

# Ecological Consequences of Ash Dieback in Western Norway

Author: Maren Stien Johansen

Master of Science in Biology

Biodiversity, Evolution and Ecology

Spring 2021

Supervisors: Fride Høistad Schei (NIBIO) and John-Arvid Grytnes (BIO)

Department of Biological sciences (BIO), University of Bergen



UNIVERSITY OF BERGEN  
*Faculty of Mathematics and Natural Sciences*



*'Every tree, therefore, is  
valuable to the community and  
worth keeping around for as  
long as possible. And that is  
why even sick individuals are  
supported and nourished until  
they recover.'*

The Hidden Life of Trees,  
Peter Wohlleben, 2015

## Acknowledgements

To my supervisors Fride Høistad Schei and John-Arvid Grytnes, I extend my gratitude for guiding and helping me through this year of writing a master thesis. And for their patient understanding with the difficulties that covid-19 brought along. To Fride for trusting in me to resample her vegetation plots.

To the people of ECKO journal club for creating an atmosphere for us students to ask all our questions, getting good answers, and for great feedback on the developing thesis. To my fellow students Frida and Halvor for help with coding in R, and for trusted feedback on parts of the thesis, and affecting me with their positive/optimistic attitude.

To my family, for support and for always encouraging me in my work. Especially to my mother and sister who accompanied me on many of my fieldtrips. This was not always easy and relaxing, but very memorable and fun, and it made the fieldwork so much easier. To Tobias, who always got my back, and knows how to encourage me when things do not go as planned. And to my friends, for support and who has been there when I needed a break from all the writing.

And finally, I want to thank UiB for the opportunity to study the forest, something that I have such interest for and really enjoy.

Thanks for all, it has been a growing experience!

*Mason S. Johansen*

## Table of contents

<b>Abstract</b> .....	6
<b>Introduction</b> .....	7
<b>Materials and Method</b> .....	11
Study area .....	11
Symptoms of Ash dieback.....	12
Fieldwork .....	13
Location.....	13
Permanent vegetation plots .....	13
Analysis of the plots.....	14
Organizing the data .....	14
Statistical analysis .....	15
Changes in species composition.....	15
Linear models.....	15
Ellenberg indicator values.....	16
<b>Results</b> .....	17
Species observation.....	17
Changes in species composition and Ellenberg .....	18
Linear models.....	20
<b>Discussion</b> .....	22
Impacts of a more open forest canopy.....	22
Impact of reduced abundance in ash .....	23
<b>Conclusion</b> .....	25
<b>References</b> .....	26
<b>Appendix A</b> -List of locations, number of plots, year of resampling and overview of increase/decrease in ash abundance .....	31
<b>Appendix B</b> – Ellenberg indicator values and abbreviation for species.....	32

<b>Appendix C-</b> Overview of species that disappeared and appeared in ground vegetation (without trees) .....	36
<b>Appendix D-</b> Species list with total number of observations .....	37
<b>Appendix E-</b> Dataset used for this thesis .....	41

## **Abstract**

Invasive forest pathogens are a global problem and are causing loss in biodiversity in forests affected. With the increased efficiency of global trade, spread of invasive pathogens has increased. Ash dieback is such a pathogen caused by the spread of an invasive species of fungi, currently threatening European ash. With a high mortality rate for ash trees, one can already tell that this disease will have major consequences for the ash populations in Europe and associated species. There is little research done on the ecological consequence of such a disease, and there is a huge knowledge gap regarding the magnitude of ecological impacts in forest habitats.

In this thesis, I am doing a resurvey in temperate deciduous forests of western Norway after the arrival of ash dieback. This is a resurvey done on plots originally sampled between 2007-2009, which is before the initial outbreak in western Norway, giving a unique opportunity to examine for changes in these forest after the arrival of ash dieback. I will be focusing on how forest structure and species composition of ground vegetation has changed during the last 10-13 years, by relating them to important biotic and abiotic variables.

I found that there is a clear trend in the decreased abundance of ash as well as the expected increase of gaps in the canopy. However, these changes were not found to be affecting the changes found in the species composition of the ground vegetation. This could still be the start of a cascade affecting understory vegetation, but more time may be needed to observe such responses. The decrease in abundance of ash certainly confirms that ash dieback is interfering with these habitats, and with an increased abundance of the invasive sycamore maple, we could be looking at the start of a change in the forest structure.

# Ecological consequences of Ash Dieback in Western Norway

## Introduction

Interference in ecosystems that causes loss of biodiversity is a global problem. Invasion and disease, overexploitation, agricultural activity and urban development are amongst the major drivers causing loss in biodiversity (Maxwell *et al.*, 2016). Invasive species and pathogens contribute to the spread of diseases affecting the biodiversity of ecosystems globally (Crowl *et al.*, 2008). Humans are the main force facilitating the spread of invasive species (Signorile *et al.*, 2016) through an increase in global trade (Hultberg *et al.*, 2020). Increases in the spread of invasive pathogens to ecosystems could be devastating to the services they provide for. For the forests worldwide, invasive forest pathogens are a major threat that causes increasing damage (Ghelardini *et al.*, 2017), and threatens the ecosystem services. The forests of Europe contribute to carbon sequestration, commercial forestry, reducing risks of flooding by storing water, the wellbeing of humans by purifying water and giving green spaces (Rigo *et al.*, 2016; Coker *et al.*, 2019), all which are essential services. Tree species of forests have undergone paradigmatic invasive forest pathogens such as Dutch elm disease (DED) on elm (*Ulmus* sp.) (Brasier *et al.*, 2004) and Chestnut blight on American chestnut (*Castanea dentata*) (Loo, 2008) to name a few. These pathogens have killed hundreds of millions of trees during the 20<sup>th</sup> century and permanently altered the affected ecosystems (Ghelardini *et al.*, 2017). However, there is a knowledge gap in documentation of the magnitude of impacts caused by invasive forest pathogens at the ecosystem level (Loo, 2008). The forests provide such important services for human health and safety, that it is important to monitor how invasive pathogens impacts our forests.

The ascomycete *Hymenoscyphus pseudoalbidus* is an invasive forest pathogen that has invaded the forests of Europe, and is currently threatening ash (*Fraxinus excelsior*) (Rigo *et al.*, 2016; Hultberg *et al.*, 2020). The disease caused by this fungus (*H. pseudoalbidus*) has been given the name ash dieback (Gross *et al.*, 2012). Spreading with ascospore dispersal (Timmermann *et al.*, 2011) it has been introduced from East Asia with the introduction of the Manchurian ash (*F. mandshurica*), which is the host for this fungus in its native area (Drenkhan *et al.*, 2014). From the Manchurian ash, the fungus has spread to the ash and through seedlings from nurseries, it has continued to spread in Europe (Kirisits *et al.*, 2010). The fungus was first observed in Poland in 1992 (McMullan *et al.*, 2018), and by 2010 it had reached 22 countries of Europe (Timmermann *et al.*, 2011). This has induced a large-scale

decline in its population all over Europe (Hultberg *et al.*, 2020) due to the 85% mortality rate for the ash (Coker *et al.*, 2019). Because of ash dieback, the ash in Norway is registered as a red-listed species in the category vulnerable (Henriksen and Hilmo, 2015). Ash dieback was detected in Norway by 2008, when nurseries were examined in the south-eastern part of Norway, and by 2010 it had also reached the western parts of Norway (Timmermann *et al.*, 2011).

The temperate deciduous forests in western Norway are mainly mixed forests dominated by the two threatened species ash and wych elm, in addition to hazel (*Corylus avellana*), and linden (*Tilia cordata*), have been greatly reduced due to great value in the nutrient-rich soil for use in agriculture in early development (Aarrestad, 2000). Total area of Norway covered with forest is approximately 40% (Timmermann *et al.*, 2018), and only 1 % of this is known as temperate deciduous forests (Larsson and Sjøggen, 2003) which is the habitats for ash. While this only makes up a small portion of the forests, these are amongst the most species-rich habitats in Norway, and host many red-listed species (Aarrestad, 2000; Kålås *et al.*, 2010; Blindheim *et al.*, 2015). The deciduous forests of Norway make up the northern part of the European temperate deciduous forest belt. Due to the housing of many red-listed species vulnerable to change in their habitats, these forests are important to monitor for better understanding and protection against diseases interfering in these habitats.

A comparable disease to ash dieback that caused major consequences, is as mentioned earlier DED. This is a pandemic that struck Europe and North America twice during the last century due to an invasive species of bark beetles who carried the fungus *Ophiostoma ulmi* (first wave) and *Ophiostoma novo-ulmi* (second wave) (Brasier *et al.*, 2004). The second and most aggressive wave arrived in Europe in the late 1960s (Webber, 1981), laying waste to millions of elms (*Ulmus* sp.) across Europe and North America. For the spread of this disease, environmental factors proved important, as it is dependent on interactions between insect vectors and the elm population for transport (Martin *et al.*, 2010). The elm population in the northern parts of Europe is the least affected by the DED (Martin *et al.*, 2010) due to lack of efficient insect vectors. With a small gene pool in the elm populations of Europe due to selective planting, and favorable environmental conditions for the insect vectors, the elm populations of Europe were largely reduced (Martin *et al.*, 2010). According to Mackenthun (2004), the elm populations of Europe have decreased by 90% after the waves of DED. As a secondary reaction, many elm-associated species have become red-listed and are considered vulnerable (Hultberg *et al.*, 2020). The consequence of ash dieback might reflect similar



responses as observed from DED should it be equally devastating for ash and could cause ash-associated species to suffer from a cascade effect, leading to loss in biodiversity.

In the case of the near extinction of ash or a significant reduction to the population, there will likely be a change in the structural composition of trees in the forests. Tree species competing to replace ash in such an event may not retain the same unique soil values in the forest as ash does (Mitchell *et al.*, 2014). Ash has a unique ability to produce nutrient-rich waste that is easily degradable, as their leaves are shed while still green, thus contributing to high soil pH, and high levels of nutrient turnover (Mitchell *et al.*, 2014) This is also an important and contributing factor to the great diversity of the ground vegetation in these forests (Mitchell *et al.*, 2014).

Ash is a keystone species, ash dieback may instigate an extinction cascade based on the number of species that are obligate and highly associated with ash (Hultberg *et al.*, 2020). Even though ash is not known to form dense canopies, due to higher penetration of light in the foliage (Emborg, 1998), wilting of leaves and eventually death resulting from dieback will lead to large openings in the tree cover. Surrounding trees may not fill sudden openings in the canopy at once, thus letting in more sunlight which may affect shade-tolerant species that thrives in the shade of the forest canopy in a negative way. This sudden access to direct sunlight may also facilitate plants that are more susceptible to light to enter these habitats and threaten existing species that are more adapted to shade and vulnerable to competition. The detrimental effect from invasive species threatening keystone species of the forests could induce a cascade of consequences leading to reduction of species diversity (Rigo *et al.*, 2016). However, information on the effects of a cascade caused by invasive alien species is limited (Hultberg *et al.*, 2020).

In this thesis, I will focus on temperate deciduous forests with ash of western Norway where ash dieback is present. In 2007-2009 before the outbreak was reported in western Norway, deciduous forests in these parts were surveyed using permanent vegetation plots. Resurvey of these permanent vegetation plots in 2018 and 2020 was used for comparison to initial sampling in this thesis. This gives a unique opportunity to examine for changes after the arrival of ash dieback. The aim of this study is to investigate ecological consequences of ash dieback in western Norway. Focusing on how forest structure and species composition has changed during the last 10-13 years, by relating them to important biotic and abiotic variables. I will test if there are any changes in general cover of trees, shrubs, vascular plants, mosses, and lichens. Also, specific tree species of interest such as ash, wych elm and the invasive

sycamore maple (*Acer pseudoplatanus*) will be tested for change in abundance. Examining the ground vegetation will be done by testing changes in species composition, and I will use change in the variables to try to explain potential change in the ground vegetation. The following hypotheses will be tested. (1) The canopy is more open today than before the arrival of ash dieback. (2) The abundance of ash was higher before the arrival of ash dieback. (3) The species composition of the ground vegetation has changed after the arrival of ash dieback. (4) Changes in species composition of the ground vegetation can be related to changes in abundance of ash.

# Materials and Method

## Study area

The study area for this thesis is restricted to the temperate deciduous forests of western Norway. The deciduous forests of western Norway are mixed forests composed of ash (*F. excelsior*), hazel (*C. avenella*), linden (*T. cordata*), wych elm (*U. glabra*), beech (*Fagus sylvatica*), oak (*Quercus* spp.), Norway maple (*Acer platanoides*), black alder (*Alnus glutinosa*) and other species such as silver birch (*Betula pendula*), common yew (*Taxus baccata*), holly (*Ilex aquifolium*), cherry (*Prunus* spp.) and rowan (*Sorbus* spp.) (Blindheim *et al.*, 2015). The invasive sycamore maple (*A. pseudoplatanus*), introduced more than 250 years ago, has now become locally common in western Norway (Fremstad and Elven, 1996). For this thesis, 62 resampled plots dispersed at nineteen locations (map Figure 1) in Vestland county were surveyed. The locations in the map are marked with yellow and blue pins, the yellow pins representing the resampling from 2018 done by Fride H. Schei and Magne Sætersdal, and the blue pins were resampled in 2020 by me. All original vegetational surveys were initially made by Fride H. Schei between the years 2007 and 2009. In all locations, there are presence of ash dieback.

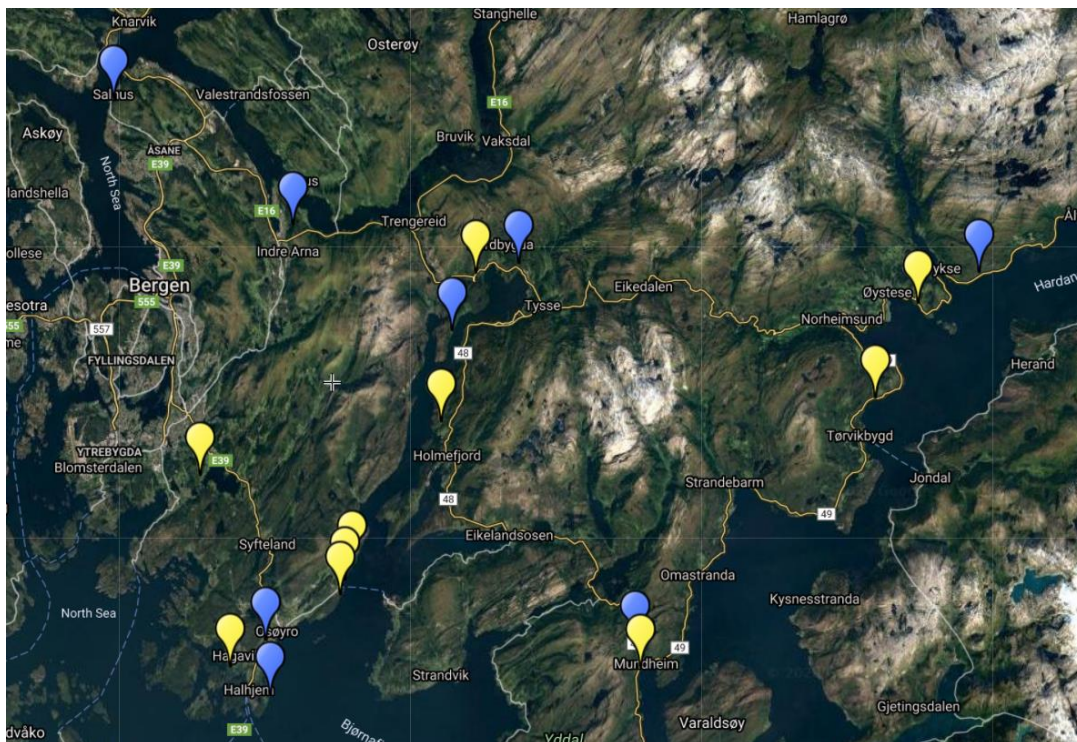


Figure 1. Map of all the locations that had plots that were resampled, all the blue pins represent resampling from 2020 and the yellow pins where resampled in 2018. See Appendix A for name of locations and year of resampling.

## Symptoms of Ash dieback

Symptoms of the fungus infecting ash can be seen in the bark and xylem of shoots, branches, stems, and in the tree's foliage (Timmermann *et al.*, 2011). Visible symptoms can be seen as eye-shaped necrotic lesions in the petioles and the bark, discoloration of leaves, petioles, and wilting of the foliage and shoots (Skovsgaard *et al.*, 2010; Timmermann *et al.*, 2011).

Elongated cankers on the tree trunk, branches, and stems are common, and with the repeated dieback of shoots in the crown, this results in the characteristic appearance with lack of foliage at the outer parts of the crown (Skovsgaard *et al.*, 2010). The disease affects trees of all ages, and usually young individuals die a few years after infection. For a mature tree, death could take about 10 years, depending on size, it can also become chronic, weakening them and make them vulnerable to other threats (Timmermann *et al.*, 2011). Affected trees are easy to discover because of their usually bushy crown and many visible symptoms (Figure 2).



Figure 2. Mature tree on the brink of death (picture to the left). Clear symptoms in the bark and in the branches along the trunk (picture to the right). Both examples are from the same location, Mundheimsdalen. Photo: Maren S. Johansen

## **Fieldwork**

### **Location**

Resampling of plots was done in deciduous forests in Western Norway where ash is the dominant tree species or previously has been the dominating. The plots that were resampled are permanent plots initially sampled from 2007-2009. During the summer of 2020, from early June until mid-August, 26 vegetation plots dispersed across 9 locations in forests of western Norway were resurveyed. These 26 plots together with 36 plots from another 10 locations, that were resurveyed in 2018, make up the total 62 plots that are the foundation for this thesis. The 19 locations are Salhus, Aldal, Asnesviki, Steinstø, Mundheimsdalen, Seimshola, Oldervollen vik, Floget, Hattvik, Hope Laupsa, Mundheimslia, Ådland, Skarvhellehola, Storomsvågen, Vangdalsberget, vest for Kalandsvatn (west of the Kalandsvatn), Mobergslia and Oldervollen (see Appendix A for a complete list of all locations with number of plots and year of resampling).

### **Permanent vegetation plots**

All original plots had coordinates and a description of the plots to help find the location. All plots are marked with an aluminum rod in the upper right corner and a nail in the bottom left corner, which was found using a metal detector. The rest of the plot was made by using the aluminum rod or nail as the corner for the plot. The nail in the bottom left corner was not found in any of the plots resurveyed in 2020, however, the aluminum rod was found. Plots were not resurveyed unless one of these permanent marks were found. The plot was set up using rope starting at the aluminum rod, with a red plastic pin in the ground, following the topography downward with a pin in each corner (Figure 3). The rope used had loops in it, marking where the plastic pin went in the ground. This rope with loops is the same as used in the original sampling, so the plot followed the exact same length and width. The permanent plots were originally put out in places of homogenous vegetation with the size of 7x3.5m, however in locations where this form was not possible, the plots were 5x5m, the total area of all plots were 25m<sup>2</sup>. This information was written in the notes from the original sampling, so there was no uncertainty in plot shape for the resampling of individual plots.

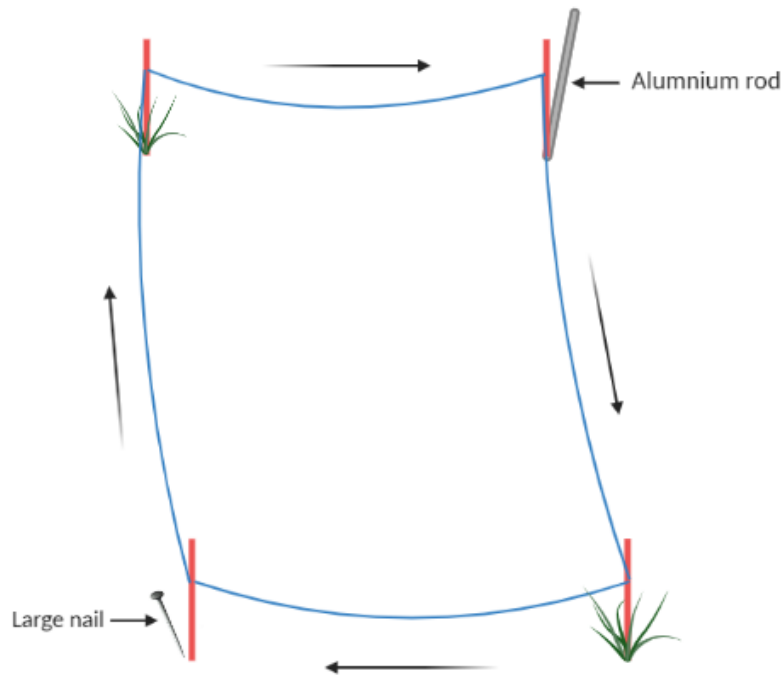


Figure 3. The permanent vegetation plot with four red plastic pins, aluminum rod in the upper right corner, and a large nail in the bottom left. The blue line represents the rope and the arrows the direction for setting it up. From the upper right aluminum rod, a rope was stretched out and mounted on four plastic pins placed in each corner of the plot to keep the rope in place. The rope had been fitted with four loops marking the length of each side of the plot. Created with BioRender.com

### **Analysis of the plots**

I registered all vascular plant species occupying the forest floor and tree species that are present in the canopy. Species in the ground vegetation were noted and given a value for the abundance. While for the tree species in the canopy the abundance was also measured for each species, and number of seedling and small individuals (less than 1.5-2 meters) were counted. The abundance of ground vegetation species and the cover of the individual tree species were measured using Braun-Blanquet scale (Braun-blanquet, 1932). In addition to measurements of specific species abundance, the total coverage of trees, shrubs, vascular plants, mosses and lichens, and rock was noted in percentage.

### **Organizing the data**

Before the data could be analyzed, they had to be organized so the resampled data would be comparable to the original data. Complete dataset is available from ECKO data consortium (Appendix E). Some species had to be merged and listed as genus, due to difficulty in

determining species late or early in the season, where some blooms early and some late in the season. Species that were merged is *Agrostis canina* and *Agrostis capillaris* to *Agrostis* sp., *Rubus fruticosus* to *Rubus* ssp. and *Taraxacum officinale* to *Taraxacum* sp.. Other species suspected of wrong determination due to lack in experience were merged with the species of the same genus if it was likely that the species was misinterpreted. Species merged with other species of the same genus are *Angelica archangelica* to *Angelica sylvestris*, *Festuca rubra* to *Festuca altissima* and *Lysimachia nummularia* to *Lysimachia nemorum*. *Polystichum aculeatum* and *Polystichum braunii* were merged to *Polystichum aculeatum/braunii*.

## **Statistical analysis**

For the statistical analysis, the R program version 1.3.1090 (R Core team, 2020) was used. Packages used were *vegan* (Oksanen *et al.*, 2019) and *tidyverse* (Wickham *et al.*, 2019).

## **Changes in species composition**

A detrended correspondence analysis (DCA) (Hill and Gauch, 1980) was done to describe the main variation in species composition for old and new sampling combined. The weighted average sample scores of the Ellenberg values were added to the DCA to help interpreting the DCA axes.

To test if the species composition changed over time, I performed a paired t-test on the DCA sample scores comparing new and old samples, to examine any change in site score along both the first and second axis. To get an overview of change in the environmental variables over time, paired t-test was done on variables of interest. These were the weighted average sample scores for the Ellenberg indicator values light, moisture, reaction of the soil (pH), and nitrogen. Other variables that were tested for change are the cover of trees, shrubs, vascular plants, mosses, and lichens, and the change in abundance of the tree species ash, wych elm, and sycamore maple.

## **Linear models**

Regressions were conducted to test if change in the environmental variables had a significant effect on the change in species composition (site score for DCA). For these models, change in cover of trees, shrubs, vascular plants, mosses and lichens, and change in abundance of specific tree species such as ash, wych elm and sycamore maple were separately set as a predictor, and change in site scores from DCA on the ground vegetation was set as response variable.

### **Ellenberg indicator values**

Ellenberg indicator values (Ellenberg *et al.*, 1992) were used to calculate average weighted sample score for four different variables. This was done to reconstruct environmental gradients based on the species data from the ground vegetation (Kapfer *et al.*, 2017), to distinguish changes between initial sampling and resampling. During the initial sampling and resampling, environmental variables such as pH and humus content were inconsistently measured, in a way that they were not useful for comparison of change over time. Therefore, Ellenberg indicator values were used instead.

These are the Ellenberg values that were used, light (L), moisture (F), nitrogen (N), and the reaction of the soil (R), also known as pH (Ellenberg *et al.*, 1992). A list of the Ellenberg values available for the species that were found can be seen in Appendix B. The values were calculated for each plot, giving a weighted average sample score for the given Ellenberg variables using this formula:

$$w_{ass} = \frac{((ab.sp\ 1 * ebv.sp\ 1) + (ab.sp\ 2 * ebv.sp\ 2) + \dots +)}{tot.sp.plot}$$

The formula represents the weighted average sample score for each Ellenberg indicator value for each plot ( $w_{ass}$ ). Where  $ab.sp$  is the abundance score for the specie in the specific plot,  $ebv.sp$  is the Ellenberg indicator value along one of the gradients for the specific species, and  $tot.sp.plot$  would be the total number of species observed in the plot. This formula was used for each of the Ellenberg variables in each plot, resulting in four weighted average samples scores for each plot.



## Results

### Species observation

In the time interval between 2007-2020, the total number of observed species in the ground vegetation has increased from 119 species to 123. 106 of these species are found in both the original and resampled plots, 13 species were only found in the original sampling and 17 species were only found in the resampled plots (see Appendix C for a list of species that have appeared and disappeared). The total number of tree species found in the original sampling was 16, and in the resampled plots, there were 18 species, the two new species were *Acer platanoides* and *Salix caprea*. The total number of observations has increased from 1246 in the original sampling, to 1297 in the resampling. The average number of species per plot when including both ground vegetation and tree species is 20.08 (without trees: 16.29) for the original sampling and 20.92 (without trees: 16.32) for the resampling. I found the number of species in each plot to be highly similar between original and resampled plots (Figure 4). Ash was present in 81% of the plots in the original sampling and 89% of plots for the resampling (see Appendix A for overview of number of plots that had increase/decrease in abundance of ash).

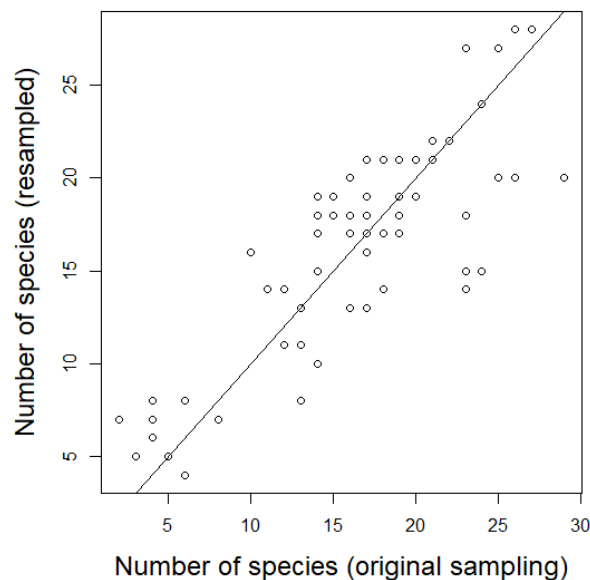


Figure 4. Comparing the number of species found in all 62 plots between the original sampling and resampled plots. The plots are following a trend along the line, indicating highly similar numbers of species found in the old and new sampling.

## Changes in species composition and Ellenberg

A DCA was conducted on the species for the ground vegetation (Figure 5). Displayed in figure 5 the Ellenberg indicator values suggest that the first DCA axis explains variance in light conditions (L) and moisture level (F), while the second DCA axis shows a slight variation in nitrogen (N) levels and soil pH (R). Analyzing the first and second axis in the DCA for the species in the ground vegetation, shows that there is a significant change in site scores over time along both the first ( $p$ -value=0.028,  $t$ -value=2.239,  $\bar{x}$ =0.073) and second axis ( $p$ -value= 0.024,  $t$ -value= -2.314,  $\bar{x}$ =-0.091).

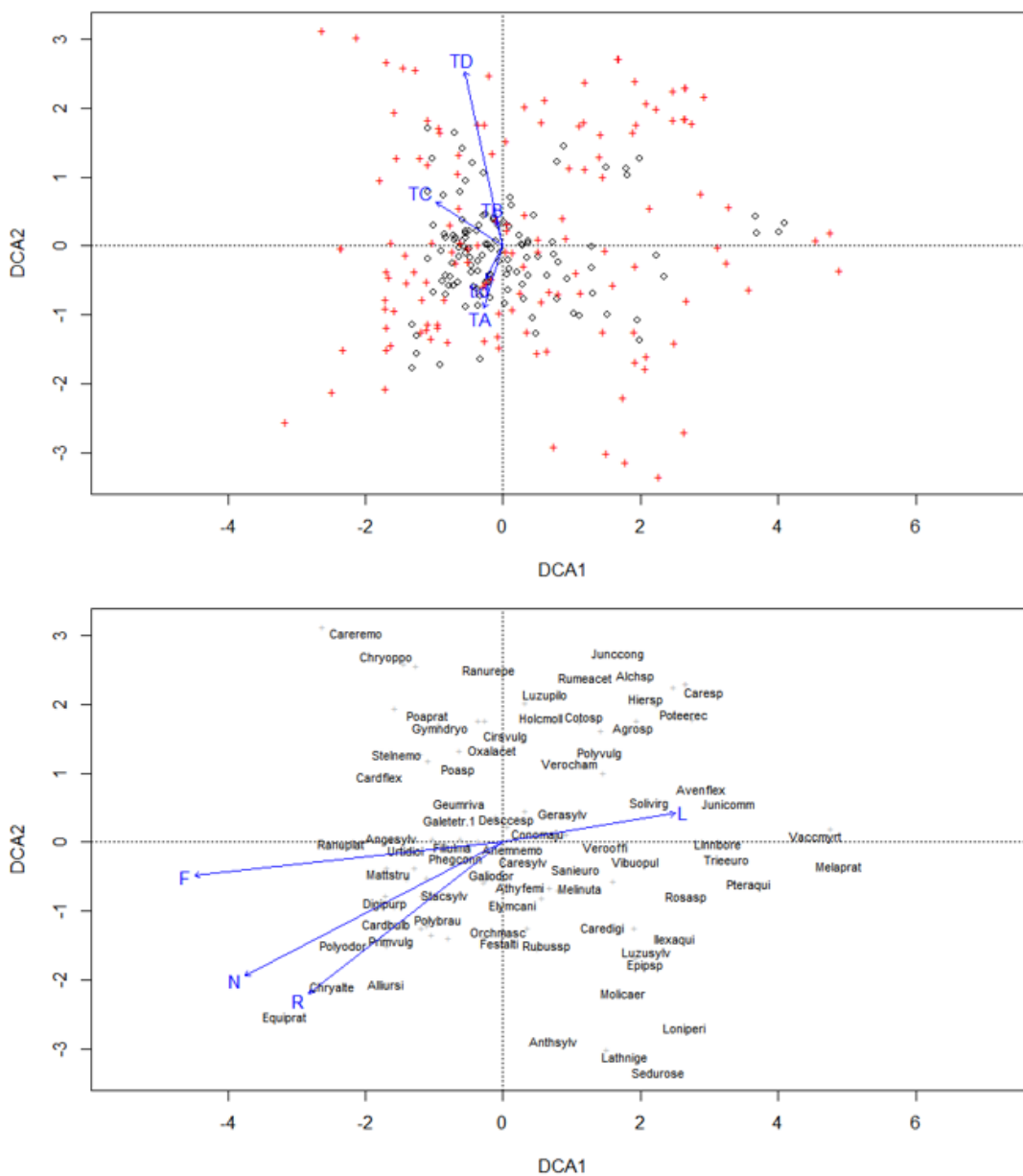


Figure 5. Detrended correspondence analysis was done on the species composition of the ground vegetation in each plot. The uppermost plot is the DCA with red crosses representing the species, and

the circles represents the plots, both original and resampled, with the added variables TA (cover of trees), TB (cover of shrubs), TC (cover of vascular plants), TD (cover of mosses and lichens) and tid (time from old to new sampling). The bottom plot illustrates the results from the same DCA, with the abbreviated species name (list of abbreviated species names and corresponding species can be found in Appendix B) for the most abundant species and the environmental variables from the Ellenberg indicator values L (light), F (moisture), R (pH) and N (nitrogen).

The average weighted sample scores for the Ellenberg indicator values had no significant change over time for the weighted average values of light (p-value= 0.851, t-value= 0.188,  $\bar{x}$ = 0.031), moisture (p-value= 0.484, t-value= -0.703,  $\bar{x}$ = -0.158), nitrogen (p-value= 0.946, t-value= 0.067,  $\bar{x}$ = 0.017) and pH (p-value= 0.248, t-value= -1.164,  $\bar{x}$ =-0.253).

### **Change in cover**

From the statistical analysis, a significant change was found in the total cover of trees (TA) in a negative direction, meaning that the canopy formed by the trees has become more open (p-value= 0.002, t-value= -3.875,  $\bar{x}$ = -8,765). However, for the change in cover of shrubs (TB), there was a significant change in a positive direction, indicating an increase in cover of shrubs (p-value= 0.002, t-value= 3.272,  $\bar{x}$ = 8.782). When testing for change in total cover of vascular plants (TC) over time, there were no significant change (p-value= 0.19, t-value= -1.33,  $\bar{x}$ = -3.152). For changes in total cover of mosses and lichens (TD), there were no significant change (p-value= 0.85, t-value= -0.188,  $\bar{x}$ = -0.869). Changes in cover of trees, shrubs, vascular plants, lichens, and mosses are illustrated using histograms (Figure 6).

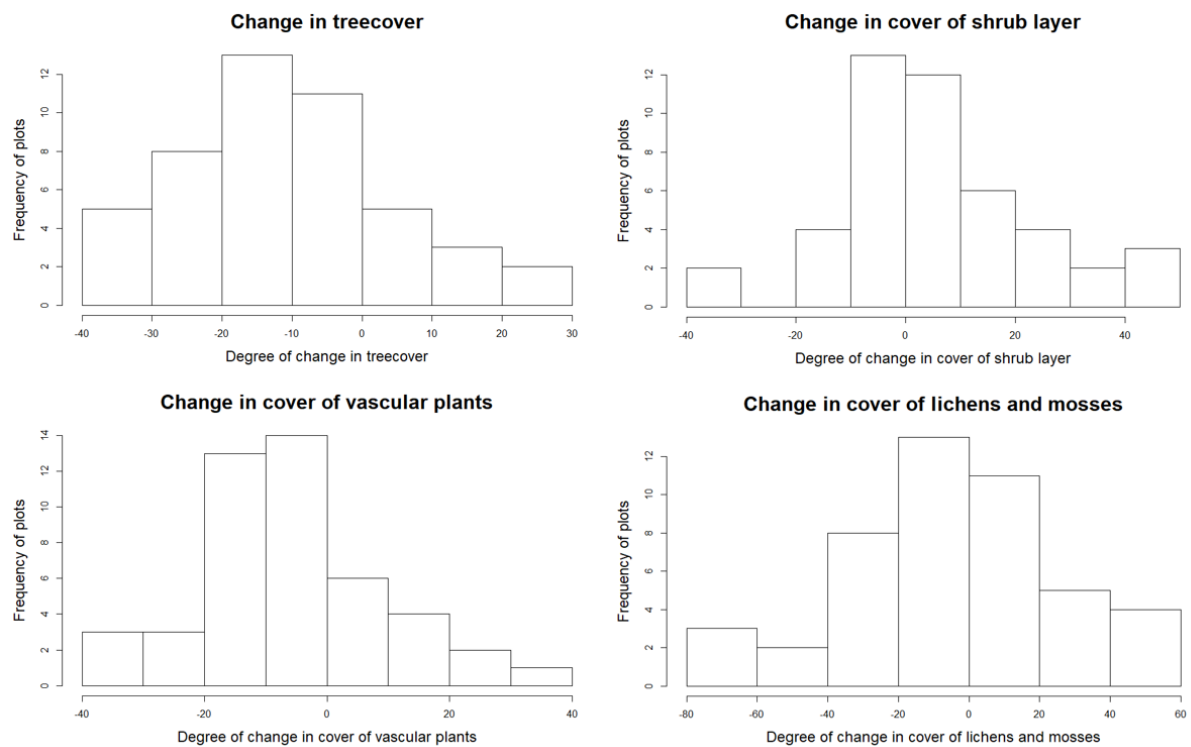


Figure 6. Histograms illustrating the amount of change in cover of the different layers that were measured for the plots. Four layers were measured for total cover, from the top layer to bottom, cover of trees, shrub layer, vascular plants and lichens and mosses.

### Change in abundance of ash, wych elm, and sycamore maple

The change in abundance of selected trees over time were tested, and for ash there has been a significant reduction in abundance (p-value= 0.018, t-value= -2.412,  $\bar{x}$ = -0.435). Change in abundance of wych elm was not significant (p-value= 0.215, t-value=1.250,  $\bar{x}$ = 0.209), while the change in abundance of sycamore maple was significant in a positive direction indicating increased cover (p-value= 0.001, t-value= 3.359,  $\bar{x}$ = 0.354).

### Linear models

The change in the total cover of trees was not significant in explaining changes in the site score of DCA axis 1 (p-value= 0.38, F-value=0.77,  $R^2 < -0.01$ ) and DCA axis 2 (p-value=0.86, F-value=0.03,  $R^2 = -0.02$ ) (Figure 7). Indicating that a more open canopy has not affected the change seen in species composition. The change in total cover of shrubs, vascular plants, mosses, and lichens were also tested, however these were also not significant in explaining change in site scores from the DCA.

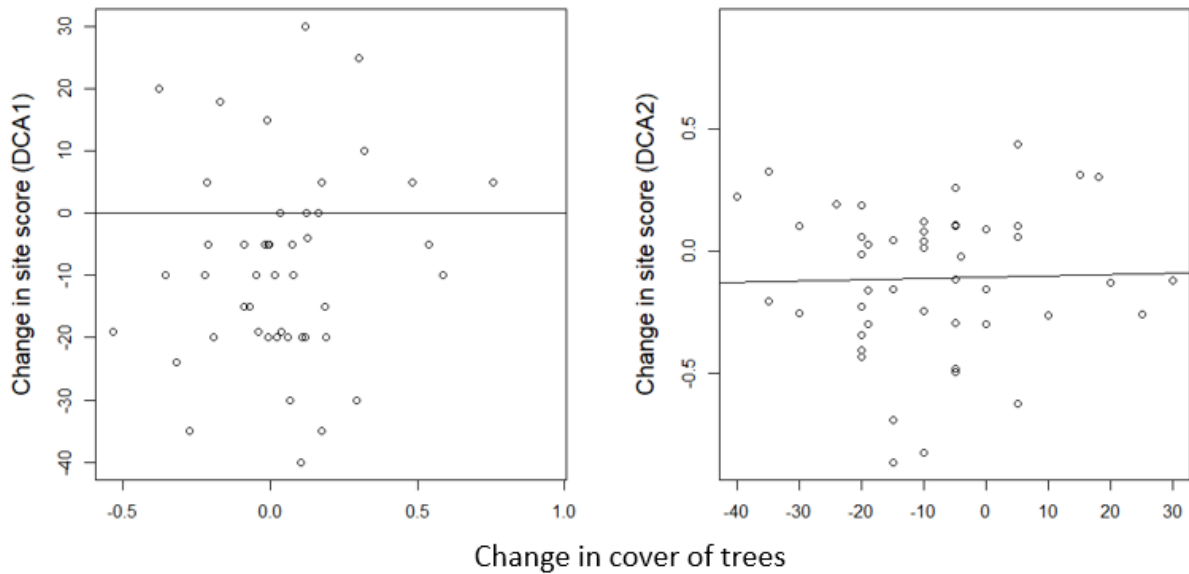


Figure 7. Change in site score of each plot against change in cover of trees along DCA axis 1 (to the left) and DCA axis 2 (to the right).

The change in abundance of ash was not significant in explaining changes in site score of DCA axis 1 (p-value= 0.76, f-value= 0.08,  $R^2 = -0.01$ ) and DCA axis 2 (p-value= 0.53, f-value= 0.39,  $R^2 < -0.00$ ) (Figure 8). For the observed reduction in ash, this has not induced the observed change in the species composition. The change in abundance for wych elm and sycamore maple was also tested for change in site score, and they were both not significant.

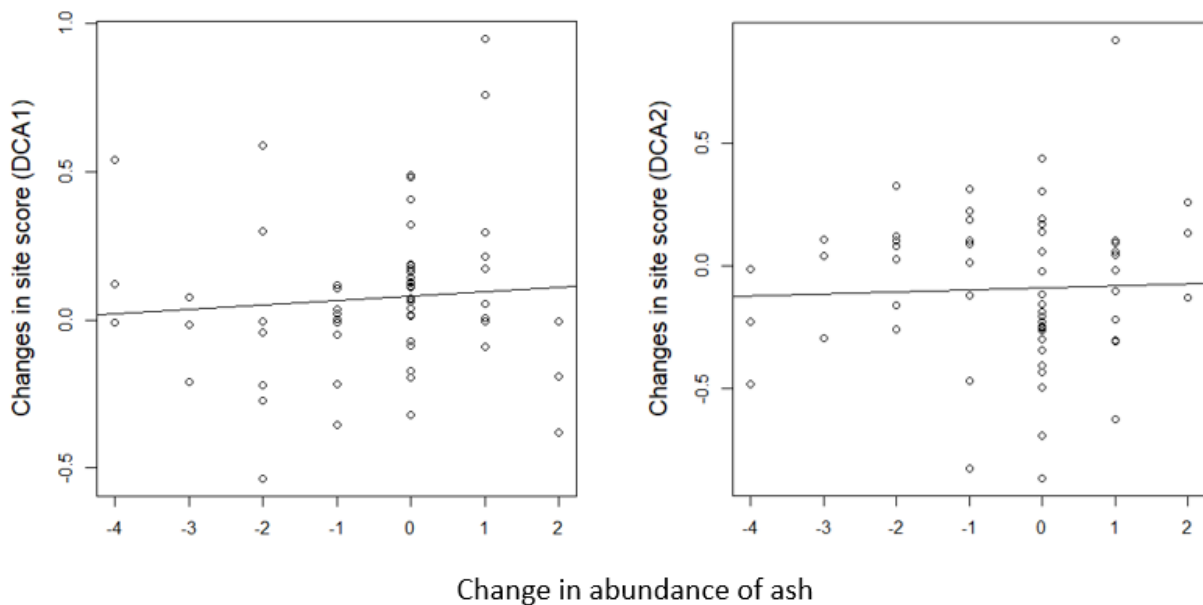


Figure 8. Change in site score against changes in abundance of ash along DCA axis 1 (to the left) and DCA axis 2 (to the right).

## Discussion

The canopy in temperate deciduous forests of western Norway has become more open since the arrival of ash dieback, and the abundance of ash has significantly decreased. This confirms hypothesis (1) and (2), that there would be a more open forest canopy and that abundance of ash would decrease with the arrival of ash dieback. There was found a change in the species composition of vascular plants in the ground vegetation after 10-13 years. This confirms hypothesis (3), that there is a change in species composition of the ground vegetation after the arrival of ash dieback. However, this change in understory vegetation was not related to change in abundance of ash, therefore rejecting hypothesis (4), that the observed change in species composition would be related to change in abundance of ash.

### Impacts of a more open forest canopy

The forest canopy has become more open since the presence of ash dieback, and it was hypothesized that this would affect species composition in the ground vegetation. However, according to the model, the reduced canopy did not explain the observed changes in the ground vegetation. From a study done in New York State on gaps in the canopy's effect on understory vegetation, it was not found large differences between species composition in a gap in comparison to vegetation under a closed canopy (Goldblum, 1997). They found however, that the species in the understory vegetation increased in size and abundance when a gap was created in the canopy, due to improved environmental conditions. Species that was not found in the seed bank already could invade these gaps, but they did not find many new species that was gap specialists in this study (Goldblum, 1997). I on the other hand, did find a significant change in the understory species composition, but as mentioned this was not explained by increased gaps in the canopy. The increased number of new species found in the resampling was 17, about 8 of these are species associated to high light conditions, however, none of these species were found in many plots and locations, and they also had a relatively low abundance. Most of them are mainly found in one location except for *Cirsium vulgare*. This could indicate that gaps are favorable for species that prefer lots of light, but it might be to early in the gap-phase for these species to properly establish.

An interesting observation, however, is that the total cover of the shrub layer has increased significantly over time. Younger trees in the shrub layer may be responding faster than the ground vegetation to sudden openings in the canopy. Sycamore maple is one of the tree species that had a significant increase in abundance over time. The growth rate of sycamore

maple is inferior to ash (Petritan *et al.*, 2007), and a potential replacement candidate to fill the sudden gaps in the canopy. A study from France on regeneration of gaps in mixed broadleaved forests with oak, ash, beech, European hornbeam (*Carpinus betulus*), field maple (*Acer campestre*), Norway maple, sycamore maple, wild service-tree (*Sorbus torminalis*) and linden, found the gaps to be occupied exclusively by sycamore maple and beech, 13 years after the gaps occurred in the canopy (Collet *et al.*, 2008). As beech was not observed in this resurvey, it can be assumed that sycamore maple is a plausible candidate to fill the gaps. According to Mitchell *et al.* (2014) sycamore maple is the most likely species to replace ash and is also a tree species that is considered a good replacement for ash associated species. If this is the case, it could indicate that the vascular plants in the ground vegetation may not have experienced that much change in light conditions. For mature ash trees to die from ash dieback it can take about 10 years (Timmermann *et al.*, 2011), so it may take more than a decade for the ground vegetation to respond to changes in forest structure, and younger trees may be responding faster. Younger trees in the shrub layer may wait decades for a mature tree to die, leaving a gap in the canopy signaling the younger trees to grow and fill these gaps.

### **Impact of reduced abundance in ash**

Ash has had a significant decrease in abundance over time, despite the observed increase in the number of plots ash is observed in. This could indicate that the larger trees that make up a greater part of the abundance are largely reduced due to ash dieback. And infected mature trees may increase flowering due to stress caused by the disease (Semizer-Cuming *et al.*, 2021), making more seedlings and saplings of ash, which could explain why there are more sightings.

With the mortality rate of 85% for ash trees (Coker *et al.*, 2019), it is a possibility that ash may face similar consequences as wych elm from DED. According to Hultberg (2020) wych elm is the species of tree that shares the highest proportion of ash associated species, a possible species to fill the gap left by ash. However, wych elm is also largely reduced in populations due to the second wave of DED and may not be potent enough to fill this niche left by ash. Many associated species of wych elm have become red-listed after DED, and secondary extinctions are assumed based on species that are obligate (only host tree is wych elm) to wych elm (Hultberg *et al.*, 2020). The model examining the reduction in abundance of ash however was not significant in explaining the observed change in the species composition of the ground vegetation. From a report in UK looking at the ecological impact of ash dieback, when examining number of vascular plants directly associated to ash, they found

none, however, there were a number of vascular plants partially associated to ash forests (Mitchell *et al.*, 2014). This may explain why the reduced abundance of ash did not affect the change in species composition of the vascular plants in the ground vegetation. Simply because many of the vascular plants in the forests are only associated to forests with ash, making them partially associated to ash trees, which could explain the moderate response to reduced abundance of ash.

However, ash is a keystone species (Hultberg *et al.*, 2020), and with a severely reduced abundance of ash it is expected to instigate a cascade of secondary reactions to species in affected ecosystems. Due to the interconnectedness between species in an ecosystem, Hultberg *et al.* (2020) assumes that there will be secondary extinctions associated with the arrival of forest pathogens. This is observed from the consequences of chestnut blight on the American chestnut which previously was a keystone species (Clark *et al.*, 2016), but due to functional extirpation in its native habitat it is not anymore (Hultberg *et al.*, 2020). The loss of this keystone species in North America has had devastating effects for the habitats of many associated species (Loo, 2008). Even though the results I found cannot confirm that this is happening in forests of western Norway to ash associated species, the reduced canopy and abundance of ash may be the beginning of a cascade effect yet to happen.

To get a complete overview of the ecological impact of reduced abundance of ash, a more extensive analysis including species that are directly dependent to ash and a longer timeframe is needed. Loo (2008) proposes approaches on how to characterize the magnitude of ecological impact from invasive pathogens, by using characteristics of both the host species and the invasive pathogen. The impacts are greater when highly successful invading pathogens attack foundation species, this causes a cascade of effects on the host and associated species (Loo, 2008). Further studies examining the effect on vegetation flora from ash dieback is needed to map the magnitude of the impact caused by this disease.

For this study permanent vegetation plots were used, therefore avoiding concern about plot accuracy. Coordinates and guidance from Fride H. Schei were used to locate the plots in advance and mark them. Sampling was done individually, however the first plots to be sampled was done with supervisor who is the original sampler so that the method in the resample would resemble the original as much as possible. To avoid seasonal variability of the vegetation to affect the plot analysis, plots were originally to be sampled within 14 days of the original sampling date. However, for three of the plots in Mobergsli, due to difficulty in finding them, they were not sampled until 51 days after the original sampling looking at date.



## **Conclusion**

In this thesis I examined the ecological impact of ash dieback in forests of western Norway. The impacts of invasive forest pathogens can be huge. And with the increased efficiency of global trade, spread of invasive pathogens has increased. From examining forests with presence of ash dieback it was not found that either a more open canopy or a decreased abundance of ash is affecting the observed change in the species composition of the ground vegetation yet.

There is, however, a clear trend in the decreased abundance of ash as well as the expected increase of gaps in the canopy. This could still be the start of a cascade, affecting understory vegetation, but more time may be needed to observe such responses. The decrease in abundance of ash certainly confirms that ash dieback is interfering with these habitats. There was, however, an interesting increase in the cover of shrubs that could indicate that the younger trees are competing to fill the gaps in the canopy. From my results there is a trend in the increased abundance of the invasive sycamore maple and a decrease in abundance of native ash. The sycamore maple could represent the younger trees in the shrub layer, indicating that we may be looking at the start of a change in the structure of temperate deciduous forests in western Norway, where sycamore maple may fill the gaps left by ash.

## References

- Aarrestad, P. A. (2000) 'Plant communities in broad-leaved deciduous forests in Hordaland county, Western Norway', *Nordic Journal of Botany*, 20(4), pp. 449–466. doi: 10.1111/j.1756-1051.2000.tb01588.x.
- Blindheim, T., Hofton, T. H., Reiso, S., Gaarder, G., Brandrud, T. E., Thylén, A., Blumentrath, S. and Hjermann, D. (2015) *Status for edelløvsskog i Norge pr 2014. Oppsummering av nasjonale kartlegginger av naturtypen 2009-2014, BioFokus Rapport*. Oslo. Available at: <http://lager.biofokus.no/biofokus-rapport/biofokusrapport2015-5.pdf>.
- Brasier, C., Paoletti, M., Kirk, S., Buck, K. and Crawford, L. (2004) 'Molecular analysis of evolutionary changes in populations of *Ophiostoma novo-ulmi*', *Investigación agraria. Sistemas y recursos forestales*, 13(1), pp. 93–104.
- Braun-blanquet, J. (1932) 'Plant sociology. The study of plant communities. First ed.', *Plant sociology. The study of plant communities. First ed.* McGraw-Hill Book Co., Inc., New York and London.
- Clark, S. L., Schlarbaum, S. E., Saxton, A. M. and Hebard, F. V. (2016) 'Establishment of American chestnuts (*Castanea dentata*) bred for blight (*Cryphonectria parasitica*) resistance: influence of breeding and nursery grading', *New Forests*. Springer Netherlands, 47(2), pp. 243–270. doi: 10.1007/s11056-015-9512-6.
- Coker, T. L. R., Rozsypálek, J., Edwards, A., Harwood, T. P., Butfoy, L. and Buggs, R. J. A. (2019) 'Estimating mortality rates of European ash (*Fraxinus excelsior*) under the ash dieback (*Hymenoscyphus fraxineus*) epidemic', *Plants, People, Planet*, 1(1), pp. 48–58. doi: 10.1002/ppp3.11.
- Collet, C., Piboule, A., Leroy, O. and Frochot, H. (2008) 'Advance *Fagus sylvatica* and *Acer pseudoplatanus* seedlings dominate tree regeneration in a mixed broadleaved former coppice-with-standards forest', *Forestry*, 81(2), pp. 135–150. doi: 10.1093/forestry/cpn004.
- Crowl, T. A., Crist, T. O., Parmenter, R. R., Belovsky, G. and Lugo, A. E. (2008) 'The spread of invasive species and infectious disease as drivers of ecosystem change', *Frontiers in*

- Ecology and the Environment*, 6(5), pp. 238–246. doi: 10.1890/070151.
- Drenkhan, R., Sander, H. and Hanso, M. (2014) 'Introduction of Mandshurian ash (*Fraxinus mandshurica* Rupr.) to Estonia: Is it related to the current epidemic on European ash (*F. excelsior* L.)?', *European Journal of Forest Research*, 133(5), pp. 769–781. doi: 10.1007/s10342-014-0811-9.
- Ellenberg, H., Weber, H. E., Dull, R., Wirth, V., Werner, W. and Paulissen, D. (1992) 'Zeigerwerte von Pflanzen in Mitteleuropa', *Scripta Geobotanica*, 18, pp. 1–258.
- Emborg, J. (1998) 'Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark', *Forest Ecology and Management*. Elsevier Sci B.V., 106(2–3), pp. 83–95. doi: 10.1016/S0378-1127(97)00299-5.
- Fremstad, E. and Elven, R. (1996) 'Fremmede planter i Norge. Platanlønn (*Acer pseudoplatanus* L.)', *Blyttia*, 2, pp. 61–78.
- Ghelardini, L., Luchi, N., Pecori, F., Pepori, A. L., Danti, R., Della Rocca, G., Capretti, P., Tsopelas, P. and Santini, A. (2017) 'Ecology of invasive forest pathogens', *Biological Invasions*. Springer International Publishing, 19(11), pp. 3183–3200. doi: 10.1007/s10530-017-1487-0.
- Goldblum, D. (1997) 'The effects of treefall gaps on understory vegetation in New York State', *Journal of Vegetation Science*, 8(1), pp. 125–132. doi: 10.2307/3237250.
- Gross, A., Zaffarano, P. L., Duo, A. and Grünig, C. R. (2012) 'Reproductive mode and life cycle of the ash dieback pathogen *Hymenoscyphus pseudoalbidus*', *Fungal Genetics and Biology*. Academic Press, 49(12), pp. 977–986. doi: 10.1016/j.fgb.2012.08.008.
- Henriksen, S. and Hilmo, O. (2015) *Norsk rødliste for arter 2015, Norwegian Biodiversity Information Centre*.
- Hill, M. O. and Gauch, H. G. (1980) 'Detrended Correspondence Analysis: An Improved Ordination Technique', *Classification and Ordination*, (Kendall 1971), pp. 47–58. doi: 10.1007/978-94-009-9197-2\_7.
- Hultberg, T., Sandström, J., Felton, A., Öhman, K., Rönnerberg, J., Witzell, J. and Cleary, M.

- (2020) 'Ash dieback risks an extinction cascade', *Biological Conservation*. Elsevier Ltd, 244, p. 108516. doi: 10.1016/j.biocon.2020.108516.
- Kålås, J. A., Henriksen, S., Skjelseth, S. and Viken, Å. (2010) *Miljøforhold og påvirkninger for rødlistearter*. Trondheim: Skipnes AS.
- Kapfer, J., Hédl, R., Jurasinski, G., Kopecký, M., Schei, F. H. and Grytnes, J. A. (2017) 'Resurveying historical vegetation data – opportunities and challenges', *Applied Vegetation Science*, 20(2), pp. 164–171. doi: 10.1111/avsc.12269.
- Kirisits, T., Matlakova, M., Mottinger-Kroupa, S., Halmschlager, E. and Lakatos, F. (2010) 'Chalara fraxinea associated with dieback of narrow-leafed ash (*Fraxinus angustifolia*)', *Plant Pathology*, 59(2), p. 1. doi: 10.1111/j.1365-3059.2009.02162.x.
- Larsson, J. Y. and Søgne, S. M. (2003) *Vegetasjon i norsk skog-vekstvillkår og skogforvaltning*. Landbuksforlaget.
- Loo, J. . (2008) 'Ecological impacts of non-indigenous invasive fungi as forest pathogens', in Langor, D. and Sweeney, J. (eds) *Ecological Impacts of Non-Native Invertebrates and Fungi on Terrestrial Ecosystems*. 1st edn. Springer, Dordrecht, pp. 81–96.
- Mackenthun, G. (2004) 'The role of *Ulmus laevis* in German floodplain landscapes', *Investigación agraria. Sistemas y recursos forestales*, 13(1), pp. 55–64. doi: 10.5424/813.
- Martin, J. A., Fuentes-utrilla, R., Gil, L. and Witzell, J. (2010) 'Ecological factors in Dutch elm disease complex in Europe-a review', *Ecological Bulletins*, (53), pp. 209–224. Available at: <https://www.jstor.org/stable/41442032>.
- Maxwell, S. L., Fuller, R. A., Brooks, T. M. and Watson, J. E. M. (2016) 'Biodiversity: The ravages of guns, nets and bulldozers', *Nature*, 536(7615), pp. 143–145. doi: 10.1038/536143a.
- McMullan, M., Rafiqi, M., Kaithakottil, G., Clavijo, B. J., Bilham, L., Orton, E., Percival-Alwyn, L., Ward, B. J., Edwards, A., Saunders, D. G. O., Garcia Accinelli, G., Wright, J., Verweij, W., Koutsovoulos, G., Yoshida, K., Hosoya, T., Williamson, L., Jennings, P., loos, R., Husson, C., Hietala, A. M., Vivian-Smith, A., Solheim, H., Maclean, D., Fosker, C., Hall,

- N., Brown, J. K. M., Swarbreck, D., Blaxter, M., Downie, J. A. and Clark, M. D. (2018) 'The ash dieback invasion of Europe was founded by two genetically divergent individuals', *Nature Ecology and Evolution*. Nature Publishing Group, 2(6), pp. 1000–1008. doi: 10.1038/s41559-018-0548-9.
- Mitchell, R. J., Bailey, S., Beaton, J. K., Bellamy, P. E., Brooker, R. W., Broome, A., Chetcuti, J., Eaton, S., Ellis, C. J., Farren, J., Gimona, A., Goldberg, E., Hall, J. and Harmer, R. (2014) (PDF) *The potential ecological impact of ash dieback in the UK, Joint Nature Conservaton Commitee*. Available at: [https://www.researchgate.net/publication/305676832\\_The\\_potential\\_ecological\\_impact\\_of\\_ash\\_dieback\\_in\\_the\\_UK](https://www.researchgate.net/publication/305676832_The_potential_ecological_impact_of_ash_dieback_in_the_UK) (Accessed: 12 November 2020).
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E. and Wagner, H. (2019) 'vegan: Community Ecology Package. R package version 2'. Available at: <https://cran.r-project.org/package=vegan>.
- Petritan, A. M., Von Lüpke, B. and Petritan, I. C. (2007) 'Effects of shade on growth and mortality of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings', *Forestry*, 80(4), pp. 397–412. doi: 10.1093/forestry/cpm030.
- Rigo, D. De, Bosco, C., Durrant, T. H., San-Miguel-Ayanz, J., Barredo, J. I., Strona, G., Caudullo, G., Leo, M. Di and Boca, R. (2016) 'Forest resources in Europe : an integrated perspective on ecosystem services , disturbances and threats', *The European Atlas of Forest Tree Species :*, (March), pp. 8–19.
- Semizer-Cuming, D., Chybicki, I. J., Finkeldey, R. and Kjær, E. D. (2021) 'Gene flow and reproductive success in ash (*Fraxinus excelsior* L.) in the face of ash dieback: restoration and conservation', *Annals of Forest Science*. Springer Paris, 78(1). doi: 10.1007/s13595-020-01025-0.
- Signorile, A. L., Reuman, D. C., Lurz, P. W. W., Bertolino, S., Carbone, C. and Wang, J. (2016) 'Using DNA profiling to investigate human-mediated translocations of an invasive species', *Biological Conservation*. The Authors, 195, pp. 97–105. doi: 10.1016/j.biocon.2015.12.026.

- Skovsgaard, J. P., Thomsen, I. M., Skovsgaard, I. M. and Martinussen, T. (2010) 'Associations among symptoms of dieback in even-aged stands of ash (*Fraxinus excelsior* L.)', *Forest Pathology*, 40(1), pp. 7–18. doi: 10.1111/j.1439-0329.2009.00599.x.
- Team, R. C. (2020) 'R: A Language and Environment for Statistical Computing'.
- Timmermann, V., Andreassen, K., Brurberg, M. B., Clarke, N., Herrero, M., Jepsen, J. U., Solheim, H., Strømeng, G. M., Talgø, V., Vindstad, O. P. L., Wollebæk, G., Økland, B. and Aas, W. (2018) *Skogens helsetilstand i Norge: resultater fra skogskadeovervåkingen i 2017, NIBIO Rapport*.
- Timmermann, V., Børja, I., Hietala, A. M., Kirisits, T. and Solheim, H. (2011) 'Ash dieback : pathogen spread and diurnal patterns of ascospore dispersal , with special emphasis on Norway \*', *EPPO Bulletin*, 41(1), pp. 14–20. Available at: <https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2338.2010.02429.x>.
- Webber, J. (1981) 'A natural biological control of Dutch elm disease', *Nature*, 292(5822), pp. 449–451. doi: 10.1038/292449a0.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, D. L., François, R., Golemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Milton, S. B., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K. and Yutani, H. (2019) 'Welcome to the tidyverse', *Journal of Open-source Software*, p. 1686. Available at: <https://doi.org/10.21105/joss.01686>.

## Appendix A -List of locations, number of plots, year of resampling and overview of increase/decrease in ash abundance

Location	Number of plots	Year of resampling	Nr. of plots with increase/decrease in ash abundance
Salhus	3	2020	1/0
Aldal	3	2020	1/0
Asnesviki	2	2020	0/0*
Steinstø	2	2020	2/0
Mundheimsdalen	5	2020	0/2
Seimshola	5	2020	0/2
Oldervollen vik	1	2020	0/0
Floget	4	2018	0/2
Hattvik	1	2018	0/1
Hope	8	2018	1/5
Laupsa	4	2018	2/0
Mundheimslia	2	2018	1/0
Ådland	6	2018	2/1
Skarvhellehola	3	2018	0/3
Storomsvågen	1	2018	0/0
Vangdalsberget	4	2018	3/0
Vest for Kalandsvatn	3	2018	1/2
Mobergslia	4	2020	0/3
Oldervollen	1	2020	0/1

Note: \* = location with no presence of ash

## Appendix B – Ellenberg indicator values and abbreviation for species

Species	L	F	R	N	Abbreviation
<i>Acer platanoides</i>	4	x	x	x	Acerplat
<i>Acer pseudoplatanus</i>	4	6	x	7	Acerpseu
<i>Alnus glutinosa</i>	5	9	6	x	Alnuglut
<i>Alnus incana</i>	6	7	8	x	Alnuinca
<i>Betula pendula</i>	7	x	x	x	Betupend
<i>Betula pubescens</i>	7	8	3	3	Betupube
<i>Corylus avellana</i>	6	x	x	5	Coryavel
<i>Fraxinus excelsior</i>	4	x	7	7	Fraxexce
<i>Picea abies</i>	5	x	x	x	Piceabie
<i>Pinus sylvestris</i>	7	x	x	x	Pinusylv
<i>Populus tremula</i>	6	5	x	x	Poputrem
<i>Prunus padus</i>	5	8	7	6	Prunpadu
<i>Quercus sp</i>	x	x	x	x	Quersp
<i>Salix caprea</i>	7	6	7	7	Salicapr
<i>Sorbus aucuparia</i>	6	x	4	x	Sorbauca
<i>Taxus baccata</i>	4	5	7	x	Taxubacc
<i>Tilia cordata</i>	5	5	x	5	Tilicord
<i>Ulmus glabra</i>	4	6	7	7	Ulmuglab
<i>Actaea spicata</i>	3	5	6	7	Actaspic
<i>Aegopodium podagraria</i>	5	6	7	8	Aegopoda
<i>Agrostis sp</i>	x	x	x	x	Agrosp
<i>Alchemilla sp</i>	x	x	x	x	Alchsp
<i>Allium ursinum</i>	2	6	7	8	Alliursi
<i>Anemone nemorosa</i>	x	5	x	x	Anemnemo
<i>Angelica sylvestris</i>	7	8	x	4	Angesyly
<i>Anthoxanthum odoratum</i>	x	x	5	x	Anthodor
<i>Anthriscus sylvestris</i>	7	5	x	8	Anthsylv
<i>Arctium minus</i>	9	5	x	8	Arctminu
<i>Asplenium trichomanes</i>	5	5	x	3	Aspltric
<i>Athyrium filix-femina</i>	3	7	x	6	Athyfili
<i>Avenella flexuosa</i>	6	x	2	3	Avenflex
<i>Blechnum spicant</i>	3	6	2	3	Blecspic
<i>Brachypodium sylvaticum</i>	3	5	6	6	Bracsylv
<i>Campanula latifolia</i>	4	6	8	8	Camplati
<i>Campanula rotundifolia</i>	7	x	x	2	Camprotu
<i>Cardamine bulbifera</i>	3	5	7	6	Cardbulb
<i>Cardamine flexuosa</i>	6	8	4	5	Cardflex
<i>Cardamine hirsuta</i>	6	5	5	7	Cardhirs
<i>Carex digitata</i>	3	5	x	4	Caredigi
<i>Carex pallescens</i>	7	6	4	3	Carepall
<i>Carex remota</i>	3	8	x	x	Careremo
<i>Carex sp</i>	x	x	x	x	Caresp



<i>Carex sylvatica</i>	2	5	6	5	Caresylv
<i>Chrysosplenium alternifolium</i>	4	8	7	5	Chryalte
<i>Chrysosplenium oppositifolium</i>	6	9	5	5	Chryoppo
<i>Circaea alpina</i>	4	7	5	5	Circalpi
<i>Circaea lutetiana</i>	4	6	7	7	Circalute
<i>Circaea x intermedia</i>	4	7	7	6	Circaxin
<i>Cirsium heterophyllum</i>	7	8	5	6	Cirshete
<i>Cirsium vulgare</i>	8	5	7	8	Cirsvulg
<i>Claytonia sibirica</i>	5	7	6	6	Claysibi
<i>Conopodium majus</i>	8	5	4	4	Conomaju
<i>Cotoneaster sp</i>	x	x	x	x	Cotosp
<i>Crepis paludosa</i>	7	8	8	6	Creppalu
<i>Dactylis glomerata</i>	7	5	x	6	Dactglom
<i>Deschampsia cespitosa</i>	6	7	x	3	Desccesp
<i>Digitalis purpurea</i>	7	5	3	6	Digipurp
<i>Dryopteris affinis</i>	3	6	5	6	Dryoaffi
<i>Dryopteris carthusiana</i>	5	x	4	3	Dryocart
<i>Dryopteris dilata/expansa</i>	4	6	x	x	Dryodili
<i>Dryopteris filix-mas</i>	3	5	5	6	Dryofili
<i>Dryopteris sp</i>	4	6	x	x	Dryosp
<i>Elymus caninus</i>	6	6	7	8	Elymcani
<i>Epilobium montanum</i>	4	5	6	6	Epilmont
<i>Epipactis sp</i>	x	x	x	7	Epipsp
<i>Equisetum pratense</i>	5	6	7	2	Equiprat
<i>Festuca altissima</i>	3	5	4	6	Festalti
<i>Filipendula ulmaria</i>	7	8	x	5	Filiulma
<i>Fragaria vesca</i>	7	5	x	6	Fragvesc
<i>Galeopsis bifida/tetrahit</i>	7	5	x	6	Galebifi
<i>Galeopsis tetrahit</i>	7	5	x	6	Galetetra
<i>Galium odoratum</i>	2	5	6	5	Galiodor
<i>Geranium robertianum</i>	5	x	x	7	Gerarobe
<i>Geranium sylvaticum</i>	6	6	6	7	Gerasylv
<i>Geum rivale</i>	6	8	x	7	Geumriva
<i>Geum urbanum</i>	4	5	x	7	Geumurba
<i>Glyceria fluitans</i>	7	9	x	7	Glycflui
<i>Gymnocarpium dryopteris</i>	3	6	4	5	Gymndryo
<i>Hedera helix</i>	4	5	x	x	Hedeheli
<i>Hieracium sp</i>	x	x	x	x	Hiersp
<i>Holcus lanatus</i>	7	6	x	5	Holclana
<i>Holcus mollis</i>	5	5	2	3	Holcmoll
<i>Hypericum maculatum</i>	8	6	3	2	Hypemacu
<i>Hypericum montanum</i>	5	4	7	3	Hypemont
<i>Hypericum pulchrum</i>	4	5	3	2	Hypepulc
<i>Hypericum sp</i>	x	x	x	x	Hypesp
<i>Ilex aquifolium</i>	4	5	4	5	Illexaqui
<i>Juncus conglomerata</i>	8	7	4	3	Junccong

<i>Juncus effusus</i>	8	7	3	4	Junceffu
<i>Juniperus communis</i>	8	4	x	x	Junicomm
<i>Lapsana communis</i>	5	5	x	7	Lapscomm
<i>Lathyrus linifolius</i>	x	5	3	2	Lathlini
<i>Lathyrus niger</i>	5	3	7	3	Lathnige
<i>Linnaea borealis</i>	5	5	2	2	Linnbore
<i>Lonicera periclymenum</i>	6	x	3	4	Loniperi
<i>Luzula multiflora</i>	7	5	5	3	Luzumult
<i>Luzula pilosa</i>	2	5	5	4	Luzupilo
<i>Luzula sylvatica</i>	4	5	4	4	Luzusylv
<i>Lysimachia nemorum</i>	2	7	7	7	Lysinemo
<i>Maianthemum bifolium</i>	3	5	3	3	Maiabifo
<i>Matteuccia struthiopteris</i>	5	8	7	7	Mattstru
<i>Melampyrum pratense</i>	x	x	3	2	Melaprat
<i>Melampyrum sylvaticum</i>	4	5	2	2	Melasylv
<i>Melica nutans</i>	4	4	x	3	Melinuta
<i>Milium effusum</i>	4	5	5	5	Milieffu
<i>Moehringia trinervia</i>	4	5	6	7	Moehtrin
<i>Molinia caerulea</i>	7	7	x	2	Molicaer
<i>Mycelis muralis</i>	4	5	x	6	Mycemura
<i>Orchis mascula</i>	6	4	8	x	Orchmasc
<i>Oreopteris limbosperma</i>	4	6	3	5	Oreolimb
<i>Oxalis acetosella</i>	1	5	4	6	Oxalacet
<i>Paris quadrifolia</i>	3	6	7	7	Pariquad
<i>Phegopteris connectilis</i>	2	6	4	6	Phegconn
<i>Plantago lanceolata</i>	6	x	x	x	Planlanc
<i>Poa nemoralis</i>	5	5	5	4	Poanemo
<i>Poa pratensis</i>	6	5	x	6	Poaprat
<i>Poa sp</i>	x	x	x	x	Poasp
<i>Poa trivialis</i>	6	7	x	7	Poatriv
<i>Polygonatum odoratum</i>	7	3	7	3	Polyodor
<i>Polygonatum verticillatum</i>	4	5	4	5	Polyvert
<i>Polypodium vulgare</i>	5	4	2	2	Polyvulg
<i>Polystichum aculeatum/braunii</i>	3	6	6	7	Polyacul
<i>Potentilla erecta</i>	6	x	x	2	Poteerec
<i>Primula vulgaris</i>	6	5	7	5	Primvulg
<i>Pteridium aquilinum</i>	6	5	3	3	Pteraqui
<i>Ranunculus acris</i>	7	6	x	x	Ranuacri
<i>Ranunculus auricomus</i>	5	x	7	x	Ranuauri
<i>Ranunculus ficaria</i>	4	6	7	7	Ranufica
<i>Ranunculus platanifolius</i>	5	6	x	7	Ranuplat
<i>Ranunculus repens</i>	6	7	x	7	Ranurepe
<i>Rosa sp</i>	x	x	x	x	Rosasp
<i>Rubus idaeus</i>	7	x	x	6	Rubuidae
<i>Rubus saxatilis</i>	7	6	7	4	Rubusaxa
<i>Rubus ssp</i>	x	x	x	x	Rubussp

<i>Rumex acetosa</i>	8	x	x	6	Rumeacet
<i>Sanicula europaea</i>	4	5	8	6	Sanieuro
<i>Scrophularia nodosa</i>	4	6	6	7	Scronodo
<i>Sedum rosea</i>	7	6	4	x	Sedurose
<i>Silene dioica</i>	x	6	7	8	Siledioi
<i>Solidago virgaurea</i>	5	5	x	4	Solivirg
<i>Stachys sylvatica</i>	4	7	7	7	Statsylv
<i>Stellaria nemorum</i>	4	7	5	7	Stelnemo
<i>Succisa pratensis</i>	7	7	x	2	Succprat
<i>Taraxacum sp</i>	x	x	x	x	Tarasp
<i>Trientalis europaea</i>	5	x	3	2	Trieeuro
<i>Urtica dioica</i>	x	6	7	9	Urtidioi
<i>Vaccinium myrtillus</i>	5	x	2	3	Vaccmyrt
<i>Vaccinium vitis-idaea</i>	5	4	2	1	Vaccviti
<i>Valeriana sambucifolia</i>	7	8	6	5	Valesamb
<i>Veronica chamaedrys</i>	6	5	x	x	Verocham
<i>Veronica officinalis</i>	6	4	3	4	Verooffi
<i>Viburnum opulus</i>	6	x	7	6	Vibuopul
<i>Vicia sepium</i>	x	5	6	5	Vicisepi
<i>Vicia sylvatica</i>	7	4	8	x	Vicisylv
<i>Viola canina</i>	7	4	3	2	Violcani
<i>Viola riviniana</i>	5	4	4	x	Violrivi

## Appendix C- Overview of species that disappeared and appeared in ground vegetation (without trees)

Species that have disappeared	Nr. Of plots	Nr. Of locations	New species that have appeared	Nr. of plots	Nr. of locations
<i>Anthriscus sylvestris</i>	2	2	<i>Aegopodium prodagaria</i>	1	1
<i>Arctium minus</i>	1	1	<i>Cardamine hirsuta</i>	1	1
<i>Campanula latifolia</i>	1	1	<i>Carex pallescens</i>	1	1
<i>Campanula rotundifolia</i>	3	3	<i>Cirsium heterophyllum</i>	1	1
<i>Equisetum pratense</i>	1	1	<i>Cirsium vulgare</i>	5	3
<i>Hypericum montanum</i>	2	2	<i>Dryopteris carthusiana</i>	1	1
<i>Juncus effusus</i>	1	1	<i>Epipactis sp.</i>	1	1
<i>Lapsana communis</i>	3	3	<i>Glyceria fluitans</i>	1	1
<i>Moehringia trinervia</i>	1	1	<i>Holcus lanatus</i>	3	1
<i>Oreopteris limbosperma</i>	2	2	<i>Hypericum pulchrum</i>	1	1
<i>Polygonatum odoratum</i>	1	1	<i>Juncus conglomerata</i>	1	1
<i>Ranunculus auricomus</i>	2	2	<i>Maianthemum bifolium</i>	1	1
<i>Ranunculus platanifolius</i>	1	1	<i>Melampyrum pratense</i>	1	1
			<i>Plantago lanceolata</i>	1	1
			<i>Sedum rosea</i>	1	1
			<i>Trientalis europaea</i>	3	3
			<i>Viola canina</i>	1	1

## Appendix D- Species list with total number of observations

Species	Nr. of observed species in 2007-2009	Nr. of observed species in 2018-2020	Total observations for species	Difference between old and new sampling	Positive/negative/stable change
<i>Acer platanoides</i>	0	1	1	1	+
<i>Acer pseudoplatanus</i>	21	26	47	5	+
<i>Alnus glutinosa</i>	3	5	8	2	+
<i>Alnus incana</i>	5	5	10	0	0
<i>Betula pendula</i>	3	6	9	3	+
<i>Betula pubescens</i>	9	6	15	-3	-
<i>Corylus avellana</i>	31	41	72	10	+
<i>Fraxinus excelsior</i>	50	55	105	5	+
<i>Picea abies</i>	5	9	14	4	+
<i>Pinus sylvestris</i>	2	1	3	-1	-
<i>Populus tremula</i>	2	5	7	3	+
<i>Prunus padus</i>	24	30	54	6	+
<i>Quercus sp</i>	7	11	18	4	+
<i>Salix caprea</i>	0	2	2	2	+
<i>Sorbus aucuparia</i>	19	22	41	3	+
<i>Taxus baccata</i>	2	3	5	1	+
<i>Tilia cordata</i>	12	14	26	2	+
<i>Ulmus glabra</i>	40	43	83	3	+
<i>Actaea spicata</i>	1	1	2	0	0
<i>Aegopodium podagraria</i>	0	1	1	1	+
<i>Agrostis sp</i>	9	8	17	-1	-
<i>Alchemilla sp</i>	2	1	3	-1	-
<i>Allium ursinum</i>	21	20	41	-1	-
<i>Anemone nemorosa</i>	25	25	50	0	0
<i>Angelica sylvestris</i>	7	4	11	-3	-
<i>Anthoxanthum odoratum</i>	7	3	10	-4	-
<i>Anthriscus sylvestris</i>	2	0	2	-2	-
<i>Arctium minus</i>	1	0	1	-1	-
<i>Asplenium trichomanes</i>	3	3	6	0	0
<i>Athyrium filix-femina</i>	42	44	86	2	+
<i>Avenella flexuosa</i>	19	16	35	-3	-
<i>Blechnum spicant</i>	3	4	7	1	+
<i>Brachypodium sylvaticum</i>	18	11	29	-7	-
<i>Campanula latifolia</i>	1	0	1	-1	-
<i>Campanula rotundifolia</i>	3	0	3	-3	-
<i>Cardamine bulbifera</i>	7	9	16	2	+
<i>Cardamine flexuosa</i>	5	5	10	0	0
<i>Cardamine hirsuta</i>	0	1	1	1	+
<i>Carex digitata</i>	2	4	6	2	+
<i>Carex pallescens</i>	0	1	1	1	+
<i>Carex remota</i>	2	2	4	0	0

<i>Carex sp</i>	3	1	4	-2	-
<i>Carex sylvatica</i>	24	13	37	-11	-
<i>Chrysosplenium alternifolium</i>	1	1	2	0	0
<i>Chrysosplenium oppositifolium</i>	5	4	9	-1	-
<i>Circaea alpina</i>	14	22	36	8	+
<i>Circaea lutetiana</i>	2	4	6	2	+
<i>Circaea x intermedia</i>	14	9	23	-5	-
<i>Cirsium heterophyllum</i>	0	1	1	1	+
<i>Cirsium vulgare</i>	0	5	5	5	+
<i>Claytona sibirica</i>	1	1	2	0	0
<i>Conopodium majus</i>	18	15	33	-3	-
<i>Cotoneaster sp</i>	2	1	3	-1	-
<i>Crepis paludosa</i>	1	1	2	0	0
<i>Dactylis glomerata</i>	10	8	18	-2	-
<i>Deschampsia cespitosa</i>	33	30	63	-3	-
<i>Digitalis purpurea</i>	2	5	7	3	+
<i>Dryopteris affinis</i>	7	7	14	0	0
<i>Dryopteris carthusiana</i>	0	1	1	1	+
<i>Dryopteris dilata/expansa</i>	7	5	12	-2	-
<i>Dryopteris filix-mas</i>	21	22	43	1	+
<i>Dryopteris sp</i>	2	0	2	-2	-
<i>Elymus caninus</i>	5	7	12	2	+
<i>Epilobium montanum</i>	14	25	39	11	+
<i>Epipactis sp</i>	0	1	1	1	+
<i>Equisetum pratense</i>	1	0	1	-1	-
<i>Festuca altissima</i>	22	23	45	1	+
<i>Filipendula ulmaria</i>	32	28	60	-4	-
<i>Fragaria vesca</i>	16	19	35	3	+
<i>Galeopsis bifida/tetrahit</i>	5	3	8	-2	-
<i>Galeopsis tetrahit</i>	1	4	5	3	+
<i>Galium odoratum</i>	22	22	44	0	0
<i>Geranium robertianum</i>	22	31	53	9	+
<i>Geranium sylvaticum</i>	22	13	35	-9	-
<i>Geum rivale</i>	20	10	30	-10	-
<i>Geum urbanum</i>	21	31	52	10	+
<i>Glyceria fluitans</i>	0	1	1	1	+
<i>Gymnocarpium dryopteris</i>	8	10	18	2	+
<i>Hedera helix</i>	7	10	17	3	+
<i>Hieracium sp</i>	3	1	4	-2	-
<i>Holcus lanatus</i>	0	3	3	3	+
<i>Holcus mollis</i>	8	12	20	4	+
<i>Hypericum maculatum</i>	1	2	3	1	+
<i>Hypericum montanum</i>	2	0	2	-2	-
<i>Hypericum pulchrum</i>	0	1	1	1	+
<i>Hypericum sp</i>	0	1	1	1	+
<i>Ilex aquifolium</i>	2	3	5	1	+

<i>Juncus conglomerata</i>	0	1	1	1	+
<i>Juncus effusus</i>	1	0	1	-1	-
<i>Juniperus communis</i>	2	2	4	0	0
<i>Lapsana communis</i>	3	0	3	-3	-
<i>Lathyrus linifolius</i>	3	3	6	0	0
<i>Lathyrus niger</i>	1	1	2	0	0
<i>Linnaea borealis</i>	1	1	2	0	0
<i>Lonicera periclymenum</i>	4	4	8	0	0
<i>Luzula multiflora</i>	2	1	3	-1	-
<i>Luzula pilosa</i>	2	3	5	1	+
<i>Luzula sylvatica</i>	12	20	32	8	+
<i>Lysimachia nemorum</i>	6	6	12	0	0
<i>Maianthemum bifolium</i>	0	1	1	1	+
<i>Matteuccia struthiopteris</i>	10	20	30	10	+
<i>Melampyrum pratense</i>	0	1	1	1	+
<i>Melampyrum sylvaticum</i>	1	1	2	0	0
<i>Melica nutans</i>	4	6	10	2	+
<i>Milium effusum</i>	2	9	11	7	+
<i>Moehringia trinervia</i>	1	0	1	-1	-
<i>Molina caerulea</i>	1	2	3	1	+
<i>Mycelis muralis</i>	12	18	30	6	+
<i>Orchis mascula</i>	5	1	6	-4	-
<i>Oreopteris limbosperma</i>	2	0	2	-2	-
<i>Oxalis acetosella</i>	43	42	85	-1	-
<i>Paris quadrifolia</i>	4	3	7	-1	-
<i>Phegopteris connectilis</i>	19	32	51	13	+
<i>Plantago lanceolata</i>	0	1	1	1	+
<i>Poa nemoralis</i>	18	11	29	-7	-
<i>Poa pratensis</i>	9	2	11	-7	-
<i>Poa sp</i>	2	2	4	0	0
<i>Poa trivialis</i>	5	1	6	-4	-
<i>Polygonatum odoratum</i>	1	0	1	-1	-
<i>Polygonatum verticillatum</i>	1	1	2	0	0
<i>Polypodium vulgare</i>	9	9	18	0	0
<i>Polystichum aculeatum/braunii</i>	20	18	38	-2	-
<i>Potentilla erecta</i>	6	6	12	0	0
<i>Primula vulgaris</i>	3	1	4	-2	-
<i>Pteridium aquilinum</i>	4	4	8	0	0
<i>Ranunculus acris</i>	3	2	5	-1	-
<i>Ranunculus auricomus</i>	2	0	2	-2	-
<i>Ranunculus ficaria</i>	6	3	9	-3	-
<i>Ranunculus platanifolius</i>	1	0	1	-1	-
<i>Ranunculus repens</i>	1	3	4	2	+
<i>Rosa sp</i>	2	3	5	1	+
<i>Rubus idaeus</i>	16	14	30	-2	-
<i>Rubus saxatilis</i>	4	2	6	-2	-

<i>Rubus ssp</i>	2	1	3	-1	-
<i>Rumex acetosa</i>	2	1	3	-1	-
<i>Sanicula europaea</i>	7	7	14	0	0
<i>Scrophularia nodosa</i>	1	1	2	0	0
<i>Sedum rosea</i>	0	1	1	1	+
<i>Silene dioica</i>	14	13	27	-1	-
<i>Solidago virgaurea</i>	7	7	14	0	0
<i>Stachys sylvatica</i>	25	23	48	-2	-
<i>Stellaria nemorum</i>	18	19	37	1	+
<i>Succisa pratensis</i>	2	1	3	-1	-
<i>Taraxacum sp</i>	11	3	14	-8	-
<i>Trientalis europaea</i>	0	3	3	3	-
<i>Urtica dioica</i>	8	11	19	3	+
<i>Vaccinium myrtillus</i>	4	4	8	0	0
<i>Vaccinium vitis-idaea</i>	2	2	4	0	0
<i>Valeriana sambucifolia</i>	17	16	33	-1	+
<i>Veronica chamaedrys</i>	14	15	29	1	+
<i>Veronica officinalis</i>	6	11	17	5	+
<i>Viburnum opulus</i>	3	5	8	2	+
<i>Vicia sepium</i>	6	6	12	0	0
<i>Vicia sylvatica</i>	10	8	18	-2	-
<i>Viola canina</i>	0	1	1	1	+
<i>Viola riviniana</i>	17	12	29	-5	-



## **Appendix E- Dataset used for this thesis**

### **For complete dataset with species composition and environmental variables:**

Johansen, Maren (2021), RE-2007-2020-NO-719545, ECKO Resurvey Data Consortium,  
<https://ecko.uib.no/datasets/RE-2007-2020-NO-719545>