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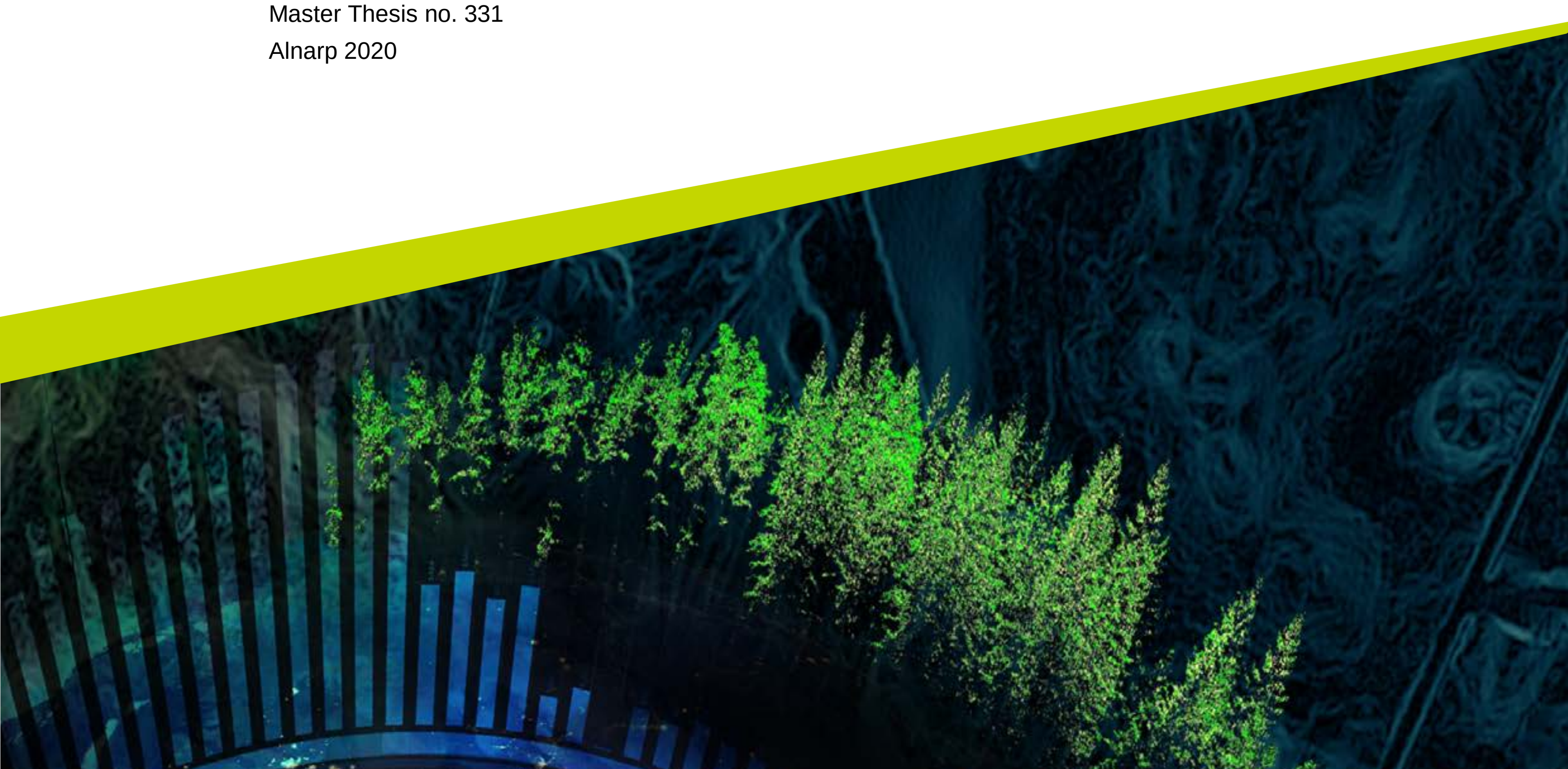

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Abstract

Dalby Söderskog is a national park situated in southern Sweden. The forest is dominated by European ash (*Fraxinus excelsior* L.), wych elm (*Ulmus glabra* Huds.), pedunculate oak (*Quercus robur* L.) and European beech (*Fagus sylvatica* L.). Due to abandonment of all types of forest management, spontaneous succession of woody species had led to an increase of shade tolerant tree species during the 20th century, in particular elm. Since 1988, the forest has been affected by Dutch elm disease and more recently by ash dieback. This study reports structural and successional changes of the main tree species in the time period of 2012 – 2020.

The inventory was carried out in 2020 and compared to an inventory from 2012. For results to be comparable, the same plots and methods were used to carry out the inventory i.e. all living trees were registered in two different size plots – 100 m^2 and 314 m^2, sharing the same plot centre. In 100 m^2 all trees from size 10 to 19 cm at 1.3 m height (dbh) were measured and identified. In 314 m^2 plots all trees above 20 cm in dbh were measured and identified.

The results show strong impact of current disturbances on tree species populations. The overall composition of the main species has not changed, but the relative proportion of each species has. Results show that ash trees with dbh >10 cm decreased from 67 to 54 individuals and elm from 178 to 98 individuals per hectare. The density of beech trees increased from 67 to 80 individuals per hectare, while oak maintained a density of 19 individuals per hectare. Regeneration of oak has increased in Dalby Söderskog lately, even though the overall regeneration of oak in southern Sweden shows a continuous decrease. The results suggest that the changes of the main tree species are direct (mortality) and indirect (changed light conditions, competition) results of ash dieback and Dutch elm disease. Oak and beech seem to benefit most from the current conditions, and are likely to increase in the future. Unfortunately, loss of large veteran ash, elm, and oak individuals will lead to loss of organisms that are dependent on habitats that these trees provide, which probably will lead to negative effects on biodiversity.

Keywords: Sweden, *Ophiostoma* spp., *Hymenoscyphus fraxineus*, *Phytophthora* spp., forest succession, forest structure

Populārzinātnes kopsavilkums

Jānis Ruks, "Ošu sēnīšu infekcijas slimības un Holandes gobu slimības ietekme uz Dalby Söderskog meža struktūru 2012-2020", Maģistra darbs, Jūnijs 2020.

Dalby Söderskog ir nacionālais parks Zviedrijas dienvidos, kurā jau vairāk kā gadsimtu nav notikusi nekāda mežsaimnieciska darbība. Šī iemesla dēļ 20. gadsimta laikā veidojās dabiska koku pēctecība, kas palielināja ēncietīgās koku sugas un to indivīdu skaitu, it īpaši parasto gobu skaitu. Citas valdošās koku sugas parkā - parastais osis, parastais ozols un parastais dižskābardis. Sākot ar 1988. gadu parku negatīvi ietekmēja Holandes slimība, kas skāra lielu skaitu gobu. Pēdējos gadus novērota arī ošu sēnīšu infekcijas slimība, kas būtiski samazinājusi ošu augtspēju.

Izmantojot iepriekš pielietotās metodes un parauglaukumus konkrētajā parkā, darbs pēta dominējošo koku sugu struktūras un pēctecības izmaiņas laika periodā no 2012. līdz 2020. gadam. Ar iegūtajiem rezultātiem būs iespējams secināt, kāda ietekme Holandes slimībai un ošu sēnīšu infekcijas slimībai būs uz citiem līdzīga tipa mežiem. Par cik Dalby Söderskog ir viens no vislabāk dokumentētajiem parkiem, ir svarīgi šo tradīciju turpināt, kā arī redzēt, kā šis parks ir mainījies laika gaitā.

Rezultāti rāda ievērojamu sakritību starp koku sugu populācijas izmaiņām un dabiskiem un cilvēku radītiem traucējumiem, piemēram, neskaitot iepriekšminētās slimības, savvaļas dzīvnieku bojājumi, drošības iemeslu dēļ nocirstie koki un citi. Laika gaitā valdošās koku sugas nav mainījušās, bet ir mainījusies to savstarpējās izplatības proporcija. Rezultāti rāda, ka parastā oša un parastās gobas populācija ir samazinājusies, parastā dižskābarža populācija ir palielinājusies, savukārt parastā ozola populācijā nozīmīgas izmaiņas nav novērotas. Bez tam, pēdējos gados parkā ir novērota ozolu reģenerācijas palielināšanās, kaut arī vidējie radītāji Dienvidzviedrijā rāda nepārtrauktu smazināšanos. Rezultāti liek secināt, ka izmaiņas dominējošo koku sugu populācijās ir gan tiešs, gan netiešs ošu sēnīšu infekcijas slimības un Holandes slimības rezultāts. Ozoliem un dižskābaržiem pašlaik ir mazāka konkurence par saules gaismu un vairāk vietas augšanai. Diemžēl, liela izmēra ošu, gobu un arī ozolu bojāeja izraisīs tādu organismu izzušanu, kas ir atkarīgi no biotopiem, ko rada šie koki. Līdz ar to tas negatīvi ietekmēs bioloģisko daudzveidību.

Table of contents

List of figures

Abbreviations

SLU	Swedish University of Agricultural Sciences
DED	Dutch elm disease
DBH	Diameter at breast height

1. Introduction

The forest succession is characterized by a continuous sequence of shifts between series of upgrading and degrading development phases (Christensen et al., 2007). When forests or individual trees reach a certain age, the degradation phase starts. It is common to see all phases in old growth forests, but some disturbances can enhance degradation of a forest, which would result in a higher percentage of degraded forest. Disturbances play a large role in changing forest structure. Biotic (pathogens, insects, wildlife), abiotic (fires, storms, floods, droughts, etc.), and anthropogenic (human) disturbances are integral parts of ecosystem dynamics, but they can cause devastating damages to forest ecosystem if they are large in size and severe. They disrupt the composition, structure, and function of the forest ecosystem, and change resource availability and the physical environment (Seidl et al., 2017). However, disturbances within themselves are different on how they impact the forest, e.g. fires and storms would kill most of the standing trees immediately, but insect and pathogen outbreaks can take years to kill trees, and some trees may survive the outbreak (Bergeron & Fenton, 2012).

Forest succession is closely linked to disturbances and describes vegetation changes on different scales in both space and time (Finegan, 1984). Any major disturbance can change the way a forest was growing before. Dalby Söderskog, which is located in southern Sweden, is a good example of an old growth forest with rapid changes in structure due to frequent disturbances in the past three decades. Nowadays Dalby Söderskog is dominated by four major tree species: European ash (*Fraxinus excelsior* L.), wych elm (*Ulmus glabra* Huds.), pedunculate oak (*Quercus robur* L.) and European beech (*Fagus sylvatica* L.) (Brunet et al., 2014). The forest was mainly dominated by human induced disturbances such as livestock grazing and wood harvest in the past centuries before it was protected in 1918. Today, however, biotic disturbances – pathogens – are dominating. Two out of four main tree species are in critical condition due to Dutch elm disease (DED) and ash dieback (Brunet et al., 2014). Previous studies (Bukina, 2012) show that Dalby Söderskog has been affected by these diseases, but mortality of *F. excelsior* has not been high until recently. This may result in loss of ash population, but the question is can ash withstand ash dieback? Mortality rate is increasing, but it may flatten, which would result in short rotation ash population. On the other hand, elm population has been decreasing for last couple of decades, but the trend line has not stopped. It is known that the diameter of an elm tree is important for the *Scolytus* vectors (Anderbrant et al., 2017), but could it become more aggressive towards smaller dimension elm trees if there is no more source of larger dimension elm trees? Oak and beech trees are affected by *Phytophthora* spp. (Sonesson & Drobyshev, 2010; Cleary et al., 2016), but increased mortality of ash and elm trees could benefit oak and beech in a way of decreased competition for space, light and nutrients.

The overall aim of this study is to analyse how the four main tree species have been affected by DED and ash dieback since the last inventory in 2012 (Bukina, 2012). The following questions are addressed concerning the fate of the main tree species:

1. Is ash able to withstand the ash dieback?
2. Does DED stop with larger elms or does it also affect gradually smaller dimensions of elms?
3. Are oak and beech trees benefiting from DED and ash dieback?

Dalby Söderskog is a well-suited forest to investigate these questions, because it has a well-documented history and one of the globally longest recorded dendrometric data series (Brunet et al., 2014). By comparing previously recorded with newly acquired data it is possible to study how structure has changed since the last inventory. To be able to predict what might be the future for this and other protected forests affected by Dutch elm disease and ash dieback, it is important to gain information on how Dalby Söderskog has been affected up to this date.

1.1. Site description

Dalby Söderskog is a 37 hectare national park situated in southern Sweden in the County of Skåne, 10 kilometres east of Lund (55°410’N, 13°200’E, 65 metres above sea level). The mineral soil is a loamy clay, derived from glacial till of the Weichsel glacial period. The soil type is eutric cambisol and the humus type is mull. The slopes next to a small stream in the south-eastern part of Dalby Söderskog are relatively well drained, but the rest of the area is moist or wet. The climate is temperate, sub-oceanic with mean annual precipitation of ca. 650 mm and a mean annual temperature of 7.5° C (Brunet et al., 2014; Oheimb & Brunet, 2007).

Most of the forest in Dalby Söderskog has experienced secondary succession due to lack of management since the area was protected in 1918. Last major cuttings were recorded in 1914 – 1916 when 1600 m^3 were taken out of a total of 8000 m^3. Since 1988 dead elms were cut down due to safety reasons around hiking paths

(Brunet et al., 2014). Dalby Söderskog was used for grazing, especially horses, but grazing ceased gradually during 19th century (Malmer et al., 1978).

1.2. Major tree species

Due to abandonment of forest management in Dalby Söderskog, spontaneous succession of woody species has led to an increase of shade tolerant tree species (elm and beech) at the expense of shade intolerant species (oak, ash and hazel) that were favoured by traditional management such as coppice and grazing (Oheimb & Brunet, 2007).

Dalby Söderskog is dominated by four major tree species: European ash, wych elm, pedunculate oak and European beech. However, due to ash dieback and Dutch elm disease forest structure and composition has drastically changed throughout the last couple of decades (Brunet et al., 2014). Beech is mainly found in the southeastern part of Dalby Söderskog, where it is relatively well drained, while the rest of the forest is moist or wet and dominated by ash, elm or oak (Brunet et al., 2016).

1.2.1. European ash

European ash is a keystone species (species that has a large effect on its natural environment relative to its abundance) in temperate Europe. It thrives on a wide range of soils except acidic soils. Even though ash is considered versatile, edaphic and hydrological factors determine on which sites it might thrive best in different parts of Europe. Soils that are preferred by ash derive from calcareous, marl or sedimentary parent material, rich in clay or silt with mean pH of 5 – 7.5. Soils also should be moist, but relatively well drained (Dobrowolska, 2011).

When it comes to nutrients, ash is considered a demanding species with high demands for nitrogen, calcium, magnesium and phosphorus (Dobrowolska, 2011). Ash is shade tolerant as a sapling, but when it matures, ash becomes light demanding (Pautasso, 2013). Winter and late spring frosts are a problem for ash. During severe winters, ash stems can crack (Dobrowolska, 2011). A major current problem for European ash is a new disease, ash dieback, which is caused by the introduced ascomycete *Hymenoscyphus fraxineus* (Hytteborn et al., 2017).

1.2.2. Wych elm

Wych elm is more common in the northern part of Europe compared to other elm species. It occurs in Norway up to the Arctic Circle and on the mountains in southern Europe, extending to the Ural Mountains in the east (Caudullo & Rigo, 2016). It can grow up to 40 m in height and 6 m in circumference (Petrokas, 2008). Wych elm is adapted to temperate and hemiboreal forests with cool summers

(Caudullo & Rigo, 2016). It thrives in moist, nutrient-rich and neutral or alkaline soils (Peterken & Mountford, 1998). Elm does not tolerate very wet and flooded areas (Caudullo & Rigo, 2016).

Despite drastic reduction of mature wych elm due to pandemic Dutch elm disease (DED), caused by fungal pathogens in genus *Ophiostoma* (*O. ulmi*, and *O. novo-ulmi*) (Hytteborn et al., 2017), some consider that elm is not endangered, even though it is red listed in Sweden and critically endangered. This is because DED initially mainly affected mature trees, especially cultivated trees in rural and urban areas. Breeding programs have selected elm hybrids that are resistant to DED for ornamental purposes, but in forests, the long-term survival of elms still may be more threatened by habitat reduction and water regulation compared to DED (Caudullo & Rigo, 2016).

1.2.3. Pedunculate oak

Pedunculate oak is a keystone species in the deciduous forests of Europe (Jensen & Hansen, 2008). Northwards it can reach southern Norway and Sweden. Southwards the distribution limit it is hard to define, because pedunculate oak can hybridise with other oaks, such as *Q. pubescens* and *Q. frainetto*. Pedunculate oak has a large ecological amplitude (limits of environmental conditions within which an organism can live and function), but grows best on fertile and moist soils (Eaton et al., 2016).

Natural regeneration of oak is one of the main problems in contemporary forestry. Competition with other vegetation for light, water and nutrients, and its high browsing sensitivity decreases natural oak regeneration (Petersson et al. 2019). Even though oak is considered intermediate shade tolerant, and it can survive under 2 % of full light during the first growing season, oak needs more sunlight so sustain survival in upcoming seasons. Therefore, light availability is the most limiting factor of oak survival (Löf et al., 2019). Due to DED and ash dieback, some areas in Dalby Söderskog have been exposed to light. In these areas, oak regeneration can be currently observed.

1.2.4. European beech

European beech is one of the most important forest trees across Europe. It can be found from the mountains of Sicily in the south to Bergen, Norway in the north. Beech is shade tolerant and it grows across wide ranges of soils with a pH ranging from 3.5 to 8.5, but it prefers moderately fertile, calcified or lightly acidic soils (Durrant et al., 2016). Beech dominates natural forests from moderate dry to moderately moist conditions, but it is replaced by other species at more extreme site conditions, e.g. in dry environments it can be replaced by *Q. robur* (Geßler et al., 2007). Since beech is sensitive to high groundwater tables and flooding, and parts of Dalby Söderskog are characterized by moist eutrophic forest soils (Brunet et al., 2014), beech only dominates the well-drained parts of the forest.

1.3. Presentation of disturbance agents

Forest structure is the vertical and horizontal distribution of multiple layers, i.e. trees, shrubs, and ground cover (Bennett, 2010), and depends on the long-term interactions of canopy disturbances and understory recruitment. In the past two centuries, the tendency has been that forests have changed from semi-open structures maintained by grazing to dense canopies. This has led to a decrease of regeneration by light demanding species, which also has been a case in Dalby Söderskog (Brunet et al., 2014). However, due to Dutch elm disease (DED) and ash dieback the forest is currently going through another phase of changes.

Dalby Söderskog has been affected by DED since end of 1980s, ten years after the disease first appeared in the surrounding Skåne region (Oheimb & Brunet, 2007; Brunet et al., 2014). The external symptoms are crown discoloration and leaf wilting, internal symptoms include formation of a brown ring in the infected sapwood, which reduces hydraulic conductivity. That results in a severe wilt syndrome, which usually kills the tree, sometimes slowly (Santini & Faccoli, 2015). Elm bark beetles of the genus *Scolytus* are the main vectors of DED. The elm bark beetle (*S. laevis*), large (*S. scolytus* F.) and small elm bark beetle (*S. multistriatus* Marsham) are respectively the common and most important species to spread DED worldwide (Santini & Faccoli, 2015; Anderbrant et al., 2017). By 2012, DED greatly had reduced the elm population in Dalby Söderskog, mainly by killing most of the large dimension elms. That led to a decrease in basal area and stem numbers (Brunet et al., 2014).

Another disease that impacted forest dynamics and structure in Dalby Söderskog is ash dieback, which is caused by the fungus *Hymenoscyphus fraxineus*. The native range of the fungus is Asia, and in Europe it was first observed in north-western Poland in 1992 from where it started to move west and was observed in the United Kingdom in 2012 (McMullan et al., 2018). First signs of ash dieback in Sweden was reported in 2002 (Stener, 2013). Ash dieback is characterized by dark brown or orange lesions on leaves followed by wilting, necrotic lesions on shoots, then diamond-shaped lesions on the stems and finally dieback of the crown (McMullan et al., 2018). Ash dieback may once again change the course of forest succession in Dalby Söderskog (Brunet et al., 2014).

A group of pathogens that cause problems for oak and beech in southern Sweden is soil-borne *Phytophthora* spp. At the end of 20^{th} century, these pathogens have been increasingly observed in Sweden, e.g. in oaks that have shown deterioration in crown conditions due to *Phytophthora quercina* (Cleary et al., 2016). The symptoms of damage are crown defoliation, formation of leaf clusters, dieback of branches, discoloration of the leaves, epicormics shoots, bark lesions and others (Sonesson & Drobyshev, 2010). In addition, since 2010 beech has been reported to have extensive crown transparency with *Phytophthora gonapodyides* as one of the main triggers, but there is not enough evidence about its effects on a large scale. Other *Phytophthora* spp are considered to have more important role such as *P. cambivora*, *P. plurivora*, and *P. cactorum* as well as associated climate triggers (Cleary et al., 2016). Other hosts that may be negatively affected by this disease and are common in southern Sweden are *Quercus petraea*, *Quercus robur* (Jung et al., 1996), *Alnus glutinosa, Picea abies, Betula* spp., *Acer* spp., *Tilia* spp. (Jung et al., 2009), and *Salix* spp (Brasier et al., 2003).

1.4. Previous inventories

In 1935 a system of transect lines and sample plots was established by Bertil Lindquist to study the forest structure and vegetation. Sixteen perpendicular transect lines were created from a straight path in the forest as a base, and 74 plots were located on these lines (fig. 1). The distance between the lines was 50 m, and the distance between the plots within the lines was 100 m with few exceptions due to margins of the forest (Lindquist, 1938). In 2010 the grid of sample plots was reconstructed using an aerial photograph of the forest with Lindquist' map as a digital overlay and the corresponding GPS coordinates. Additional inventory data was available from 1909, 1916, 1935 and 1970. Data from 1909 only included species-wise total stem numbers above 20 cm in dbh. Data from 1916, 1935 and 1970 were published in 10 cm diameter classes (Brunet et al., 2014).

Figure 1. Transect lines and sample plots in Dalby Söderskog (from Brunet et al., 2014)

The latest inventory of tree species in Dalby Söderskog so far was done in late 2011 and early 2012. The inventory was carried out in all 74 plots. All trees from 10 to 19 cm at 1.3 m height (dbh) were measured and identified to species in 100 m^2 (5.64 m radius) plots using the centre of the plot as a starting point. In 314 m^2 (10 m radius, same centre point) plots all trees above 20 cm in dbh were measured and identified. Trees below 10 cm in dbh were not measured. Vitality of trees was assessed. All stems were classified as living or dead. Alive wych elms and European ashes were classified as alive or sick, in regards whether they showed symptoms of Dutch elm disease or ash dieback (Brunet et al., 2014; Bukina, 2012).

2. Materials and methods

2.1. Inventory 2020

The inventory was carried out in Dalby Söderskog in the end of January 2020. The previously created 74 plots were used as sample plots. To locate the plots handheld GPS and a map were used. The plot centre was marked with plastic sticks in earlier inventories, but due to uprooting by wild boar, some sticks had been removed. Centres were relocated with a help of marked trees and pictures of plots from previous inventories. Uncertainty of plot relocation was estimated as below 0.25 m from the original plot centre.

Field work was carried out the same way as it was done in 2012, so the data would be comparable. All living trees were registered in two different size plots – 100 m^2 (5.64 m radius) and 314 m^2 (10 m radius), sharing the same plot centre. In 100 m^2 all trees from size 10 to 19 cm at 1.3 m height (dbh) were measured and identified. In 314 m^2 plots all trees above 20 cm in dbh were measured and identified (fig. 2). Diameter at breast height (dbh) was registered for all individuals using cross-calliper method. For trees that were larger than 50 cm in dbh, measuring tape was used. Vitality of each living wych elm and European ash tree was assessed (section 2.2.).

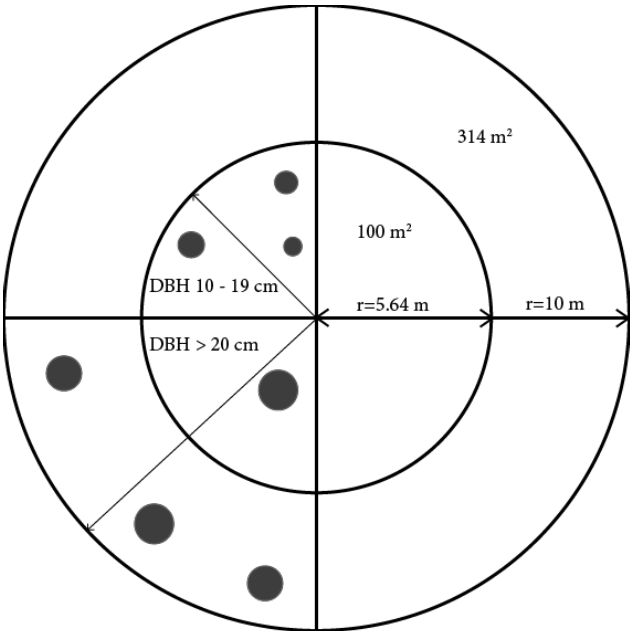


Figure 2. Representation of a sample plot.

2.2. Vitality classes and assessment

Five vitality classes were created for European ash to assess the condition of each individual found in sample plots regarding ash dieback. Vitality classes are as follows:

Table 1. Classes for classification of vitality of ash.

Class	Vitality class description
0	symptomless
1	slightly symptomatic
2	clearly symptomatic
3	declining
4	severely affected; dying or dead

First, it was assessed whether an individual tree was looking healthy, diseased or dead. Afterwards, the more detailed characteristics were looked upon and noted. Some of the characteristics were also assessed quantitatively. Dead ashes were also noted. Characteristics were as follows:

- stunted shoots;
- adventitious shoots;
- reduced crown;
- abundant fruiting;

- dead branches;
- dead crown;
- high stump.

Vitality for wych elm was assessed by noting whether it was healthy or diseased.

2.3. Analyses

The inventory data were analysed to assess basal area, stem density, dbh classes for each species and the whole area, and dominating species in each plot for both years 2012 and 2020. Some of the results were available from 2012 (Bukina, 2012).

While comparing *F. excelsior* data with data from 2012, some dead ashes were missing. Most likely, they were fallen and not found in the present inventory, but to assess mortality these missing dead ashes were added to year 2020 data during data analyses.

To create dominant tree species maps, the grid of 74 sample plots was used. Dominance was defined as the species with the highest number of trees in the plot, or the highest basal area, respectively. Dominating tree species were marked each with a specific colour. In cases, where there was equal dominance between two or more species, the circular plot was divided in equal sections and coloured accordingly.

All calculations were done by using Microsoft Excel (2016). Dominant tree species maps were created in illustration application Paint 3D.

3. Results

3.1. European ash

In the time period from 2012 to 2020, the density of ash trees decreased by 20 %, which led to 8 % decrease to the basal area. The number of ash trees decreased from 67 to 54 trees per hectare. The highest decrease can be seen in the 20 – 29 and 30 – 39 cm diameter classes, where on average six trees per ha have been lost in both classes (fig. 3).

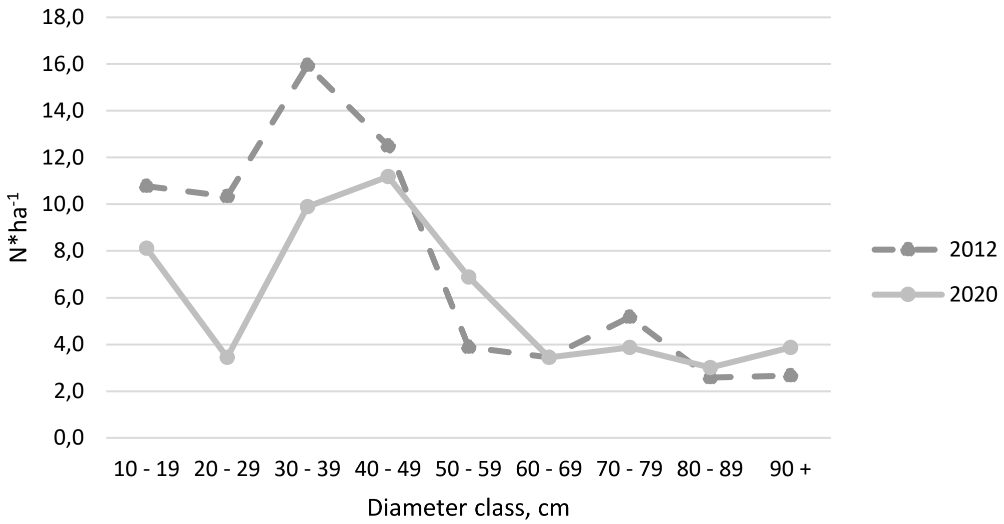


Figure 3: Diameter class distribution of Fraxinus excelsior (stems per hectare) in 2012 and 2020 in Dalby Söderskog.

There was also a clear decrease in overall vitality of ash. There were almost no healthy ashes left in Dalby Söderskog, while the amount of dead ashes increased by 24 %. The percentage of diseased ash trees grew from 55 to 73 % (fig. 4).

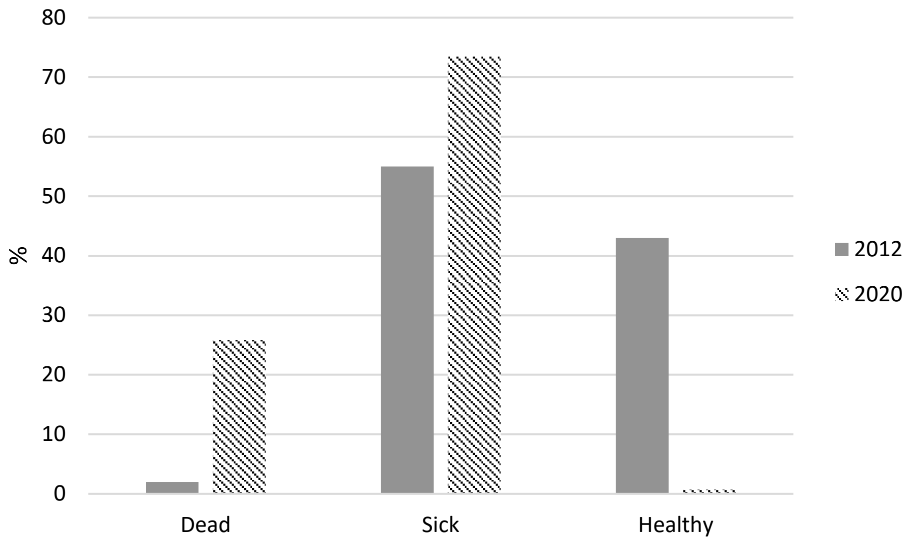


Figure 4: Changes in Fraxinus excelsior status in Dalby Söderskog between 2012 and 2020.

Vitality class assessment showed that only one percent of ashes were considered symptomless in 2020. Most of the ashes were either slightly symptomatic (31%), or severely affected, dying or dead (30 %). The second vitality class – ashes that were clearly symptomatic accounted for 20 %. The third class – declining, was assigned to 18 % of the ash trees (fig. 5).

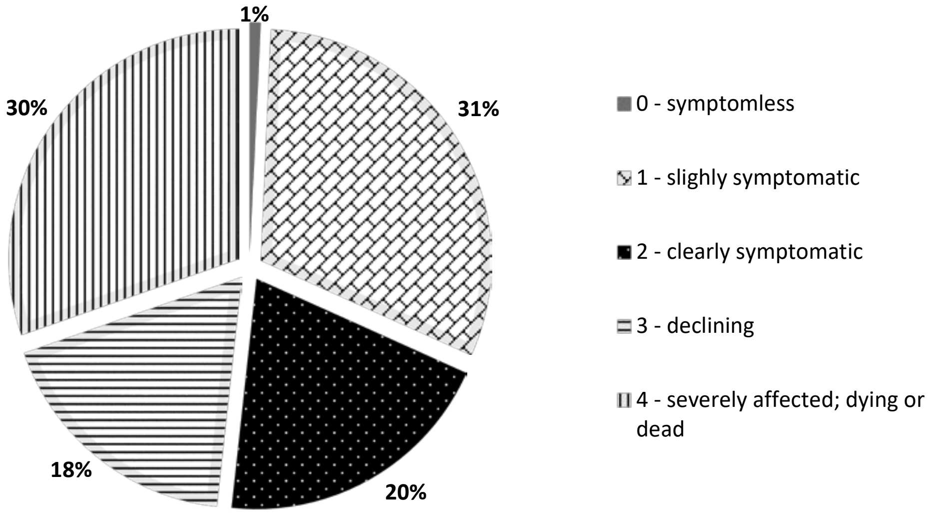


Figure 5: Vitality class distribution of Fraxinus excelsior in Dalby Söderskog 2020.

3.2. Wych elm

For wych elm, inventory data still showed an ongoing decrease in total numbers of trees. Wych elm stem density decreased by 45 % from 2012 to 2020, which led to 68 % decrease of basal area of elm in Dalby Söderskog during this period. The number of elm trees decreased from 178 to 98 trees per hectare. Diameter class distribution shows the highest decrease in the 20 – 29 cm diameter class. The largest number of individuals can be seen in 10 – 19 cm diameter class (fig. 6). The number of elms in other diameter classes was low, which means that wych elm in Dalby Söderskog does not reach larger dimensions anymore (fig. 7).

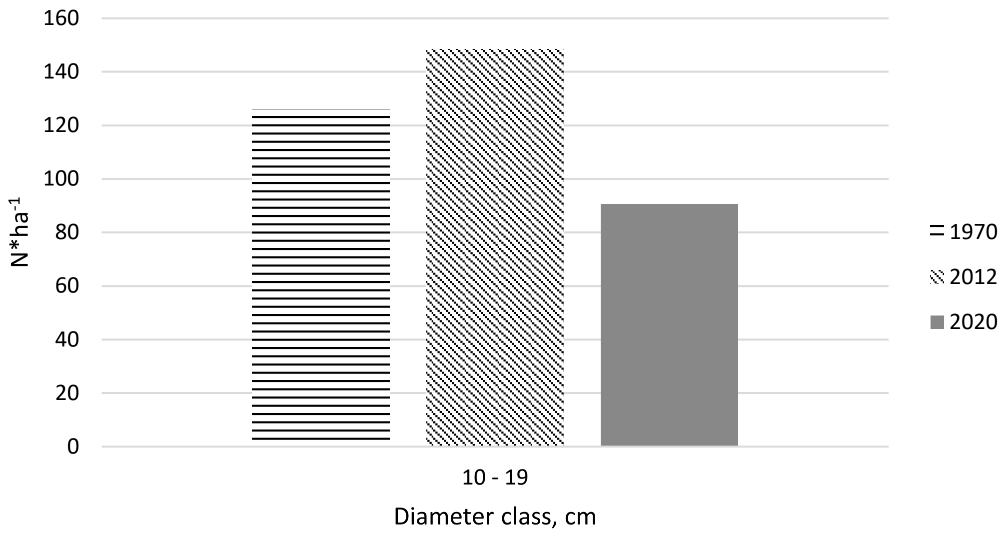


Figure 6: Density (stems per hectare) of Ulmus glabra with 10 – 19 cm diameter in 1970, 2012 and 2020 in Dalby Söderskog.

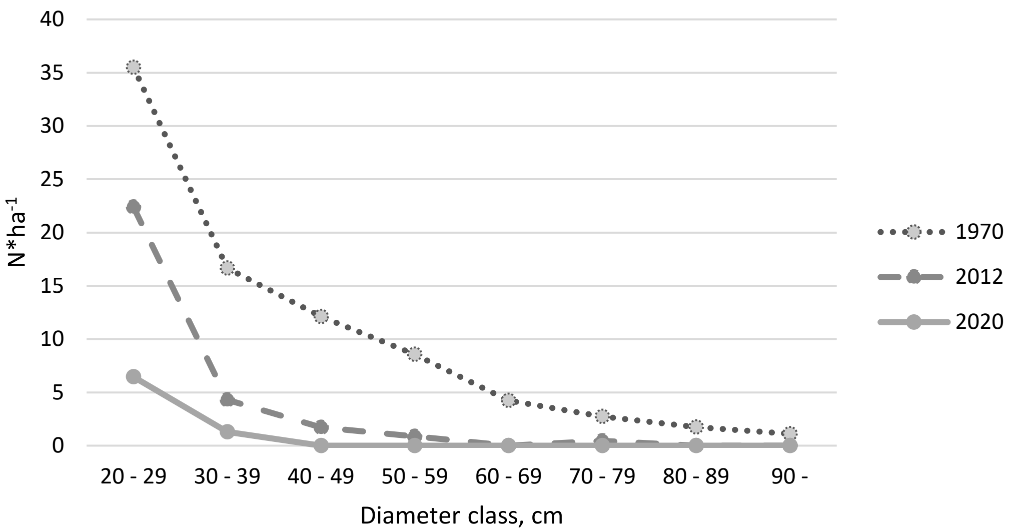


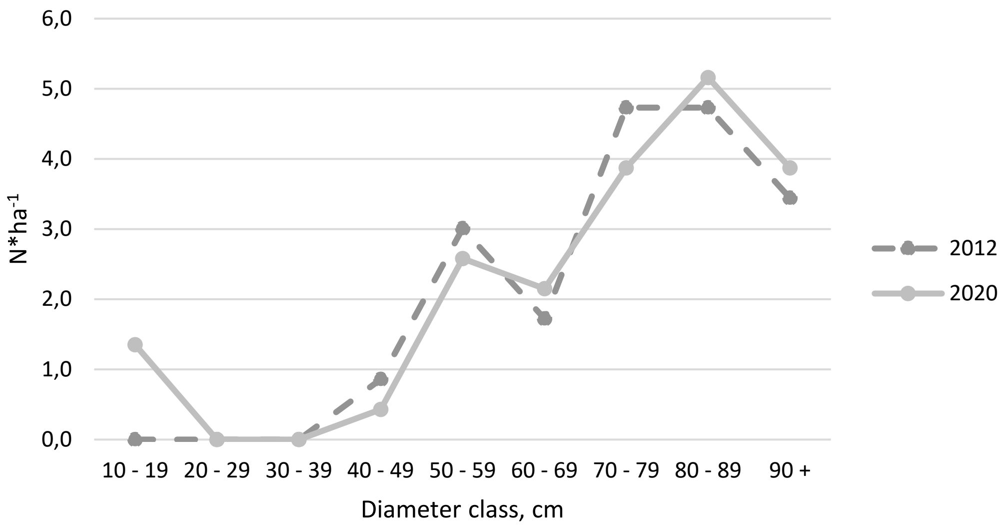
Figure 7: Diameter class distribution of Ulmus glabra (stems per hectare) in 1970, 2012 and 2020 in Dalby Söderskog.

Vitality assessment of 2020 showed that 64 % of inventoried alive elm were healthy and the remaining 36 % are diseased. It is worth to mention that 92 % of all alive elms were found in the 10 to 19 cm diameter class.

3.3. Pedunculate oak

The overall density of pedunculate oak did not change from 2012 to 2020, with 19 individuals per hectare in both years. On the other hand, basal area increased by eight percent. Respectively, basal area of oak increased from 8.79 to 9.53 m^3 per hectare. Oak diameter distribution did not show significant changes (fig. 8), but diameter class 10 – 19 cm increased from 0 to 1.4 trees per hectare as one young oak was found in one of the sample plots in 2020.

Figure 8: Diameter class distribution of Quercus robur (stems per hectare) in 2012 and 2020 in Dalby Söderskog.



3.4. European beech

The overall density of European beech trees increased by 19 %, therefore, basal area also increased by almost 15 %. Respectively, the density of beech trees increased from 67 to 80 trees per hectare. The diameter distribution did not show any larger changes, except for the 10 – 19 cm diameter class. Some of the increase of individuals in diameter classes were due to growth of trees during the study period (fig. 9).

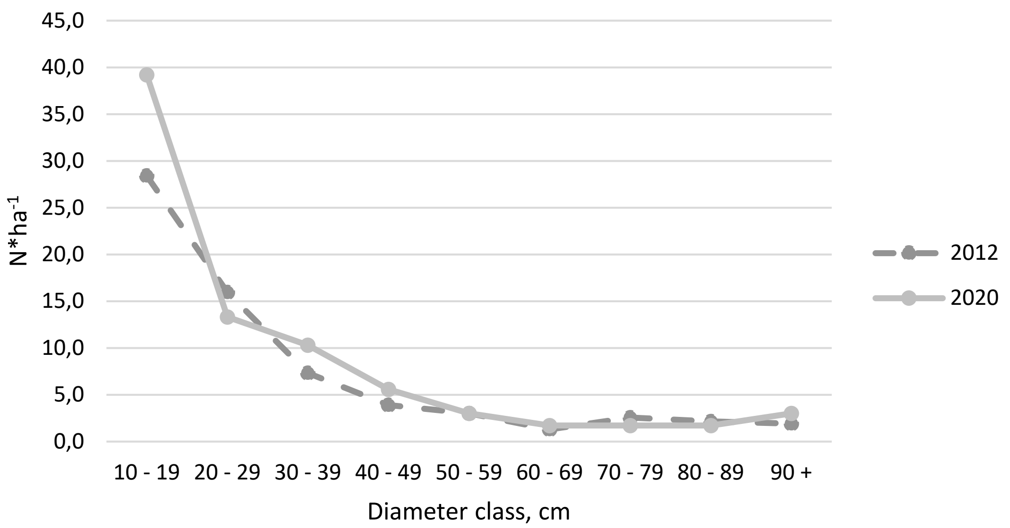


Figure 9: Diameter class distribution of Fagus sylvatica (stems per hectare) in 2012 and 2020 in Dalby Söderskog.

3.5. Other tree species

Tree species apart from main four, i.e. black alder (*Alnus glutinosa*), Norway maple (*Acer platanoides*) and crab apple (*Malus sylvestris*) decreased by 15 % in density. The stem number decreased from 18 to 15 trees per hectare. On the other hand, basal area increased from 1.15 to 1.29 m^2 per hectare. The diameter distribution did not show any larger changes (fig. 10).

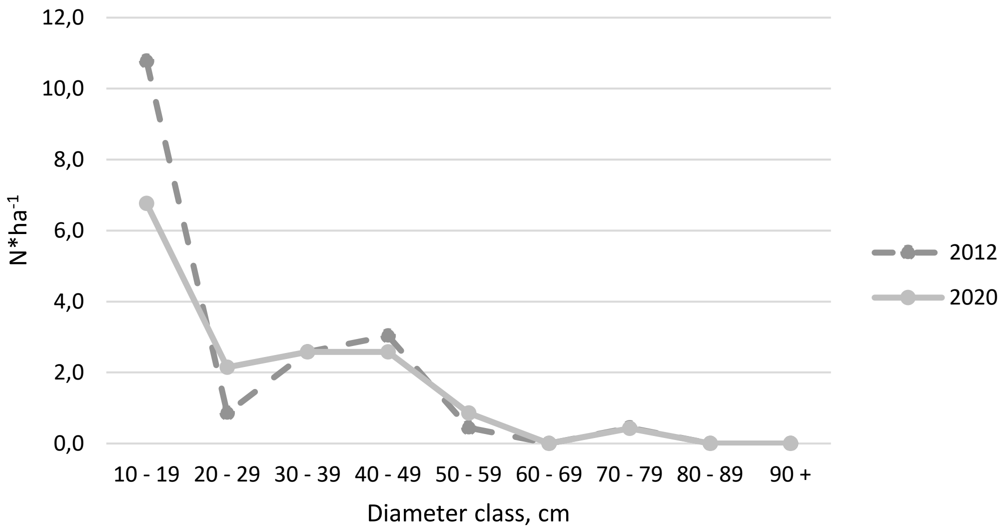


Figure 10: Diameter class distribution of other tree species (stems per hectare) in 2012 and 2020 in Dalby Söderskog.

3.6. Dominating tree species

Species dominance in all 74 sample plots was determined by number of individuals above 20 cm in diameter at breast height. Maps were created for both 2012 (fig. 11) and 2020 (fig. 12). The most frequent dominant species was European ash, which dominated 31.5 plots in 2020, three plots more compared to 2012. European beech dominated in 23 plots in 2020 and in 21 plots in 2012. Pedunculate oak dominated in 7.5 plots in 2020 and in five plots in 2012, while other species apart from four main ones dominated in 6.5 plots in 2020 and in five plots in 2012. The least frequent dominant was wych elm, which dominated in only 1.5 plots in 2020, compared to 11.5 plots in 2012 (fig. 13). There were four plots with no trees in 2020, which is one more compared to 2012.

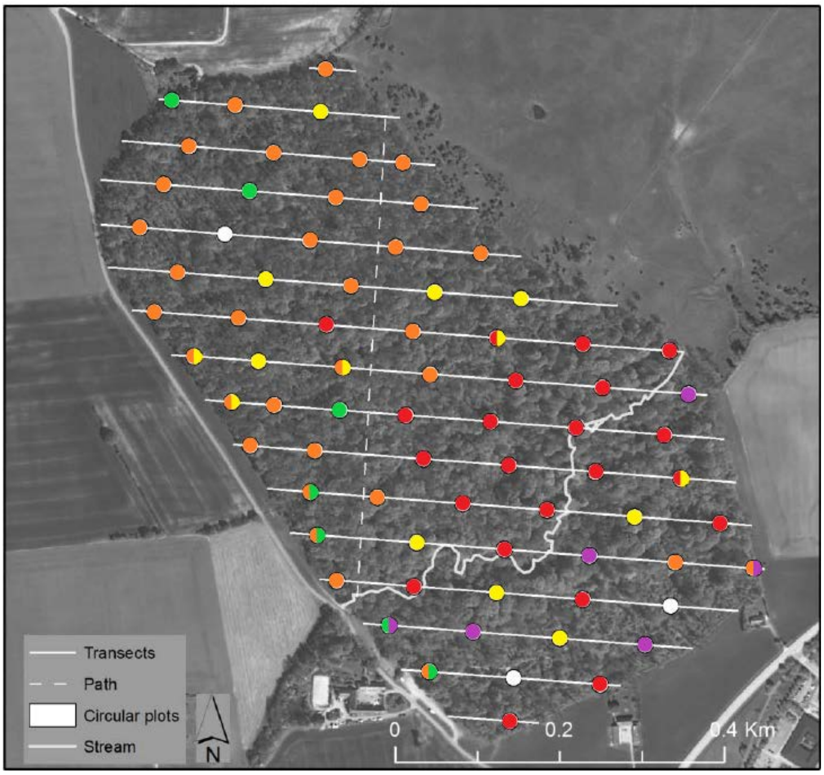


Figure 11: Dominant tree species above 20 cm dbh in permanent plots of Dalby Söderskog 2012,

● *F. excelsior;* ● *F. sylvatica;* ● *U. glabra;* ● *Q. robur;* ● *other;* ○ *no trees.*

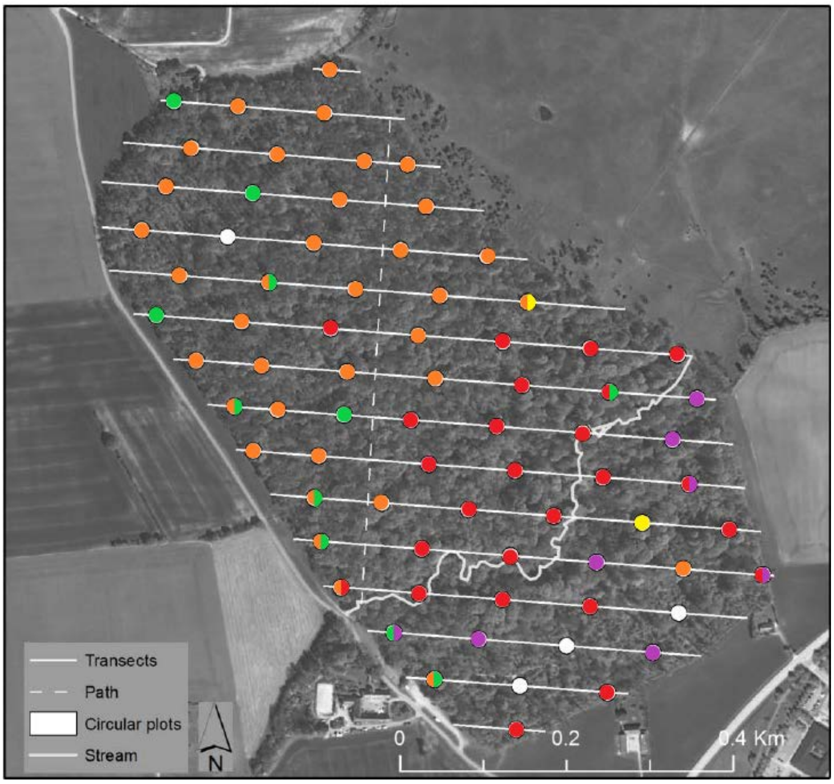


Figure 12: Dominant tree species above 20 cm dbh in permanent plots of Dalby Söderskog 2020,

● *F. excelsior;* ● *F. sylvatica;* ● *U. glabra;* ● *Q. robur;* ● *other;* ○ *no trees above 20 cm dbh.*

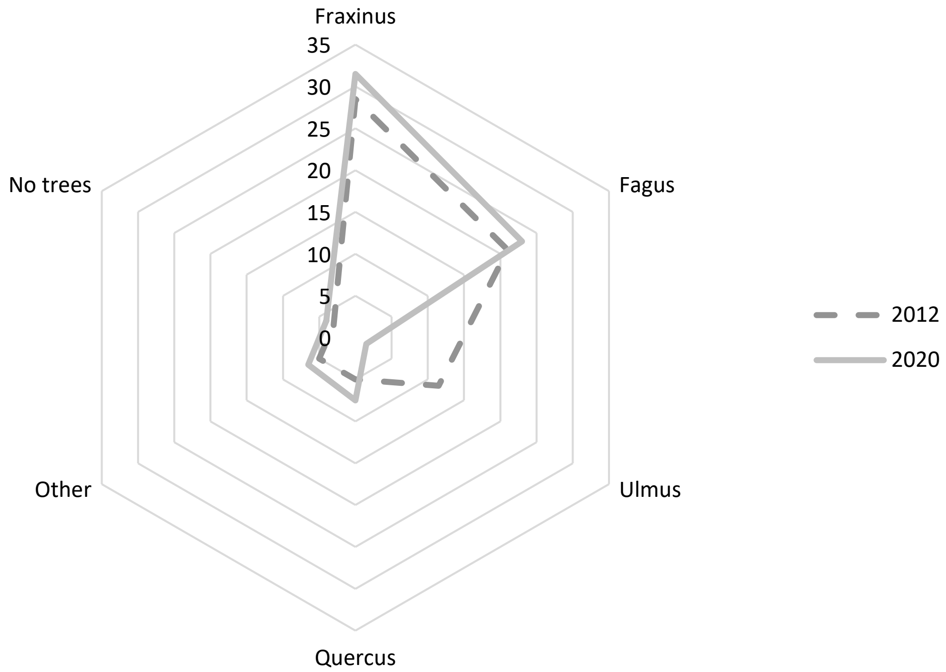


Figure 13: Changes in dominance by number of trees per hectare in permanent plots of Dalby Söderskog in the period from 2012 to 2020.

On the other hand, if dominance in Dalby Söderskog is evaluated by basal area, changes from 2012 to 2020 affected less tree species than changes in number of individual trees (fig. 14; fig. 15). For wych elm, dominance decreased from seven to two plots. European beech increased dominance from 17 to 21 plots. European ash, pedunculate oak and other tree species have not changed dominance (fig. 16). Plots with no trees have increased from zero to one.

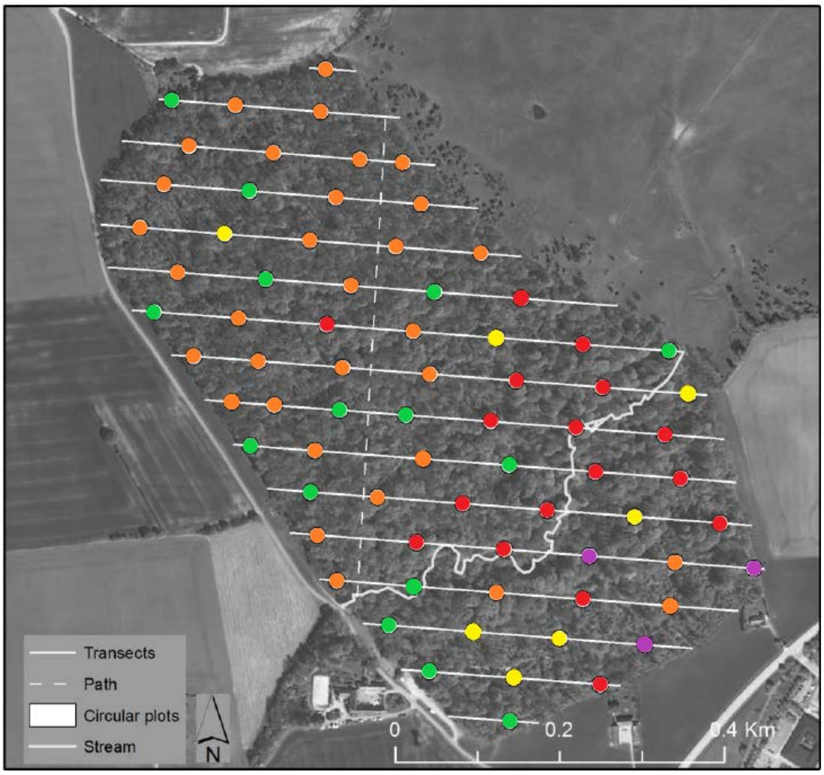


Figure 14: Dominant tree species according to basal area in permanent plots of Dalby Söderskog 2012,

● *F. excelsior;* ● *F. sylvatica;* ● *U. glabra;* ● *Q. robur;* ● *other;* ○ *no trees.*

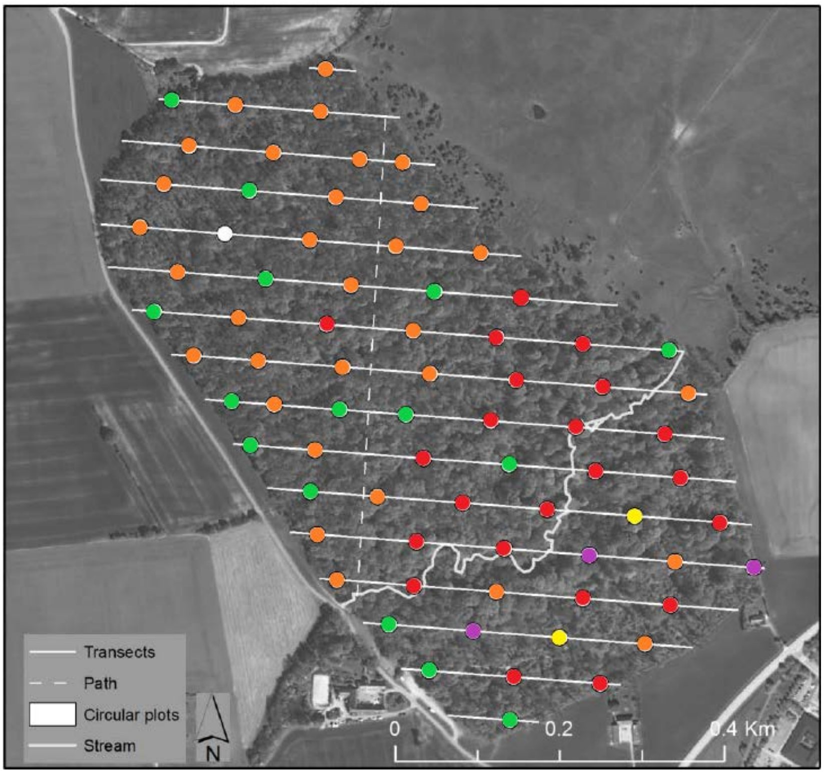


Figure 15: Dominant tree species according to basal area in permanent plots of Dalby Söderskog 2012,

● *F. excelsior;* ● *F. sylvatica;* ● *U. glabra;* ● *Q. robur;* ● *other;* ○ *no trees.*

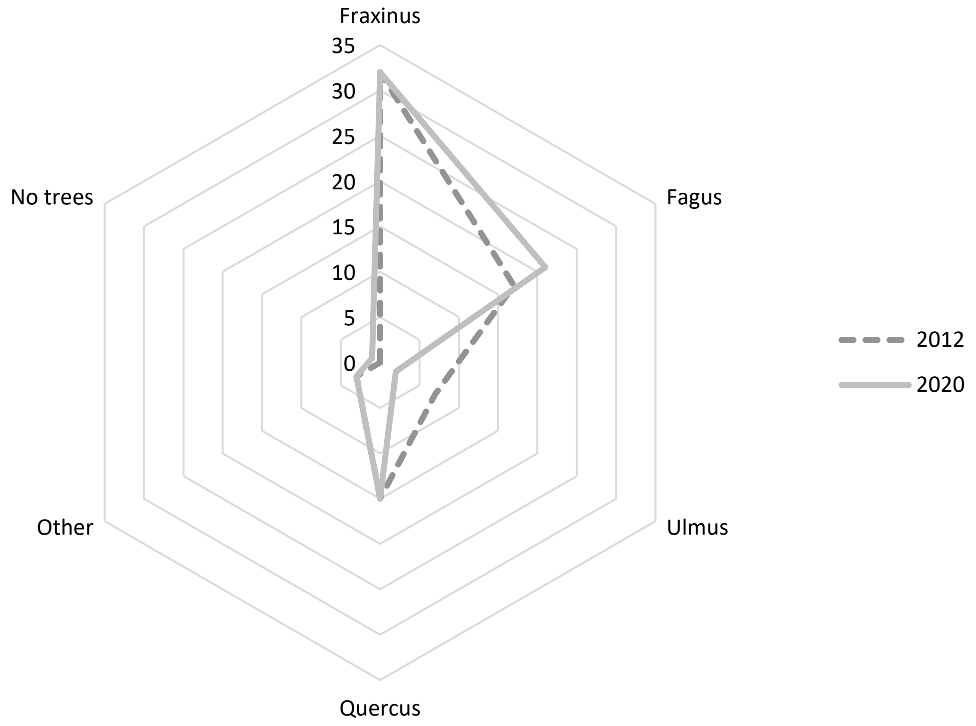


Figure 16: Changes in dominance by basal area in permanent plots of Dalby Söderskog in time period of 2012 to 2020.

3.7. Species composition and overall stand structure

The overall species composition did not change, but the relative proportions of the four main tree species changed (fig. 17). A decline of the total number of trees was seen for wych elm and European ash. If ash in 2012 was almost at the same amount as beech, then, due to ash dieback, it is clearly less in 2020. Ash has decreased by 20 %, while beech has exploited the situation and increased its population by 19 %. Pedunculate oak has not increased nor decreased, while other species i.e. black alder, Norway maple and crab apple have decreased by 15 % in number of trees per hectare. The total stem density has decreased from 349 to 266 individuals per hectare.

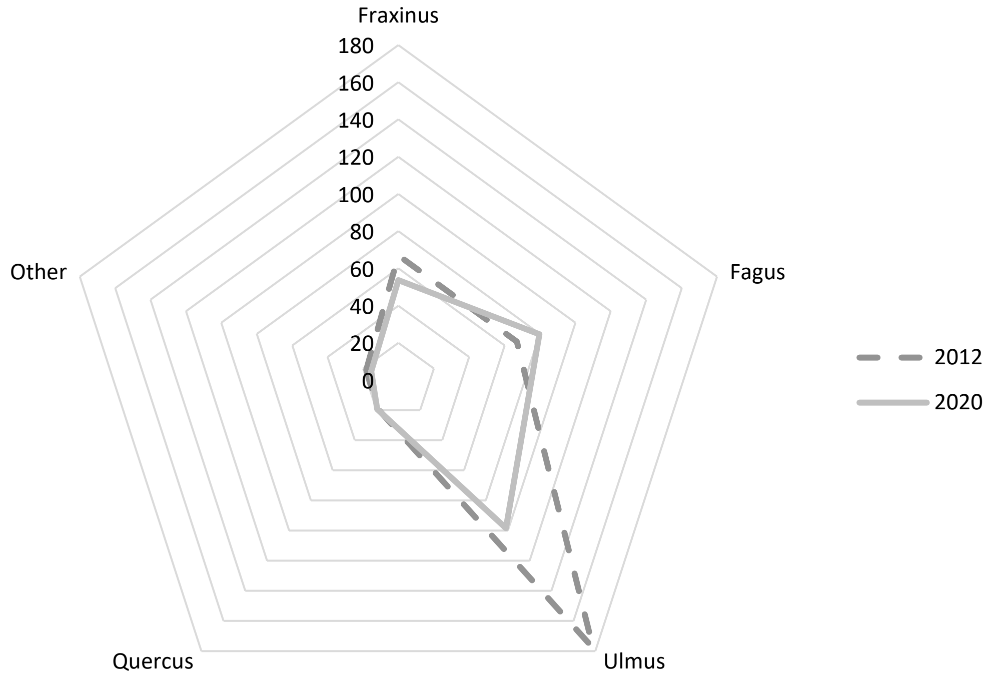


Figure 17: Species composition of tree species above 10 cm diameter in units per hectare in Dalby Söderskog 2012 and 2020.

The diameter distribution in 2012 can be described as an inversely J-shaped curve (fig. 18). In 2020 the diameter distribution is still similar as it was in 2012, but there is a large decrease in smaller diameter trees in the 10 – 19 and 20 to 29 cm diameter classes. A slight decrease can also be seen in diameter classes up to 49 cm. In diameter classes above 50 cm changes are relatively small (fig. 18).

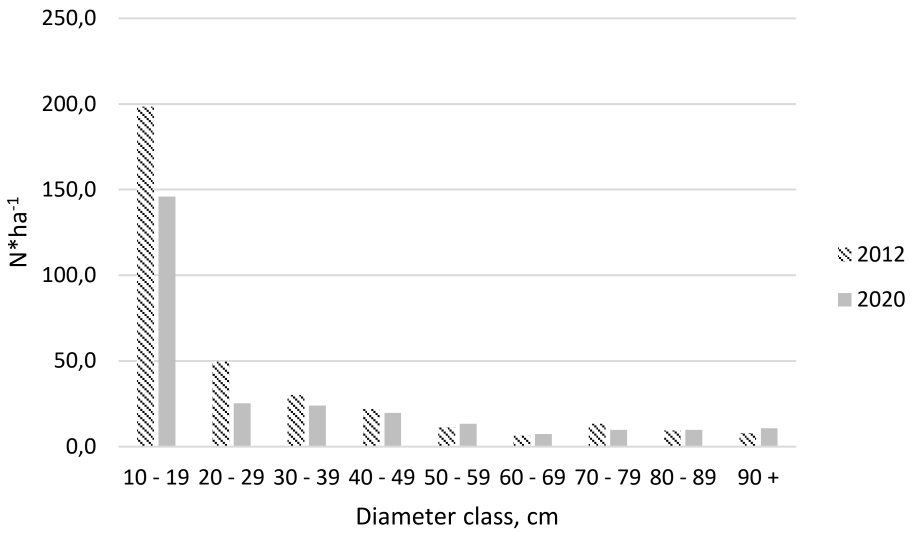


Figure 18: Diameter class distribution of all tree species in Dalby Söderskog in 2012 and 2020.

Figure 19 shows gains and losses throughout the period 2012 to 2020. Highest losses can be seen in the diameter class 10 – 19 and 20 – 29 cm. The largest increase can be seen in diameter group 50 – 59 and 90 + cm (fig. 19).

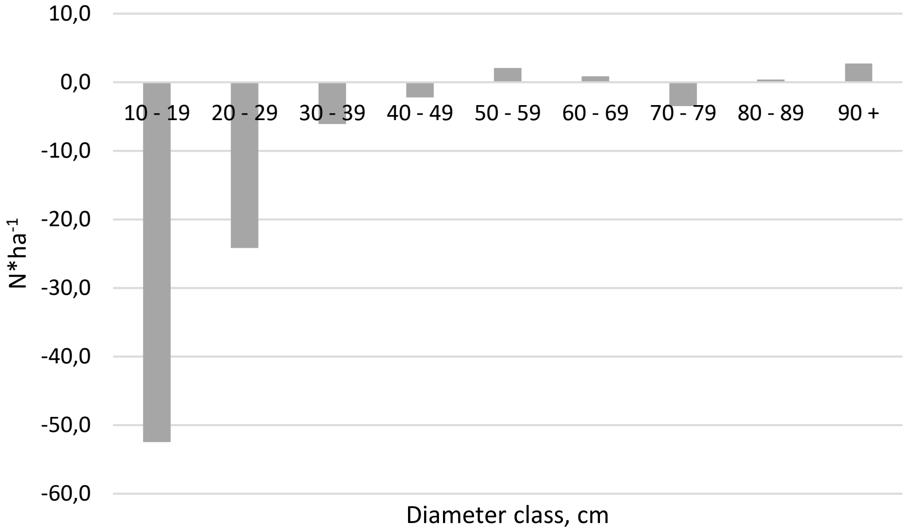


Figure 19: Gains and losses in each diameter class from period of 2012 to 2020.

4. Discussion

4.1. European ash

All inventories of Dalby Söderskog throughout the years show that European ash has continuously increased until 2012 (Brunet et al., 2014). According to the inventory carried out in 2020, ash shows a decrease in number of individuals. The diameter distribution figure shows that the decrease is seen mainly in two diameter classes, 20 – 29 and 30 – 39 cm. This decrease of European ash is mainly a result of ash dieback caused by the fungus *Hymenoscyphus fraxineus*. Other reasons that could be considered are storm damage and anthropogenic damage i.e. cutting down trees due to safety reasons. Ash decline may have been a predisposing factor that weakened the trees before storm or a person took them out. When it comes to the smaller 10 – 19 cm diameter class, a decrease already can be seen since the inventory that was done in 1970 up until 2012 (Brunet et al., 2014) and 2020 is no exception. This is mainly due to weak regeneration when tree canopies grew denser (Brunet et al., 2014), but on the other hand ash dieback has also affected almost all of the trees in this diameter class in 2020.

A succession of ash in the shrub layer has been observed for the time period of 1970 to 2012 (Brunet et al., 2014). This is a period when elm was declining due to Dutch elm disease. The disease created gaps, which were utilized by ash more than by any other species (Brunet et al., 2014). Since the elm decline has only continued, situation of young ash has most likely continued the same path. A master thesis study in 2016 found that in Dalby Söderskog ash trees below 1.3 m height are rarely affected, but trees above 1.3 m and until nine cm in dbh are severely affected by ash dieback (Dietrich, 2016). Similar results have also been obtained in Latvian study (Pušpure et al., 2017) which showed that 15 years after ash dieback, natural regeneration has been in sufficient quantities. Seventy five percent of ash in age of two to six years were healthy (Pušpure et al., 2017). Another possible factor that has been found to affect ash regeneration in the herbaceous layer is uprooting by wild boar (*Sus scrofa*). A study shows that in the time period of 2010 to 2013 the amount of ash seedlings/saplings significantly decreased from 11.6 % to 8.2 % mean ground cover because of wild boar damage (Brunet et al., 2016).

Almost all (99 %) of the ash trees larger than 10 cm dbh in Dalby Söderskog are currently affected by ash dieback. Only one individual was found that did not show any clear signs of disease. The percent of diseased ash has increased from 55 % in 2012 to 73 % in 2020, but the largest increase is seen in ash mortality. If in 2012 only two percent of all registered ashes were dead, then in 2020 it has increased to 26 %. The previous inventory showed that the largest percentage of affected trees were in lower diameter classes (Bukina, 2012). This is explainable by that the larger ash trees could have been more vigorous. Unfortunately, this is not the case anymore. In 2020 almost all of the trees are affected by ash dieback and many of them have died or will die in the near future. If this tendency continues in Dalby Söderskog, this would not only lead to a strong reduction of the ash population in the long run, but it would also cause local extinction of epiphytes (Hultberg et al., 2020).

4.2. Wych elm

Inventories from Dalby Söderskog show that wych elm has been increasing up until 1970 (Malmer et al. 1978). Dutch elm disease started to affect the forest around 1988, and this can clearly be seen in data from the later inventories. Elm decreased almost by two thirds in the time period from 1970 to 2012 (Brunet et al. 2014). From 2012 to 2020 wych elm has decreased by almost a half. Worth to mention that most of the individuals are in the 10 – 19 cm diameter class. As a result, elm is still the most abundant species if the 10 to 19 cm diameter class is included, but if not included it is the most scarce tree species of the main four in Dalby Söderskog. The diameter class distribution shows that there has been a decrease in all diameter classes, where still some individuals were found. It is the same pattern as from 1970 to 2012. Data collected for estimating vitality of elm shows that DED has affected 36 % of all registered living elms. Sixty four percent of elms seemed to show no signs of disease yet, but it is worth to mention that almost all of the healthy elms are in the smallest diameter class. The continuous mortality of larger individuals has influenced elm dominance in Dalby Söderskog. In 2020, only one and a half plot is dominated by elm, compared to 11.5 in 2012. Increased death rate of elm has resulted in creation of gaps in the tree canopy, but elm has utilized these gaps themselves. Many young elm saplings can be observed in the shrub layer, which means that successful regeneration is their main remaining mechanism to escape Dutch elm disease (Oheimb & Brunet, 2007). This phenomenon has also been noticed in Lady Park Wood, western Britain, where Peterken and Mountford (1998) observed that while about 65% of the elm population has been killed by DED, the population has increased 1.4 times due to increased rate of regeneration. Emborg et al. (2000) also observed a similar tendency in Suserup Skov, Denmark. Emborg et al. also suggested that it was a result of DED.

Due to the current situation and examples from other places, Dalby Söderskog will most likely follow the same path (Oheimb & Brunet, 2007). Even though inventory data show that elm in the smallest diameter class were being affected more compared to previous years, the production of seeds and successful regeneration in the gaps of fallen trees will and are resulting in short rotation, fast growing wych elms. In this way, elm will probably continue to maintain itself and continue to be an important part of Dalby Söderskog for upcoming decades even with a presence of DED.

4.3. Pedunculate oak

The number of oak has shown a decreasing trend since 1935. When canopies closed and there were no gaps to grow in, regeneration of the light-demanding oak drastically decreased. In the time period from 1970 to 2012 oak decreased by a half, respectively from 38 individuals to 19 individuals per hectare (Brunet et al., 2014). The 2020 inventory shows that oak has not increased nor decreased, respectively in both survey years 19 individuals per hectare were found. On the other hand, the frequency of oak regeneration in the ground layer has significantly increased in the time period from 1970 to 2012 (Brunet et al., 2014; Finnström, 2016). It seems that from the last inventory up to today this tendency has continued, because Dutch elm disease and ash dieback have not stopped affecting the forest, and the gaps are still being created every year. The diameter class distribution figure shows that there was a lack of regeneration in the past, but now the first young oak tree of the 10 – 19 cm diameter class has entered one of the permanent sample plots. Lindquist (1938) and Malmer et al. (1978) suggested that oak might disappear from Dalby Söderskog in the future, but the results of the current study indicate that the diseases on ash and elm have helped oak to regenerate.

The increase of dominance of the oak is largely a result of loss of ash and elm due to ash dieback and DED. If the dominance of the oak would be taken according to basal area, then it would dominate a much larger proportion of Dalby Söderskog, due to the many large individual oak trees in the forest.

The future of oak is hard to foresee. Not only regeneration of oak has significantly decreased in last couple decades in southern Sweden (Petersson et al., 2019), but there are also other factors that have induced oak mortality. In southern Sweden extreme weather conditions play a large role e.g. droughts during the vegetation season (Sonesson & Drobyshev, 2010). Studies show a correlation between droughts and oak mortality (Drobyshev et al., 2007). This results in defoliation, and in 1999 in southern Sweden 59 % of oaks were considered damaged, which means that oaks showed at least 25 % crown defoliation. However, during 2000 to 2008 a trend was observed of improving crown conditions. In addition, *Phytophthora* species may play a role. In southern Sweden most of the soils are acidic, which may suppress the ability of some of these pathogens to exploit and affect the oaks (Sonesson & Drobyshev, 2010). Therefore, it is hard to predict the future, because a large percentage of dead oaks have shown that growth has been affected multiple years before the death of a tree (Drobyshev et al., 2007).

In addition, the current situation of oak regeneration is alarming. Petersson et al. (2019) found that in southern Sweden during last six decades the number of larger oak trees and standing volume have continuously increased, but the natural regeneration has rapidly declined after the early 1980s. The authors explain these results with denser and darker forests as well as with increasing abundance of deer populations (Petersson et al., 2019). At the stand level, natural oak regeneration could be expected after strong disturbance events, which is also being reported in Dalby Söderskog. In most forest reserves experiencing gap creation after disturbances, however, browsing pressure from ungulates is suppressing oak regeneration more than in Dalby Söderskog. This can lead to large gap in diameter distribution, which would result in loss of species that are dependent on old and large oaks, and thereby negatively affect biodiversity (Petersson et al., 2019).

4.4. European beech

The European beech population remained relatively stable in the time period from 1916 to 1970. Then up until 2012 the population of beech increased both by basal area and number of stems (Brunet et al., 2014). This shows that beech was one of the first species that was favoured by decline of wych elm due to DED. The diameter distribution has not markedly changed compared to 2012. When it comes to shrub layer and ground layer, beech has increased its frequency almost two times (Oheimb & Brunet, 2007). This tendency will not most likely continue, because of soil conditions that are present in Dalby Söderskog. Beech is more sensitive to high groundwater tables and flooding, compared to ash and elm. This limits occurrence of beech in floodplain forests and other moist eutrophic forests. Therefore, it is more likely that oak will be the one of the major tree species that might take the place in the moister parts of the forest after decrease of ash and elm due to ash dieback and DED (Brunet et al., 2014). In addition, a study by Brunet et al. (2016) of the herbaceous layer shows that beech has been decreasing in places where wild boar has been uprooting the herbaceous layer.

Beech is one of the most dominant tree species in Dalby Söderskog. It has increased its dominance by two plots since 2012, respectively, 21 plots in 2012 to 23 plots in 2020. In dominance beech currently only falls behind the ash. In addition, beech mainly dominates the southeastern part of the forest, and it is likely that the beech will stay on that side and not move to the west, because the western side is much wetter and not favourable for beech (Brunet et al., 2014). Beech dominance is still less pronounced when it comes to basal area, which is mainly due to large oaks that are present in Dalby Söderskog.

Cleary et al. (2016) reported that European beech currently is under threat from the *Phytophthora gonapodyides* in southern Sweden, but also other *Phytophthora* spp. such as *P. cambivora, P. plurivora and P. cactorum* are considered as the main contributors of declining health of beech. *Phytophthora* spp. also can affect larger variety of hosts (Schoebel et al., 2014). Some of the symptoms of the disease are crown deterioration and bleeding canker, which have been spotted in Dalby Söderskog. This causes a concern. Even when *Phytophthora* spp. rarely kill the host quickly compared to ash dieback and DED, it still might lead to increasing mortality of mature beech trees in the future.

5. Conclusion

The results show that there is a strong connection between current disturbances and tree species population dynamics in Dalby Söderskog. Even if the overall composition of the main species in Dalby Söderskog has not changed yet, the relative proportion species has. The European ash population has strongly decreased since the last inventory in 2012 as a result of ash dieback. The amount of declining ash trees has strongly increased, which may threaten the existence of the species in Dalby Söderskog in the future.

The wych elm population has also continued to decrease as a result of the Dutch elm disease. DED has almost killed all of the large dimension trees, therefore the majority of elm population trees are in the lowest diameter class, which seems to be less affected by the disease. Thus, the chance for long-term survival of elm may be higher than for ash. Still, the current decrease of small elm may indicate increasing overall effects of DED. More research should be done to explore if this tendency is due to *Scolytus* vectors affecting smaller dimension trees or due to root graft transmittance from one tree to another.

Previous studies also show an increase in pedunculate oak regeneration, but the effects are still weak in the current tree inventory. The data also shows an increase of the European beech populations. Ash dieback and DED have made more growing space available for these species to thrive and regenerate, which indicates that oak and beech is benefiting from both diseases.

Consequences of DED, ash dieback and possibly also reduced vitality of old oak and beech trees may lead to loss of species that are dependent on habitats that these trees provide. As a result, overall biodiversity of Dalby Söderskog will probably be negatively affected.

Researches still should be done in a similar manner to predict what may happen with Dalby Söderskog and other similar protected forests in future. This could help creating trend lines that show a course of changes due to ash dieback and DED.

References

Anderbrant, O., Yuvaraj, J.K., Martin, J.A., Gil, L., Witzell, J. (2017). Feeding by *Scolytus* bark beetles to test for differently susceptible elm varieties. *Journal of Applied Entomology*, vol. 141, pp. 417 – 420.

Bennett, K.P. (2010). Forest structure. In: Bennett, K.P. (eds) *Good Forestry in the Granite State: Recommended Voluntary Forest Management Practices for New Hampshire* (2nd edition). University of New Hampshire Cooperative Extension, Durham, N.H. pp. 34 – 37.

Bergeron, Y., Fenton, N.J. (2012). Boreal forests of eastern Canada revisited: old growth, nonfire disturbances, forest succession, and biodiversity. *Botany*, vol. 90(6), pp. 509 – 523.

Brasier, C.M., Cooke, D.E.L., Duncan, J.M., Hansen, E.M. (2003). Multiple new phenotypic taxa from trees and riparian ecosystems in *Phytophthora gonapodyides-P. megasperma* ITS Clade 6, which tend to be high-temperature tolerant and either inbreeding or sterile. *Mycological Research*, vol. 107, pp. 277 – 290.

Brunet, J., Bukina Y., Hedwall, P.O., Holmström, E., Oheimb, G.v. (2014). Pathogen induced disturbance and succession in temperate forests: Evidence from a 100-year data set in southern Sweden. *Basic and Applied Ecology*, vol. 15, pp. 114 – 121.

Brunet, J., Hedwall, P.O., Holmström, E., Wahlgren, E. (2016). Disturbance of the herbaceous layer after invasion of an eutrophic temperate forest by wild boar. *Nordic Journal of Botany*, vol. 34, pp. 120 – 128.

Bukina, Y. (2012). *Long-term Succession and Loss of Foundation Species in a Temperate Broadleaved Forest in Southern Sweden*. Diss. Swedish University of Agricultural Sciences: Alnarp.

Caudullo, G., de Rigo, D. (2016). *Ulmus* - elms in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, pp. 186 – 188.

Christensen, M., Emborg, J., Nielsen, A.B. (2007). The forest cycle of Suserup Skov - revisited and revised. *Ecological Bulletins*, vol. 52, pp. 33 – 4.

Cleary, M., Ghasenkhani, M., Blomquist, M., Witzell, J. (2016). First report of *Phytophthora gonapodyides* causing stem canker on European beech (*Fagus sylvatica*) in southern Sweden. *Plant Disease*, vol. 10, pp. 2174.

Dietrich, M. (2016). *The impact of ash dieback on ash regeneration in the forest reserve Dalby Söderskog*. Diss. Swedish University of Agricultural Sciences: Alnarp.

Dobrowolska, D., Hein, S., Ooserbaan A., Wagner, S., Clark, J., Skovsgaard, J.P. (2011). A review of European ash (*Fraxinus excelsior* L.): implications for silviculture. *Forestry*, vol. 84, pp. 133 – 148.

Drobyshev, I., Linderson, H., Sonesson, K. (2007). Temporal mortality pattern of pedunculate oaks in southern Sweden. *Dendrochronologia*, vol. 24, pp. 97 – 108.

Durrant, T.H., Rigo, D., Caudullo, G. (2016) *Fagus sylvatica* and other beeches in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, pp. 94 – 95.

Eaton, E., Caudullo, G., Oliveira, S., de Rigo, D. (2016). *Quercus robur* and *Quercus petraea* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, pp. 163 – 160.

Emborg, J., Christensen, M., Heilmann-Clausen, J. (2000). The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. *Forest Ecology and Management*, vol. 126, pp. 173 – 189.

Finegan, B. (1984). Forest succession. *Nature*, vol. 314, pp. 109 – 114.

Finnström, O. (2016). *Regeneration dynamics of pedunculate oak in natural temperate forests: a case from southern Sweden*. Diss. Swedish University of Agricultural Sciences, Alnarp.

Geßler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., Rennenberg, H. (2007). Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees*, vol. 21, pp. 1 – 11.

Hultberg, T., Sandström, J., Felton, A., Öhman, K., Rönnberg, J., Witzell, J., Cleary, M. (2020). Ash dieback risks an extinction cascade. *Biological Conservation*, vol. 244, pp. 1 – 9.

Hytteborn, H., Svensson, B.M., Kempe, K., Press, A., Rydin H. (2017). Century-long tree population dynamics in a deciduous forest stand in central Sweden. *Journal of Vegetation Science*, vol. 28, pp. 1057 – 1069.

Jensen, J.S., Hansen, J.K. (2008). Geographical variation in phenology of *Quercus petraea* (Matt.) Liebl and *Quercus robur* L. oak grown in a greenhouse. *Scandinavian Journal of Forest Research*, vol. 23, pp. 179 – 188.

Jung, T., Blaschke, H., Neumann, P. (1996). Isolation, identification and pathogenicity of *Phytophthora* species from declining oak stands. *European Journal of Forest Pathology*, vol. 26, pp. 253 – 272.

Jung, T., Burgess, T.I. (2009). Re-evaluation of *Phytophthora citricola* isolates from multiple woody hosts in Europe and North America reveals a new species, *Phytophthora plurivora* sp nov. *Persoonia*, vol. 22, pp. 95 – 110.

Lindquist, B. (1938). Dalby Söderskog, en skånsk lövskog i forntid och nutid. *Acta Phytogeographica Suecica*, vol. 10, 1 – 273.

Löf, M., Castro, J., Engman, M., Leverkus, A.B., Madsen, P., Reque, J.A., Villalobos, A., Gardiner, E.S. (2019). Tamm Review: Direct seeding to restore oak (*Quercus* spp.) forests and woodlands. *Forest Ecology and Management*, vol. 448, pp. 474 – 489.

Malmer, N., Lindgrem, L., Persson, S. (1978). Vegetational succession in a south Swedish deciduous wood. *Vegetatio*, vol. 36, pp. 17 – 29.

McMullan, M., Rafiqi, M., Kaithakottil, G., Calvijo B.J., Bilham, L., Orton, E., … Clark, M.D. (2018). The ash dieback invasion of Europe was founded by two genetically divergent individuals. *Nature Ecology & Evolution*, vol. 2, pp. 1000 – 1008.

Oheimb, G.v., Brunet, J. (2007). Dalby Söderskog revisited: long-term vegetation changes in a south Swedish deciduous forest. – *Acta Oecologica*, vol. 31, pp. 229 - 242.

Pautasso, M., Aas, G., Queloz V., Holdenrieder O. (2013). European ash (*Fraxinus excelsior*) dieback – A conservation biology challenge. *Biological Conservation*, vol. 158, pp. 37 – 49.

Peterken, G.F., Mountford, E.P. (1998). Long-term change in an unmanaged population of wych elm subjected to Dutch elm disease. *Journal of Ecology*, vol. 86, pp. 205 – 218.

Petersson, L.K., Milberg, P., Bergstedt, J., Dahlgren, J., Felton, A.M., Götmark, F., Salk, C., Löf, M. (2019). Changing land use and increasing abundance of deer cause natural regeneration failure of oaks: Six decades of landscape-scale evidence. *Forest Ecology and Management*, vol. 444, pp. 299 – 307.

Petrokas R. (2008). Growth vigor in wych elm (*Ulmus glabra* Huds.). *Baltic Forestry*, vol. 14, pp. 204 – 215.

Pušpure, I., Matisons, R., Laiviņš, M, Gaitnieks, T., Jansons, J. (2017). Natural regeneration of common ash in young stands in Latvia. *Baltic Forestry*, vol. 23, pp. 209 – 217.

Santini, A., Faccoli, M. (2015). Dutch elm disease and elm bark beetles: a century of association. *iForest*, vol. 8, pp. 126 – 134.

Schoebel, C. N., Stewart, J., Grünwald, N. J., Rigling, D., Prospero, S. (2014). Population history and pathways of spread of the plant pathogen *Phytophthora plurivora*. *PloS one*, vol. 9, pp. 1 – 11.

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., … Reyer, C.P.O. (2017). Forest disturbances under climate change. *Nature Climate Change*, vol. 7, pp. 395–402.

Sonesson, K., Drobyshev, I. (2010). Recent advances on oak decline in southern Sweden. *Ecological Bulletins*, vol. 53, pp. 197 – 207.

Stener, L.G. (2013). Clonal differences in susceptibility to the dieback of *Fraxinus excelsior* in southern Sweden. *Scandinavian Journal of Forest Research*, vol. 28:3, pp. 205 – 216.

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