add buds, twigs, leaves, or branches. Do not remove buds, twigs, leaves, or branches. Use the photograph as a tracing reference, not as inspiration. Output only a solid black silhouette of the tree/sapling on a pure white background. The silhouette must be geometrically identical to the photographed sapling. Any uncertainty should remain visible rather than being reconstructed. No artistic interpretation."*

- *Grammarly was used to identify and correct grammatical errors and fin synonyms for words that were repeated too many times.*

- *Google NotebookLM (Gemini Notebook) was used to systemize sources so as to have a searchable database with selected sources. This was used to re-locate specific sources when needed and quickly get an overview of which sources were relevant for specific topics.*

2) Work phase (when in the process did you use GAI?)

- *NotebookLM was used in the start and middle of the thesis process, to structure all the sources needed for the writing process.*
- *OpenAI was used after datacollection, for image generation of oak trees and shrubs, based on pictures taken at the locations.*
- *Grammerly was used at the very end, to correct grammar and refine selected sentences.*

3) What did you do with the output? (including any editing of or continued work on the output)

- *I added the silhouettes to the thesis as a visual representation of the oaks and their shrub-like characteristics.*
- *I changed some words to give a better reading experience for the reader.*

4.d) The 1996 amendment: Lov nr. 392 af 22. maj 1996 om ændring af skovloven.

Miljø- og Energiministeriet (1996)(1995 LSF 151 FORSLAG TIL LOV OM ÆNDRING AF SKOVLOVEN, 1996).

Retsinformation.dk: https://www.retsinformation.dk/eli/ft/199512K00151?utm_source=chatgpt.com

> *" I skovloven, lov nr. 383 af 7. juni 1989, som senest ændret ved § 16 i lov nr. 284 af 27. april 1994, foretages følgende ændringer:*
>
> *...*
>
> *ad stk. 8*
>
> *Den første del af bestemmelsen (egekrat skal bevares) er uændret i forhold til den gældende lovs § 17, stk. 2. Ved administrationen af den gældende bestemmelse er det lagt til grund, at egekrat er karakteriseret ved at have krat præg. Krat Præget kan f.eks. bestå i, at træerne er mere lavstammede, krogede eller flerstammede i forhold til, hvad der er normalt for plantede bevoksninger. Efter gældende lov må skovejere ikke aktivt gennemføre en skovbehandling, der fremskynder egekrattets ændring til egeskov.*
>
> *Hvis bevoksningen mister sit kratpræg, og f.eks. vokser op til egeskov, er der i henhold til gældende lov ikke længere tale om egekrat i lovmæssig forstand. Bevoksningen er herefter omfattet af de almindelige bestemmelser for fredskovspligtige arealer og kan ved hugstmodenhed erstattes med andre træarter. Sådanne konverteringer forekommer, selvom der ikke er indlysende økonomiske eller miljømæssige fordele forbundet hermed.*

Bestemmelsen i den gældende lov har ikke betydet en arealmæssig binding af de eksisterende egekrat. Der har heller ikke været en lovmæssig forpligtelse til aktivt at bevare et areal som egekrat ved f.eks. stævnings- eller plukhugstdrift.

Den gældende lovs bestemmelse om, at egekrat skal bevares, videreføres med de samme lovmæssige forpligtelser som hidtil. Ved administrationen af den gældende lov er det lagt til grund, at egekrat ikke må konverteres til andre bevoksningstyper, f.eks. ved at foretage plantning eller anvende gødning eller pesticider, der kan skade den flora og fauna, der er karakteristisk for egekrat.

Til den gældende bestemmelse føjes, at ministeren gennemfører en registrering af bevaringsværdige egekrat. Intentionen med tilføjelsen er at sikre, at bevaringsværdige egekrat ikke konverteres til andre træarter i de situationer, hvor bevoksningen ikke længere er omfattet af lovens generelle beskyttelse af egekrat, og at en del af de bevaringsværdige egekrat aktivt, ved pleje, bevares som krat. Bevaringen forventes især at ske i form af konkret aftale, eller alternativt f.eks. ved rejsning af fredningssag efter naturbeskyttelsesloven.

De nærmere retningslinier for registreringen af de bevaringsværdige egekrat, herunder hvilke kriterier, der skal ligge til grund, forelægges Skovrådet. Den endelige fastlæggelse af kriterier vil tage udgangspunkt i følgende generelle kriterier for bevaringsværdige egekrat:
- større end 0,5 ha
- helt overvejende stedlige, selvsåede træarter og -racer
- beliggenhed i Jylland på især mager jordbund
- dominans af eg, men gerne væsentlig andel af asp, lind m.m.
- præges af, at være eller have været udsat for påvirkning i form af græsning, stævning og/eller opvækst under særlig frost- eller vindpåvirkede forhold.

Kriterierne indebærer, at bevaringsværdige egekrat både kan være bevoksninger af eg med kratpræg og bevoksninger af eg uden kratpræg.

De bevaringsværdige egekrat udgør en enestående naturressource og har stor betydning set ud fra en genetisk, botanisk, kulturhistorisk og landskabelig synsvinkel. Bevarelsen falder i tråd med de internationale bestræbelser for at bevare oprindelige skove.

Ifølge naturskovsstrategien fra 1994 er der ca. 4.000 ha egekrat i Danmark, overvejende i Midt- og Vestjylland. En del er ejet af staten. De statslige egekrat er sikret i forbindelse med driftsplanlægningen.

Registrering af de bevaringsværdige egekrat vil blive iværksat efter lovens vedtagelse og forventes afsluttet i løbet af ca. 3 år. Registreringen vil tage udgangspunkt i eksisterende data- og kildegrundlag.

Registreringen skal tilvejebringe det nødvendige grundlag for lovens administration og være tilstrækkelig detaljeret til at:
- den naturvidenskabelige og kulturhistoriske værdi kan vurderes

- den aktuelle tilstand og den potentielle risiko for ændring kan vurderes
- lokaliteterne kan prioriteres
- forslag til fremtidig drift kan udarbejdes.

Registreringen vil danne grundlag for indgåelse af konkrete aftaler for at sikre de bevaringsværdige egekrat. I hvert enkelt tilfælde vil det være nødvendigt at tage stilling til, hvordan det bevaringsværdige egekrat bedst kan bevares. Bevaringen kan f.eks. ske i form af en aftale om, at foryngelse kun må ske med eg fra samme bevoksning (f.eks. ved stævning eller selvforyngelse), eventuelt kombineret med en plejeaftale (f.eks. stævning, græsning eller plukhugst) eller aftale om urørt skov. Aftalerne vil blive tinglyst.

Ud fra en konkret vurdering af aftalens økonomiske betydning for ejeren kan der, når det er relevant, udbetales en kompensation for træartsbindingen. Størrelsen af kompensationen afhænger blandt andet af boniteten og størrelsen af træerne på arealet. Der kan også forekomme, boniteter og arealer, hvor kompensation ikke er relevant. Dansk Skovforening har foreslået op til 8.000 kr./ha som kompensation for, at egekrat skal fastholdes som eg og forynges med eg fra samme bevoksning. Herudover kan der blive tale om tilskud til skovpleje. Retningslinier for tilskuds- og kompensationssatser forelægges for Skovrådet.

Efter lovens § 19, stk. 1, nr. 1, kan der ydes tilskud til pleje af egekrat.

ad stk. 9

Bestemmelsen er ny og skal understøtte, at stævningsskov kan drives efter de gamle driftsformer. Skovtypen kan være bevaringsværdig i henhold til naturskovsstrategien. Stævningsdrift (også kaldet lav- og mellemskovsdrift) er kendt fra det gamle danske bondeskovbrug, men er også kendt fra resten af Europa.

Bestemmelsen retter sig navnlig mod de skovarealer, hvor spor af stævningsdrift stadig kan konstateres, eller hvor der er mulighed for, at rester af den flora og fauna, der er karakteristisk ved netop denne driftsform, stadig findes. At et areal har været stævningsskov ses især på træernes basis, hvor den gamle, ofte hule stub endnu står, samt ved at træerne ofte er flerstammede.

Stævningsdrift betyder, at skovarealet drives i kort omdrift, med træarter, der egner sig til at skyde fra stubben og/eller rødderne. Det er typisk hassel, rødel, ask og eg, men også andre arter kan der være lokal tradition for at stævne. Alt efter formål blev skuddene tyndet og endeligt afdrevet efter 15-20 år, når de havde nået arms- eller benstykkelse. Der har ofte været overstandere på arealet, og arealet kan have været drevet i kombination med kreaturgræsning, jf. bemærkningerne til § 16, stk. 10.

Egekrat og bøgepur kan være eksempler på stævningsskove. Egekrat findes hovedsagelig i Midt- og Vestjylland, og bøgepur findes blandt andet i de nordøstjydske skove. Der er tale om natur- og/eller kulturbetingede krat af eg og bøg. Ellesumpe er en anden værdifuld type stævningsskove, der findes på fugtige eller oversvømmede arealer.

Stævningsskovene har med den relativt lysåbne skov, hvor de afdrevne arealer har skiftet rundt i skoven, et helt særligt dyre- og planteliv. Ligeledes har jordbunden under de gamle stævningsskove oftest aldrig været udsat for jordbearbejdning. De enkelte træer i stævningsskoven kan, som det kendes fra egekrat, have en betydelig alder som individer, selv om den nystævnede skov ser ung ud. De kan derfor ofte betragtes som de gamle skoves efterkommere."

4.e) The Percentage Occurrence of Trees and Shrubs in the Main Types of Oak Shrub

Den procentiske Forekomst af Træer og Buske i Hovedtyperne af Egekrat, (Gram et al., 1944).

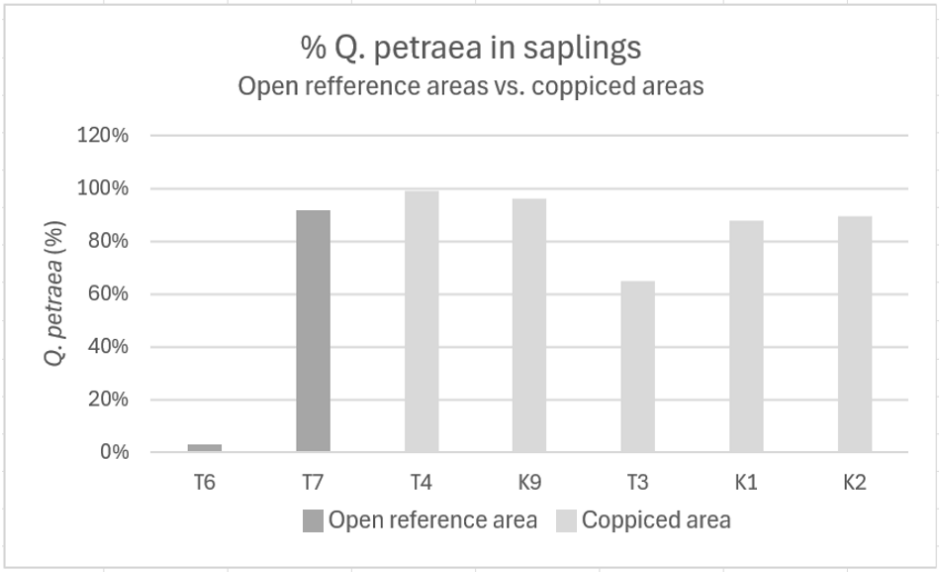
Tabel 1. Den procentiske Forekomst af Træer og Buske i Hovedtyperne af Egekrat.

Krattype	Kystkrat	Skovkrat	Bakke-Aa-Krat	Bakkekrat	Slette-Aa-Krat	Slettekrat
Antal Krat	20	30	23	35	27	7
Quercus robur	100	100	100	91	100	100
Populus tremula	70	87	87	97	85	100
Frangula alnus	45	73	87	69	78	43
Sorbus aucuparia	70	93	78	83	59	43
Lonicera periclymenum	80	83	78	69	74	57
Quercus petraea	15	53	35	57	52	29
Crataegus sp.	90	70	52	29	44	14
Juniperus communis	50	53	43	43	22	14
Pyrus malus	55	53	39	23	30	14
Corylus avellana	85	70	26	14	11	..
Salix aurita	25	7	30	23	37	..
Betula sp.	40	43	22	17	11	..
Hedera helix	40	37	17	14	4	..
Viburnum opulus	55	40	17	3	7	..
Tilia cordata	15	20	9	..	19	..
Prunus spinosa	50	17	..	3	4	..
Carpinus betulus	..	7	..	..	..	..
Rhamnus catharticus	10	..	4	..	..	..
Ilex aquifolium	5	..	..	3	..	..
Euonymus europaea	5	..	..	..	..	..
Cornus sanguinea	5	..	..	..	..	..

5. Data

5.b) Percentage Q. petraea in saplings

Average percentage *Q. petraea* in saplings per plot. Open reference areas vs. areas coppiced <20 years ago.



5.c) Raw data from Kollemorten and Tinnet Oak Shrub

The data collected from Kollemorten and Tinnet Oak Shrubs are available upon request. This data is based on 170 trees from 20 different plots. Data includes:

- Plottypes
- Year of coppicing
- Plot numbers
- Tree numbers
- Shrub scores
- Height
- Stem number
- DBH of up to five stems per tree
- Age differentiation of the trees (young/old)
- GPS location of each tree
- Weather the tree is single-stemmed or multi-stemmed
- Notes