Assessing the Potential of Natural Regeneration of *Fraxinus excelsior* that have been selected for tolerance of the Ash Dieback Pathogen *Hymenoscyphus fraxineus*:

Implications for Forest Conservation

Urszula Bogusławska

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Assessing the Potential of Natural Regeneration of Fraxinus excelsior that have been selected for tolerance of the Ash Dieback Pathogen Hymenoscyphus fraxineus: Implications for Forest Conservation

Bedömning av potentialen för naturlig föryngring av Fraxinus excelsior som har valts ut för tolerans mot askskottsjukan Hymenoscyphus fraxineus: Konsekvenser för skogsbevarande.

Urszula Boguslawska

Supervisor:	**Michelle Cleary, Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre**
Assistant supervisor:	Ana Paula Gamba, Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre
Examiner:	Emma Holmström, Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre

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Abstract

European ash (*Fraxinus excelsior*) is a noble broadleaf of significant cultural and biological importance in Europe. In past years, its population has been in rapid decline due to an invasive fungal disease known as ash dieback, caused by the pathogen *Hymenoscyphus fraxineus* which causes necrosis and eventual death of the tree. The stability and existence of ash in the landscape of Europe are in danger. In this study, we inventoried 27 sites from an existing database of 1300 trees that show signs of resistance. The selection was based on the presence of at least one tree showing signs of resistance to the disease and their distribution in Sweden. Around each selected tree, we established eight circular sample plots of 2,78 m with centres located 8 and 20 meters away in the North, South, East and West directions. In each plot, we counted the number of naturally regenerated seedlings, higher than 25 cm, and categorized them into three size strata, six health classes (from No symptoms of disease to dead) and three stem forms. Later data about the site properties was extracted from online databases. The purpose of the study is to analyze the status of the understory seedlings and saplings of phenotypically tolerant ash trees, considering their potential for tolerance, as well as to grasp a better understanding of the joint effects of the disease and other environmental and site factors on ash natural regeneration. It was found that the natural regeneration surrounding ash trees selected for tolerance differed in health between sites. Correlation was found between ash dieback symptoms and stem form of the regeneration.The disease severity of the three size strata differed from each other, with trees higher than 4m exhibiting significantly worse health. In this study we have found that while the there is large potential in the natural regeneration, environmental and site factors may in complex ways affect the success and health of natural regeneration under the pressure of ash dieback.

Keywords: ash dieback ; regeneration ; resistance

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1. Introduction

1.1 The European ash

European ash or common ash (*Fraxinus excelsior L.)* is a medium-sized tree in the noble broadleaves group. It grows to a height of 25-35 m, with some of the tallest specimens measuring as high as 45 m in Białowieża National Park (*Common Ash in the National Park of Białowieża, Białowieża, Podlaskie, Poland*, 2014). It has a broad, usually high-situated crown with a thick root crown. The trees have smooth, greenish-grey coloured bark, which can harden and develop fissures with time, gaining both a furrowed and more brown appearance. It has compound leaves of 20-35 cm, consisting of 9-13 individual leaflets growing in opposite pairs and measuring 0.8-3 cm (Beck et al. 2016). It is one of the last trees to flush, and it is also one of the first wild trees to lose its leaves, which turn fleetingly pale yellow or fall even when still green (Johnson and More, 2004).

There are three species of ash in Europe, of which the European ash (*F. excelsior*) is the most prevalent one, with its range covering most of the continent with the exception of its most northern and southern regions, extending past the Volga River and into south-west Asia (Beck et al., 2016) (Figure 1). Range of the European ash overlaps with the distribution of pedunculate oak (*Quercus robur*), marking the region of Europe's nemoral forests. Ash reaches its northernmost distribution in Scandinavia, along the so-called limes norrlandicus, a border between the nemoral and boreal zones (Dobrowolska et al., 2011). It is generally thought to be limited in the north by the number of days with temperatures above 5,6°C needed to complete its yearly life cycle (Kerr & Cahalan 2004).

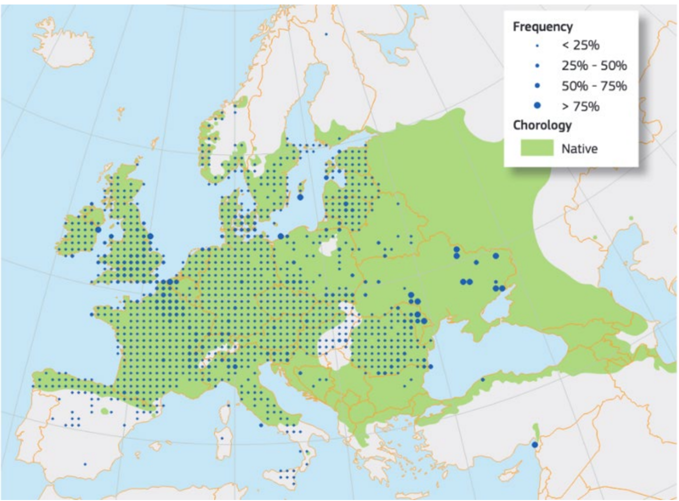

Figure 1 Distribution of Common Ash in Europe with the frequency of occurrence by Beck et al.,2016

Historically, *F. excelsior* is a tree acknowledged for both its wood, as well as its cultural and historical significance in many European cultures. In Norse mythology, it is the ash tree that is imagined as an axis for different dimensions, called Yggdrasil, that holds up the worlds and from which the first man emerged (Dumont, 1992). In the Slavic cultures, ash trees were worshipped in the sacred groves and later remained in folklore, as it was believed that sleeping under an ash tree gives strength to the human mind and that its leaves facilitate conflict resolution. Ash traditionally existed close to humans as it was widely planted near homes and gardens due to not only its shade-giving properties (Marszałek, 2017) but also as it was believed to ward off evil spirits and scare off snakes (Seneta et al., 2021).

Ash timber is widely valued for its properties as it has a bright colour, durability and flexibility. Some traditional uses include tool handles, cart axles, arrow shafts, spears, ploughs, rakes and other everyday equipment that required strong materials that could handle large tensions. Ash has also found its usage in many areas of life; its extracts could be used to promote digestion to treat rheumatism. Different parts of the trees were also used for dying fabrics and tanning. The white ashes that were left after burning the wood could be utilised for bleaching linen. (FRAXIGEN, 2005; Seneta et al., 2021).

1.2 Site requirements

European ash is sometimes called the king's tree, mostly in relation to its leaves flushing late and senesce early, but a connection could also be made to its site requirements as it thrives in deep, nutrient-rich and well-drained but moist soils and does not tolerate drought. Within those limits, ash can, however, occupy a wide range of habitats. *Fraxinus excelsior* has properties between a permanent forest component, in most of its range, to pioneer, for example in Sweden (Dobrowolska, 2011). The growth potential of the species and its regeneration is closely related to the physical properties of the soil on which it grows.

European ash can occur on lime-rich calcareous soils, often originating from calcareous marls or sedimentary parent material rich in silt or clay (Dobrowolska, 2011). It is not suited to acidic soils and thrives on soil with a pH higher than 5.5 but tolerates a minimum pH of 4.5 (Pliûra and Heuertz, 2003). Optimal ash sites can have a fast turnover of organic material as it has a high demand for nitrogen as well as calcium, magnesium and phosphorous. Understory species that can be used as indicators of soils suitable for ash are *Mercurialis perennis*, *Allium ursinum*, *Urtica dioica*, *Circaea lutetiana*, *Festuca rubra*, *Arrhenatherum elatius, Dactylis glomerata* and *Poa trivialis* (Thomas, 2016) (see Figure 2).

Figure 2 Indicators of suitable ash soils from the left: Allium ursinum, Mercurialis perennis, Urtica dioica, Circaea lutetiana, Festuca rubra, Arrhenatherum elatius, Dactylis glomerata and Poa trivialis adapted from Mossberg et al. 2018

When it comes to soil moisture, ash thrives when it ranges from ‘fresh’ to ‘very moist’. Seedlings can tolerate moderate flooding but are sensitive to limitations in water supply and prolonged drought seasons (Kerr and Calahan, 2004). The natural range of ash is limited because of its temperature requirements with a minimum of 1614 annual growing degree days (accumulated mean daily temperatures > 5 °C) occurring in Sweden and a mean growing season temperature for most sites at 13.0 °C (Kollas et al., 2013). Seedling mortality has been found to be related to harsh winters and the occurrence of late frost (Tapper, 1992) with the buds on the top shoots of seedlings dying after 18 h exposure at -3°C (Wardle, 1961). Climate however, is less related than the soil to the growth of *F. excelsior* and it can grow under a wide range of climatic conditions.

1.3 Ash silviculture

1.3.1 Traditional usage

Fraxinus excelsior traditionally was widely utilised in many ways, some of which prevail in modern times. Firstly, it had its place in the human-made landscape. Ash trees could be commonly found in swampy places, growing by roads or mixed into hedges, as they were thought to stabilise the terrain (Seneta, 2021). To use their branches and leaves as animal fodder, coppice forests of ash were created. The ability of the tree to sprout from the stump, even at old age, was used to create low forests of multi-stemmed trees. In many stands, it was customary to cut down the tree between 60 and 90 cm from the ground, which creates a characteristic pollarded look (Rackham, 2016).

Secondly, the timber itself has unique properties that distinguish it even among other noble broadleaves. It is ring porous, has a straight grain and is pretty uniform in colour, which makes it useful for one of the most profitable timber products – veneer, furniture and flooring (Pliûra and Heuertz, 2003). It is the physical properties of the wood, however, that determined most of its usage. F. excelsior timber is shock-resistant, doesn't produce splinters, is bendable and does not taint the taste of foods and drinks (Rackham, 2016), which made it essential before the introduction of man-made materials and tropical woods in Europe (FRAXIGEN, 2005). Its value used to be lowered only by black heart of ash, a non-fungal stain that occurs in some trees and is influenced by their age and the site they grow on (Kerr, 1998).

1.3.2 Stand establishment

Regeneration of *F. excelsior* can be either natural, conducted through planting or a combination of those two (FRAXIGEN, 2005). Vegetative forms of regeneration are also possible for the species and are related to the traditional uses of ash, such as coppicing (Matthews, 1997). Planting practices vary between different countries, with the numbers ranging from 300 to 6000 trees per hectare, with equal spacing in between. The planting material is usually 2-year-old seedlings, with rare exceptions (Dobrowolska,2011).

The European ash is trioecious or subdioecious, meaning its flowers and trees can be female, male and hermaphrodite (Thomas, 2016). The trees start to produce seeds at the age of around 20-30 years, with 2-5 years between heavy crops. The seeds that usually fall between September and March, but can be held up on trees for a whole year (Kerr, 1995). They are, for the most part, wind-dispersed, but they can float and be transported long distances along waterways. Seed dormancy can last from 2 to 6 years as the trees require a warm and a cold period to germinate (Pliûra and Heuertz, 2003), resulting in regeneration emerging in the second spring after seedfall. The expansion and abundance of the natural regeneration depend on soil conditions and relate to the water balance gradient (Dobrowolska, 2011). Deer browsing has been found to have little effect on the recruitment of ash saplings. In Sweden, the species composition of the surrounding forests has been found to influence the density and establishment of natural ash regeneration. It has been found to have biggest regeneration success in noble broadleaf forests of low productivity (Götmark et al., 2005).

1.3.3 Stand management

After successful stand establishment through either planting or natural regeneration, the objective of ash sylviculture is to produce high-quality timber. The ideal, desired outcome are boles, free of defects, 6 meters in length and with diameter at breast height of 40-60 cm. On more fertile sites, achieving this will take around 50 years, but on poorer sites it could take up to 80 years (Kerr, 1995). In light of this timeframe, the typical rotation length has been 60 years, as the ash trees also tend to slow down their growth after that age (FRAXIGEN, 2005) and the risk of black heart occurring is increased after the age of 80 (Kerr, 1998). One of the commonly listed issues in ash sylviculture is insufficient thinnings, as stands should be at their final spacing by age 30 to 35. Pruning and crown thinnings are also recommended to ensure clear wood of high quality (Savill, 2019).

1.4 Ash dieback

Since the early 1990s, the population of the Common Ash in Europe has dwindled significantly, with an estimated loss of nearly 90% of all *F. excelsior* trees due to a disease known as ash dieback (Beck et al., 2016; Carrol and Boa, 2024). Symptoms of the disease include discolouration and wilting of foliage, premature shedding of leaves, wilting of shoots, necrotic cankers and discolouration in the bark, diamond-shaped lesions on stems and petioles and from afar visible dieback of the upper parts of the crown (Skovsgaard, 2010; Needham and Weber, 2022). The disease was observed on many ash trees, particularly in Central Europe, which was initially thought to be caused by combined ecological factors, which could be the case, especially as many of the symptoms can be associated with other factors (Skovsgaard et al. 2017a). It was later, however, found to be independent of environmental factors and associated with certain fungi (Przybył, 2002).

The pathogen was identified as an ascomycete and described as *Chalara fraxinea* (Kowalski, 2006). Further research revealed a more complex nature of the fungus, as it was shown to be the anamorph of another fungus, *Hymenoscyphus pseudoalbidus* (Gross et al., 2014), which was later identified as *Hymenoscyphus fraxineus,* the current name for the causative agent of ash dieback (Baral and Bemmann, 2014). The pathogen is believed to have originated in East Asia (Zhao et al., 2013), as confirmed by studies regarding its genetic diversity in various regions and its interactions with species native to the area (

Cleary, 2016; Orton et al., 2018).

The pathogen infects the trees through their leaves and spreads downwards into twigs and branches, which leads to dieback. It is agreed upon that the infectious propagules of *Hymenoscyphus fraxineus* are its ascospores. The pathogen overwinters in leaf remnants on the forest floor (Marçais et al. 2022) and forms its apothecia predominantly on dead pseudosclerotial petioles and rachises there (Gross et al. 2014). Given that the conditions are unfavourable, for example, they are too dry, *H. fraxineus* can sporulate up to five years after the leafshed and withstand an adverse environment (Kirisits 2015). The main form of dispersal for the pathogen is wind (Timmermann et al. 2011; Gross et al. 2014), but it can also be transferred via the movement of infected ash plants (Marçais et al. 2022). It was also suspected to be possible by seeds (Cleary et al. 2013); yet, it was deemed improbable to germinate from this vector (Marčiulynienė et al. 2018).

According to a database updated in February 2025, the presence of H. fraxineus has been reported in over 30 countries across Europe (Needham and Weber, 2022), which means the majority of the continent is affected by it. The disease spread even before its identification in 2006 (Kowalski, 2006) and is believed to have reached the continent many years prior, in the 1960s. Its first reports in Sweden date back to 2001 (Pagad and Wong, 2022), and by 2009, a fourth of the ash trees in Sweden were severely damaged or dead. The severity of the disease, combined with the resulting discontinuation of planting and replanting of ash (Cleary et al. 2019), has significantly impacted the *F. excelsior* population in Sweden, placing the species on the red list as endangered (SLU, 2025). The crisis is far from over, with mortality rates reaching up to 70% in ash woodlands across Europe, and 82% among naturally regenerated saplings (Coker et al. 2019).

1.5 Tolerance to the disease

1.5.1 Observed tolerance and its mechanism

With the severity of the disease and the subsequent effect on the landscape and ash-dependent ecosystems (Hultberg et al. 2020), a question is raised about possible solutions. Some hope may come in the form of high genotypic variability in susceptibility between individual hosts. Long-term observations confirm that some ash trees can be found in relatively good state even after many years of exposure to the pathogen (Madsen et al. 2021; Matisone et al. 2021), as do different trials (Stener 2013; Liziniewicz et al. 2022; Seidel et al. 2025).

The percentage of ashes estimated to be tolerant to *H. fraxineus* infections ranges from 1% in most trials (Enderle et al. 2019) to 5% (Carroll & Boa 2024). Trials in Denmark and Sweden have proven that the phenology of the tree, along with active defence mechanisms, is significantly correlated with ash dieback tolerance (McKinney et al. 2014). It is the ability of the host to stop the spread of the pathogen into the woody parts of the tree that plays the key role in tolerance mechanisms (Landolt et al. 2016). An important finding is that tolerance is in high degree inherited from parents to offspring (Lobo et al. 2014; McKinney et al. 2014; Muñoz et al. 2016; Enderle et al. 2019). McKinney et al.(2014) conclude that variation in ash dieback tolerance is controlled by many additively operating genes. The aspect of inheritance has both practical and evolutionary importance, as the trees can be identified, tested and used for seed production (Marçais et al. 2022).

1.5.2 Environmental factors influencing tolerance

Part of the variation in tolerance between *F. excelsior* trees can be explained by environmental factors, as the pathogen itself and its life cycle are influenced by its environment (see Table 1). *Hymenoscuphus fraxineus* has been found to have limited growth at high summer temperatures (Hauptman et al. 2013; Grosdidier et al. 2018). The structure of the surrounding landscape has been found to have a significant effect, as forest stands with low density and open growth conditions tend to display fewer symptoms of the disease (Marçais et al. 2016; Skovsgaard et al. 2017b; Grosdidier et al. 2020).

The species composition of the surrounding forest can influence the health status, as a negative correlation has been found with the presence of *Quercus* spp. And positive with *Acer* spp. in an infected ash stand (Havrdová et al. 2017; Pušpure et al. 2017). High site moisture has a positive correlation with the spread of the pathogen and disease severity (Dvorak et al. 2015; Enderle et al. 2017; Havrdová et al. 2017; Skovsgaard et al. 2017b; Erfmeier et al. 2019). With drought periods, however, the plants' immune response can be weakened (Hauptman et al. 2013; Skovsgaard et al. 2017). No consistent results have been obtained so far with soil type or pH (Marçais et al. 2022).

Based on different studies and trials on the environmental influences of the disease, the following pattern was observed by Skovsgaard et al.(2017): the well-being of trees on suitable sites leads to their improved recovery potential, and seasonal unsuitable conditions for the pathogen could hamper the conditions of infection.

Table 1 Environmental factors influencing ash dieback symptoms, adapted from Enderle et al. (2019)

Environmental factor	**Symptoms are more severe with…**	**Reference(s)**
Temperature	…low and moderate temperatures (below 28°C)	(Hauptman et al. 2013; Grosdidier et al. 2018)
Surroundings	…closed, dense stands	(Marçais et al. 2016; Havrdová et al. 2017; Chumanová et al. 2019)
Presence of *Quercus* spp.	…present	(Havrdová et al. 2017)
Presence of *Acer* spp.	…not present	(Havrdová et al. 2017)
Drought	…occurance	(Hauptman et al. 2013)
Site moisture	…more humidity	(Dvorak et al. 2015; Marçais et al. 2016; Havrdová et al. 2017; Pušpure et al. 2017; Erfmeier et al. 2019 Keßler et al., 2012; Koltay et al., 2012)
Forest type	…broadleaf, ash dominated	(Havrdová et al. 2017; Pušpure et al. 2017; Chumanová et al. 2019; Enderle et al. 2019; Erfmeier et al. 2019; Grosdidier et al. 2020)

1.6 Study aim

European ash reaches its northern range limit in Sweden, and of all tree species in Sweden, it accounts for about 0.1% of the total stem volume (SLU, 2024). Despite that, it is considered an important broadleaved tree, both culturally and ecologically. Ash dieback has made a huge impact on the population of European ash which is already marginalised by the past silvicultural practices (Götmark et al. 2005). Due to the ownership structure of Swedish forests, a uniform policy or recommendation protecting the ash in the landscape is difficult to achieve and implement, especially with the dynamics of the disease in the local conditions still not fully investigated.

Potential for the ash tree's survival can come in the form of its natural regeneration, as various studies and trials revealed that tolerance can be inherited from parent to offspring (Kjær et al. 2012; McKinney et al. 2012; Stener 2013; Lobo et al. 2014; McKinney et al. 2014; Muñoz et al. 2016; Enderle et al. 2017; Liziniewicz et al. 2022; Haupt et al. 2024).Another important fiding is how the offspring of the relatively healthy trees is overrepresented in stands infected with *H. fraxineus* which could potentially give hope for local restoration of infected populations (Semizer-Cuming et al. 2021).

Natural regeneration of ash differs among sites differing in soil pH, moisture and fertility(Kerr & Cahalan 2004). So far, only a few studies have explored the relation between site conditions and the health of naturally regenerated saplings (Lygis et al. 2014; Enderle et al. 2017; Pušpure et al. 2017; Turczański et al. 2021, 2022). However, there is still potential for this complicated relation to be investigated, as firstly, none of the studies took into account the regeneration of surrounding trees selected for tolerance, which could potentially reveal how sites could influence the inheritance or expression of the trait. Secondly, none of them took place in Sweden, which, as the northern border of *F. excelsior*'s range, could prove to be an interesting case study.

A better understanding of the joint effects of the disease and other environmental and site factors on ash natural regeneration is needed to make necessary steps towards recommendations for stakeholders. I have investigated if ash regeneration around the tolerant focal trees can be used to promote restoration of sites decimated by the disease. The purpose of this study is to investigate the health status of the offspring surrounding a known tolerant ash tree.

In this study following research questions were posed:

1. How much natural regeneration can we find around tolerant trees on forest land? And what size (3 strata) and distance from tree?
2. What health status does the regeneration have in different strata?
3. Is there a difference in average health and abundance of regeneration on different sites?
4. Is there a relationship between the Health Class and Stem Form?
5. Does the tree size of the focal tree and the regeneration have a significant effect on the health status of the natural regeneration?

6. Is there a significant correlation between the distance from the tolerant focal tree and the health status of the regeneration around it?
7. What is the relationship between the forest type and the health status of the regeneration around the focal trees?
8. What is the effect of soil type and soil moisture on the severity of ash dieback infections in natural regeneration surrounding tolerant ash trees?
9. What is the relationship between environmental factors like tempeature and precipitation and the health and abundance of the natural regeneration surrounding a tolerant ash tree?
10. What is the relationship between the naturally occurring competition of woody tree species and the health of the regeneration around the focal ash tree?
11. What is the relationship between the occurrence of nitrophyllic species (*Urtica dioica, Anemone nemorosa*) and the health and abundance of the natural regeneration surrounding the focal ash tree?
12. What is the relationship between the occurrence of alien species (*Acer pseudoplatanus, Amelanchier* spp.*, Impatiens glandulifera*) and the health and abundance of the natural regeneration surrounding the focal ash tree?

2. Methodology

2.1 Study area

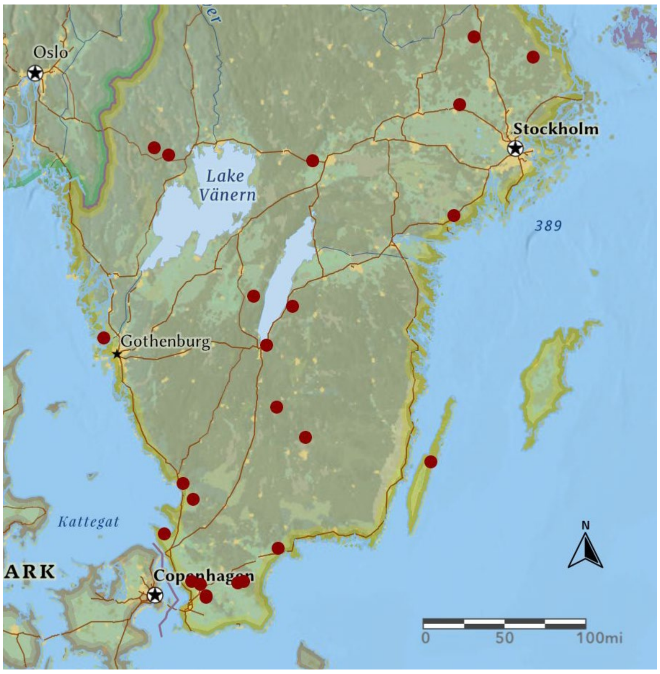

Figure 3 All the established plots

The sample plots (Fig. 3) were established based on the knowledge from the resistant inventory database from an ongoing project called 'RäddaAsken' made as a cooperation between Forestry Research Institute of Sweden (Skogforsk) and Swedish University of Agricultural Sciences. For this initiative, a database was made containing trees that exhibit tolerance to ash dieback, whereby at least 80% of the tree's crown is intact (non-symptomatic) relative to surrounding ash trees. The inventory was made by project leaders Michelle Cleary, Lars-Göran Stener and Mateusz Liziniewicz throughout the natural range of ash in Sweden. This pre-existing database of was the basis for further selection and analysis.

Using that dataset, buffer zones of 100 m were created around each trees coordinates and data was extracted form National Land Cover Database (Swedish Environmental Protection Agency, 2025, NMD2018). A list of potential stands was generated based on the pixels in the buffer zones meeting the following criteria (also see Fig. 4):

1. minimum 70% falls under one of the 16 forest categories (see Fig. X).
2. category 'road/railway' does not occur

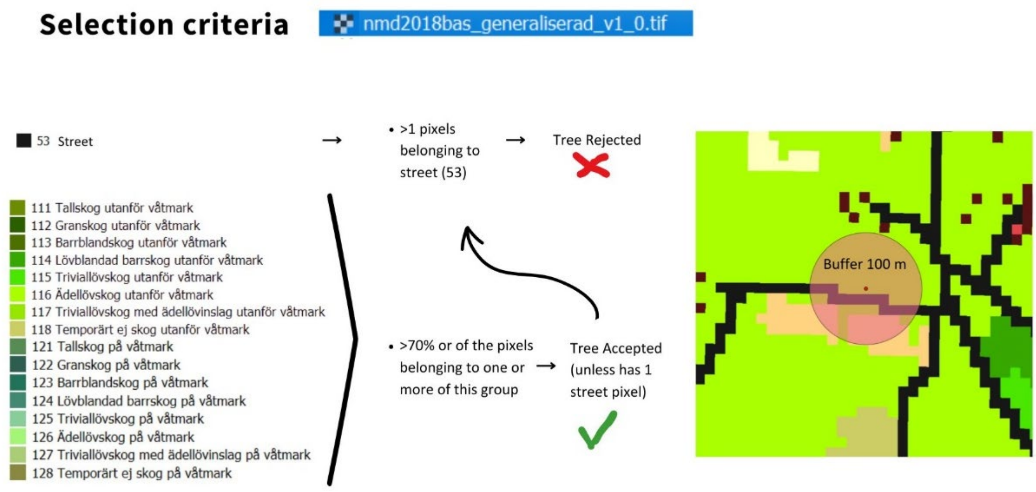

Figure 4 Selection criteria for the buffer zones

The buffer zone was motivated by the approximate ash seed dispersal distance according to Wagner (1997). It was done firstly, to be able to observe saplings and seedlings that could be presumed to be offspring of the selected trees.Secondly, to ensure that the regeneration is growing on land classified as forest Later, sites were selected to ensure good geographic representation across the natural range of ash in Sweden, and therefore across a climatic gradient.

From the list of candidate sites, the health and vitality of the tolerant ash tree was assessed visually and only those ash trees that appear to exhibit tolerance based on the original criteria for selection were considered as candidate sites for establishing plots. In instances where on a site, more than one tree form the database met the selection criteria (see Fig 4) and the observations were less than 100 meters from each other, the more vital tree was selected as a centre for plot establishment.

2.2 Materials and methods

2.2.1 Experimental plot design and establishment

The tolerant tree represented the center location from which sample plots were established. Owners of the land on which the selected trees were found were contacted and asked for consent to establish a semi-permanent plot. Each tree was marked with tape and a tag with short project description as well as a plastic marking stick, which was put in the ground next to it to mark the side that made the actual center of the plot. To conduct the inventory, circular sample subplots with the radius of 2,78 m, to have plots with surfaces around 25 m^2, were established at eight and 20 meters distance from the center tolerant tree in the North, South, East and West directions (Figure 5). At each plot center, a plastic marking stick was placed along with four others in cardinal directions to mark the radius of each plot.

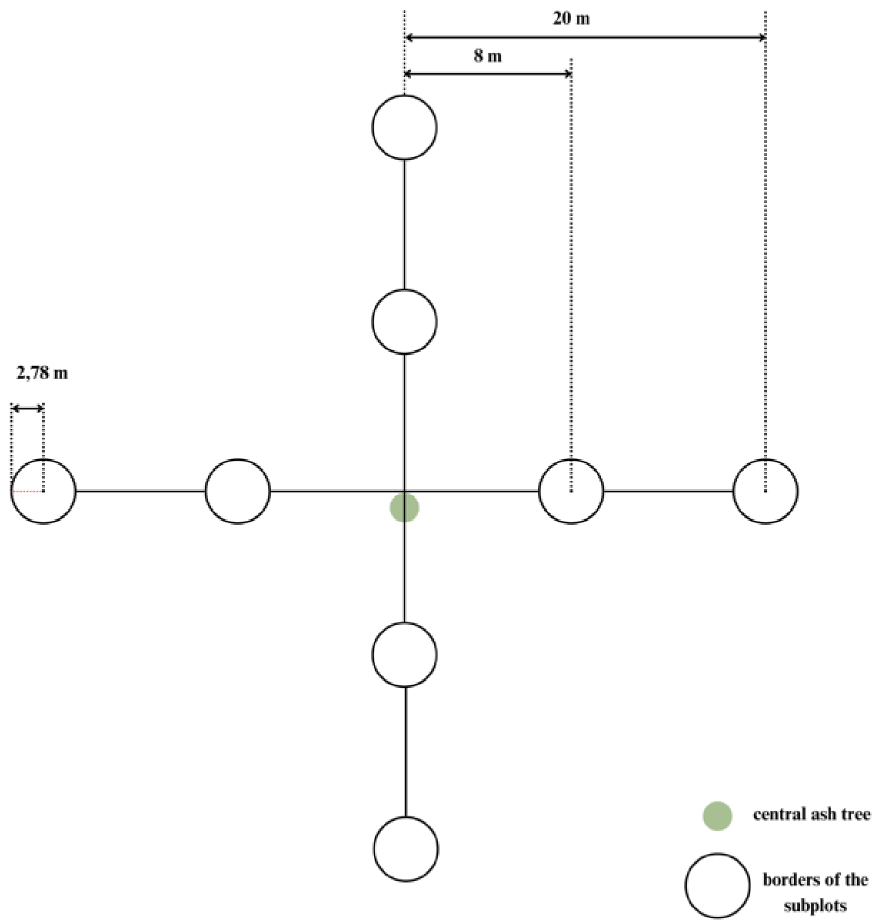

Figure 5 A schematic rendition of the established sample plots surrounding a mature tolerant ash tree

2.2.2 Data collection

In each subplot, naturally regenerated seedlings, regardless of tree species, that were higher than 25 cm were counted and categorized into size strata 1,(0,25–1,3m); 2,(1,3–4,0m); 3, (>4,0m). An assessment was conducted of health of all ash trees and assigned to a health class rating based on previous studies of tolerant ash clones whereby 1=healthy to 6 =dead (see Table 2). As well as information about the stem form of the trees in categories 1 – one top shoot, 2 – a for forming, 3- more than two competing top shoots.

Table 2 Criteria of health class assessment

Health class	Criteria of damage symptoms
1	Healthy-no signs of infection
2	Less than 1/3 of the crown is damaged
3	Less than 1/3 of the crown is damaged and the leader shoot of the main stem is necrotic
4	Between 1/3-2/3 of the crown is damaged Two or more leader shoots of stems are necrotic Two or three leisons on the main stem
5	More than 2/3 of the crown is damaged Several leader shoots necrotic Four or more necrotic leisons on the main stem
6	Dead

In addition, competing tree species and ground vegetation was identified. To register more information about the sites, photographs were taken of both the tree and its surroundings together with descriptions of other mature ash trees in the area.

2.2.3 Online databases

To supplement field-collected data, additional site parameters were obtained from official online databases. Soil type and site characteristics were accessed through the GIS database maintained by Länsstyrelsen (County Administrative Boards) and SLU's map services. This data included information on soil type, soil moisture classification for the sites. Land cover information, crucial for site selection and identifying forest type, was retrieved from the Swedish National Land Cover Database (NMD) provided by the Swedish Environmental Protection Agency (Naturvårdsverket, 2025). Temperature and precipitation data were retrieved from the Swedish Meteorological and Hydrological Institute (SMHI), specifically annual values for the years 2015-2024 for every site. A site location map was created using ArcGIS Online (Esri, 2025), incorporating geospatial data from SLU's map services.

2.3 Data analysis

All statistical analyses were conducted using R (version 2024.12.1+563). Packages used for the analysis and visualisation were: dplr (Wickham et al. 2022), ggplot2 (Wickham 2016), tidyr (Wickham 2024), readxl (Wickham and Bryan 2025).

2.3.1 Preparation of the data

The data collected in the field was put in three different data frames in Microsoft Excel. First one on site-level with average health and abundance of different size strata of regeneration, as well as values for the studied variables for each site. These included: forest type (Naturvårdsverket, 2025), soil type (Sveriges geologiska undersökning 2001) , soil moisture, temperature and precipitation for the years 2023 – 2024 (SMHI, 2025), as well as values of 0 – not present or 1 – present for nitrophyllic plants, sycamore (*Acer pseudoplatanus*), foreign species (*Acer pseudoplatanus, Amelanchier, Impatiens glandulifera.* The second data frame included data on health and abundance of each of the 8 subplots in every site. In the third one, all individual field observations were put together in a large Excel file. In all data frames, raw character columns were converted to numeric format, and incomplete rows were excluded to ensure model validity.

To analyse the site factors, some variables were regrouped, and the following were created: forest group (grouping forest types to ‘wetland’ and ‘outside wetland’ as well as “decidiuous’ and ‘broadleaf’, dbh classes were created for the focal trees: small (<250cm), medium (250-500cm), large (>500cm).

2.3.2 Variable justification

The variables were picked based on the general finding that vigorous trees can better compensate for the effects of *H. fraxineus* (Havrdová et al. 2017; Skovsgaard et al. 2017b; Enderle et al. 2019). The factors that were selected for analysis could be generally grouped into two categories: the indicators that the site is suitable for ash and factors influencing the severity of the disease symptoms based on the published literature.

Seedling and sapling size

In the field observations, a trend could be observed, where smaller regeneration seemed to be in better health. In mature trees, some authors, recorded a relation between tree size and disease severity (Skovsgaard et al. 2010).

Distance from the tree

The distance from the adult tree could help capture potential variation in microclimatic conditions, root zone influence, or pathogen exposure gradients around the focal tree. Could also check the occurrence of the Jentzen-Conell effect (Turczański et al. 2022).

Adult tree size

A relation has been found in different studies between the tree’s diameter and the severity of *H. fraxineus* symptoms (Skovsgaard et al. 2010). It is interesting to explore how that relationship transfers to its supposed offspring and if it is possible that some trees just show signs of tolerance due to their size but the trait is not apparent in the next generation.

Forest type

Forest types have been recorded to influence the abundance of ash regeneration (Götmark et al. 2005) as well as its health (Erfmeier et al. 2019).
The forest types were taken from the Swedish National Land Cover Database (NMD) provided by the Swedish Environmental Protection Agency (Naturvårdsverket, 2025).

The types of forest included in the database, describe mostly the specie composition of the stand in two categories of moisture: 'Forest on wetland' and 'Forest not on wetland'. Distinguishing within both those categories by specie composition: Pine forest, Spruce forest, Mixed coniferous forest, Mixed forest, Deciduous hardwood forest, Deciduous forest with hardwood forest, Temporarily nonforest. The forest types recorded on our sites are listed in Table 3.

Table 3 Definitions of all the recorded forest types for the sites (Naturvårdsverket, 2025)

Code	Forest type	Description
225	Deciduous forest on wetland	Tree-covered areas on wetlands with a total crown cover of >10% where >70% of the crown cover consists of deciduous trees (primarily birch, alder and/or aspen). Trees are higher than 5 meters.
115	Deciduous forest not on wetland	Tree-covered areas outside of wetlands with a total crown cover of >10% where >70% of the crown cover consists of deciduous trees (primarily birch, alder and/or aspen). Trees are higher than 5 meters.
116	Deciduous hardwood forest not on wetland (Broadleaf forest outside wetland)	Tree-covered areas outside of wetlands with a total crown cover of >10 where >70% of the crown cover consists of deciduous trees, of which >50% is broad-leaved deciduous forest (mainly oak, beech, ash, elm, linden, maple, cherry and hornbeam). Trees are higher than 5 meters.
117	Deciduous forest with deciduous hardwood forest not on wetland (Deciduous Forest with deciduous hardwood forest elements not on wetland)	Tree-covered areas outside of wetlands with a total crown cover of >10 where >70% of the crown cover consists of deciduous trees, of which 20 - 50% is broad-leaved deciduous forest (mainly oak, beech, ash, elm, linden, maple, cherry and hornbeam). Trees are higher than 5 meters.
118	Temporarily non forest not on wetland	Open and re-growing clear-felled, storm-felled or burnt areas outside of wetlands. Trees are less than 5 meters.
114	Mixed forest not on wetland	Tree-covered areas outside of wetlands with a total crown cover of >10% where neither coniferous nor deciduous crown cover reaches >70%. Trees are higher than 5 meters.

Soil moisture

Soil moisture has been one of the main factors recorded to influence the development of the disease ((Havrdová et al. 2017; Pušpure et al. 2017; Erfmeier et al. 2019). It has been found to promote leaf infection and the growth of apothecia raiches in the leaf litter (Skovsgaard et al. 2017).
In our dataset two categories were recorded: 'moist' and 'mesic-moist', these two categories from the National Forest Inventory. The two categories include areas with shallow groundwater (<1m), with the first category exhibiting pools of standing water, while the later (mesic-moist) only has seasonally standing water. More details about the specific differences are described by Ågren et al. (2021).

Soil type

Soil type alone has not been found to influence the health directly (Enderle et al. 2019; Turczański et al. 2021). The properties of the soil however can influence overall seedling health and moisture retention in the area (Kerr & Cahalan 2004; Skovsgaard et al. 2017).

Temperature and Precipitation

Multiple studies found the influence of those evironmental factors on development of the pathogen, severity of symptoms and regeneration abundance (Dvorak et al. 2015; Marçais et al. 2016; Havrdová et al. 2017; Pušpure et al. 2017; Erfmeier et al. 2019; Hauptman et al. 2013; Grosdidier et al. 2018).

Competition

Competition from other tree species is known to influence the natural regeneration of ash (Kerr & Cahalan 2004; Götmark et al. 2005; Dobrowolska et al. 2011; Thomas 2016a).

Nitrophyllic species

Ash has been found to thrive on sites rich in nitrogen and with the presence of some of the included species like U*rtica dioica* for example(Kerr & Cahalan 2004; Dobrowolska et al. 2011; Thomas 2016b) . And it has been pointed out, that the more suitable sites could support plants immune response (Skovsgaard et al. 2017b). Moreover, an indicator like that could prove useful for making recommendations for sylvicultural practices, as it could be easily used as identificators by foresters. From the recorded understory plants *Urtica dioica, Anemone nemorosa* were selected based on their nitrophyllic properties (Witkowska-Żuk 2021).

Foreign species

The presence of alien and invasive species has been documented to influence the densities of natural regeneration (Dyderski & Jagodziński 2020). Few species non-native to Sweden were identified, both in the tree and understory layer, namely: *Acer pseudoplatanus, Amelanchier* spp. and *Impatiens glandulifera*. Their potential relation to the health of the regeneration was tested. It was hypothesised that they could have negative effects on the vigour and through it indirectly on health of the natural regeneration.

2.3.3 Statistical tests and models

The tests and analysis tools for every variable will be stated below.

Seedling and sapling size

To assess whether tree size is associated with health condition, regenerating individuals were grouped into size strata based on height and categorized into health classes ranging from 1 (healthy) to 6 (dead) as explained in Figure 7. A contingency table and stacked bar plots were used to explore how size strata are distributed across health classes. As the values for health and class in this case could be treated as categorical, a chi-squared test was conducted to check the statistical significance of the relationship.

Distance from the tree

To assess whether sapling health differed by distance from the tolerant ash tree (8 m vs. 20 m), an initial ANOVA was performed. However, Shapiro–Wilk tests indicated non-normal distributions in both groups so a Wilcoxon rank-sum test was used instead. This non-parametric test is appropriate for comparing non-normally distributed or ordinal data between two independent samples.

Stem form

To explore the relations between the Stem Form treated here as a categorical variable and Health Class, an ordinal variable, a Chi-squared test of independence was performed and later standardized residuals were analised.

Adult tree size

A linear regression was used to assess whether the diameter at breast height (DBH) of tolerant ash trees was associated with the health of surrounding natural regeneration. Three different size categories were established: small (<250cm), medium (250-500cm), large (>500cm), a linear model was used to test whether the diameter class (DBH) of the parent ash tree was associated with the health of surrounding regeneration.

Sites

To analize the differences in health and abundance for the sites a one way ANOVA was run with the subplots treated as replications within each site. From the subplots 24 were excluded due to lack of regeneration on them.

Forest type

Forest type was tested in three different ways. Firstly, each distinct forest type was taken into consideration, then they were grouped into inside and outside of wetland categories. Lastly, they were grouped by specie composition into groups 'Broadleaf'= 'Broadleaf forest outside wetlands' and 'Broadleaf forest on wetlands'; 'Deciduous' = 'Deciduous forest outside wetlands' "Decidous forest on wetlands" and 'Deciduous forest with deciduous elements outside wetlands'; 'Other' = for forest types not previously stated. This was done because the individual forest types were underrepresented because of the sample size (sometimes containing one or two observations), in an attempt to increase the significance and reliability of the analysis. Later an ANOVA was conducted on the three earlier stated groups.

Soil type and Soil moisture

Soil type and soil moisture were included in multiple models predicting the average health and abundance of ash regeneration. Firstly, simple, separate models of soil type interaction with average health were produced. Secondly, their interaction was examined in a linear model. Thirdly, they were included in models with combined environmental factors (Temperature, Precipitation, Forest type) for both health and abundance with different models for the general studied population and with division into different size strata (Size staratum 1, Size stratum 2, Size stratum 3).

Temperature and Precipitation

To analyse the relationship temperature and health of the regeneration an ANOVA was performed. Later it was included in the multivariate linear models alongside other environmental factors.

Combined environmental factors

To evaluate how climate and site conditions jointly influence regeneration health, a multiple linear regression model was used. Predictors included average temperature, average precipitation (climatic variables), soil type, soil moisture, and forest type (site conditions). This approach allowed for assessing the relative contribution of each environmental factor while controlling for the others. Due to the limited sample size ($n = 27$), interaction terms were not included in this model to prevent overfitting.

Nitrophyllic species and foreign species

Linear models were used to investigate the relation between the presence of Nitrophyllic species and foreign species and health of regeneration for each site.

Competition

A percentage was calculated of the number of woody plants observed on the plots that were not *F. excelsior*. Later, a linear model was used to investigate the relation between the percentage of competition and health and abundance of regeneration for each site.

3. Results

3.1 Relation between seedling size and health

In this study 28 trees were inventoried on 27 different sites. In total, an assesement of 7103 young ash trees was done. Seedlings in size stratum 1 (n=3572) had 52 % seedlings classified as Health class 1, with no visible signs of disease, stratum two (n=586) included 16% of saplings with no symptoms and size stratum 3 (n=134) represented only 3%. Dead individuals (Health Class 6) comprised 4% of size stratum 1, 13% of size stratum 2, and 43% of size stratum 3. The details are reported in Table 4 and visualised in Figure 6.

A Chi-square test of independence confirmed a statistically significant relationship between size strata and health condition ($\chi^2 = 661.53$, $df = 10$, $p < 0.001$), which indicates that health status is not independent of tree size in the regenerating ash population. Residuals from the test highlighted an overrepresentation of small (size stratum 1), healthy individuals and a corresponding underrepresentation of small trees in the more damaged or dead categories.

Table 4 Number and percentage of each Health Class in each Size Strata for all sites combined

Size Stratum	**Health Class**	**Count (n)**	**Percentage [%]**
1	1	1867	52
	2	454	13
	3	414	12
	4	346	10
	5	358	10
	6	133	4
2	1	96	16
	2	109	19
	3	127	22
	4	103	18
	5	72	12
	6	79	13
3	1	4	3
	2	22	16
	3	30	22
	4	16	12
	5	5	4
	6	57	43

Figure 6 Percentage distribution of Health classes within Size Strata for all sites combined

3.2 Differences between sites

One-way ANOVA revealed that the average health between the sites differed significantly ($F(26, 127) = 5.91$, $p < 0.001$) with the scores ranging from 1,39 to 5,14 (see Table 5). The abundance of regeneration has also been found to differ significantly depending on the site in ANOVA ($F(26, 127) = 5.91$, $p < 0.001$) with the values ranging from 5 to 643 with different representation of size strata (Figure 7).

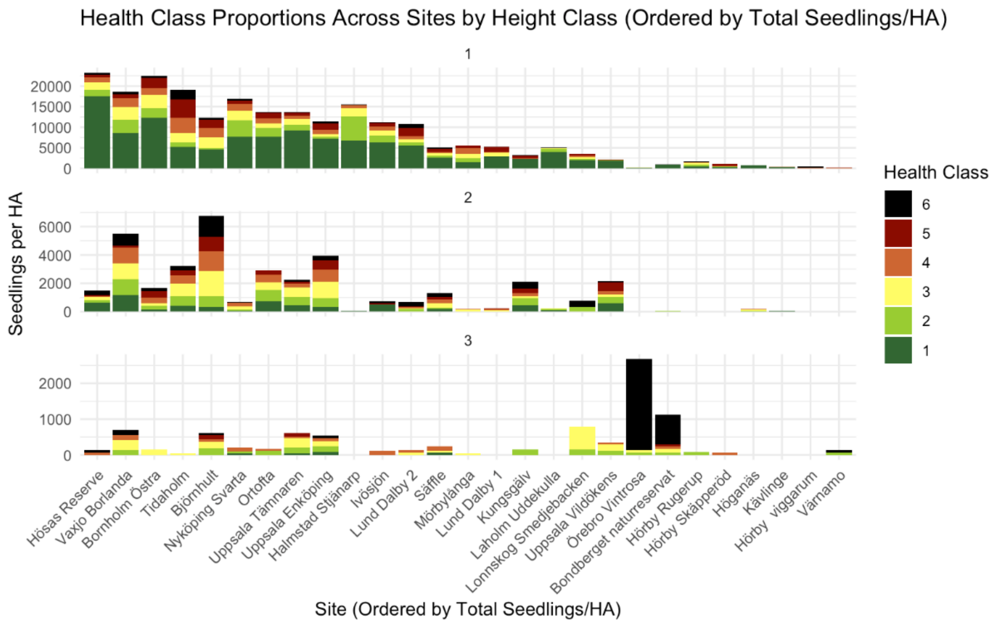

Figure 7 Health class proportions in different size strata (horizontal panels) through the examined sites, ordered from highest to lowest number of seedlings per hectare (from the left

Table 5 Average values for Health Class and Number of Trees for every established plot

Location	**Average Health Class**	**Quantity**
Björnhult	3,24	395
Bondberget Naturreservat	3,44	44
Bornholm Östra Sörby	2,27	348
Halmstad Stjänarp	1,83	279
Höganäs	1,40	18
Hörby Rugerup	2,35	43
Hörby Skäpperöd	3,45	22
Hörby viggarum	5,14	11
Hösas Reserve	1,69	504
Ivösjön	2,07	112
Kungsgälv Torsby	2,61	78
Kävlinge	1,63	10
Laholm Uddekulla	1,39	130
Lonnskog Smedjebacken	2,56	40
Lund Dalby	2,72	268
Lund Dalby	2,44	97
Mörbylånga LillaVickleby	2,78	114
Nyköping Svarta gård	2,20	347
Ortofta	2,17	308
Säffle gillberga-torp	2,66	112
Tidaholm strakaskogen	3,39	437
Uppsala Enköping	2,52	239
Uppsala Tämnaren	1,95	323
Uppsala Vildökens	2,32	88
Vaxjo Borlanda	2,44	643
Värnamo Svensbygd	3,60	5
Örebro Vintrosa	5,53	43

3.3 Distance from the tolerant focal tree

Sapling health was compared between plots located 8 m and 20 m from tolerant ash trees. Mean health at 20 m approached 2.86 and at 8 m it had the mean of 2.48. This difference did not reach statistical significance ($F(1, 152) = 3.59$, $p = 0.060$).

3.4 Stem form and health

Statistically significant association between sapling health class and stem form was found ($\chi^2 = 363.04$, $df = 10$, $p < 0.001$). The distribution of stem forms varied significantly across health conditions, suggesting that certain stem forms may be more prevalent among individuals with differing levels of ash dieback severity. Standardized residuals revealed overrepresentation in several combinations. Saplings with Stem Form 2 were overepresented in health class 2, 3 and 4 and saplings with Stem Form 1 were overrepresented in Health Class 1.

Table 6 Overrepresented combinations of stem form and health class based on standardized residuals from the Chi-square test of independence

Stem Form	Health Class	Residual
2	3	7.191721
2	2	6.283476
1	1	5.584573
3	5	5.255561
3	2	4.353171
2	4	3.690768
3	4	2.544575
2	5	2.26415

3.5 Diameter at breast height of the tolerant focal tree

The diameter at breast height for the tolerant trees ranged from 11 to 75 cm with an average 32,8 cm. There was no significant correlation between tree size and seedling mean health.
Linear regression showed no significant relationship between parent tree size and average health of the surrounding regeneration ($p = 0.75$). The effect was minimal ($R^2 = 0.004$) as visualized in Figure 8. This suggests that, within this dataset, DBH of the focal tree is not a reliable predictor of regeneration health.

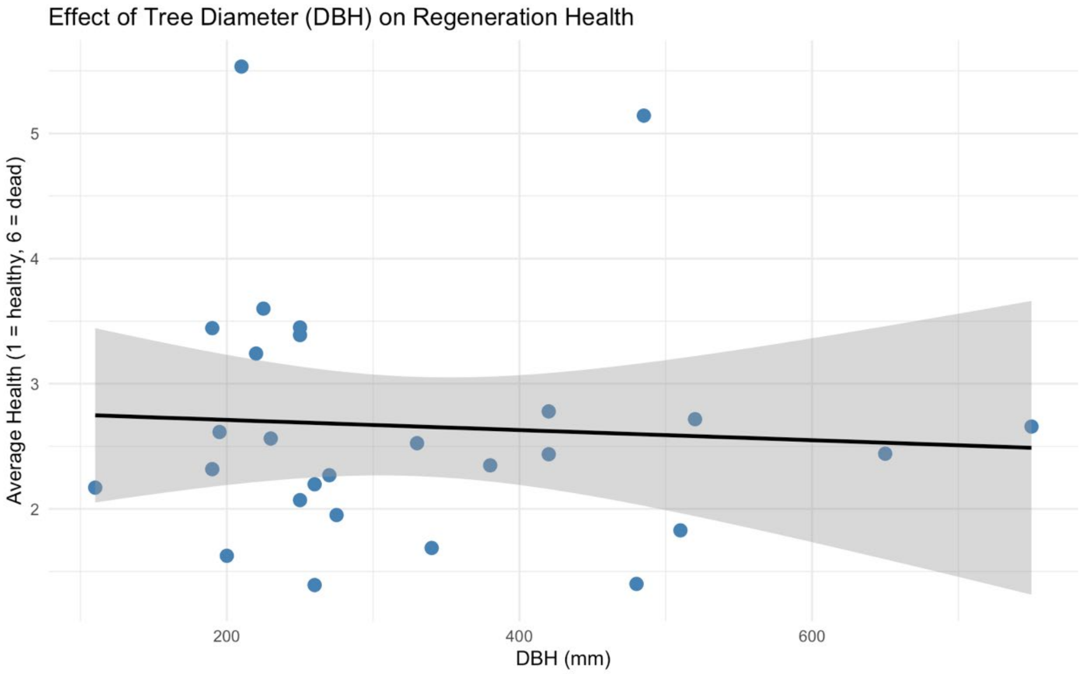

Figure 8 Effect of Diameter at breast heigh on Average health of the regeneration

After establishing three different size categories the overall model was not statistically significant ($F(2, 24) = 1.30$, $p = 0.29$), it explained ~10% of the variation in average health scores.

The regeneration around medium and large trees had higher health scores (Estimate = +0.62 and +0.75, respectively), indicating poorer health compared to regeneration around small trees (see Fig. 9). However, neither comparison reached statistical significance (p > 0.16).

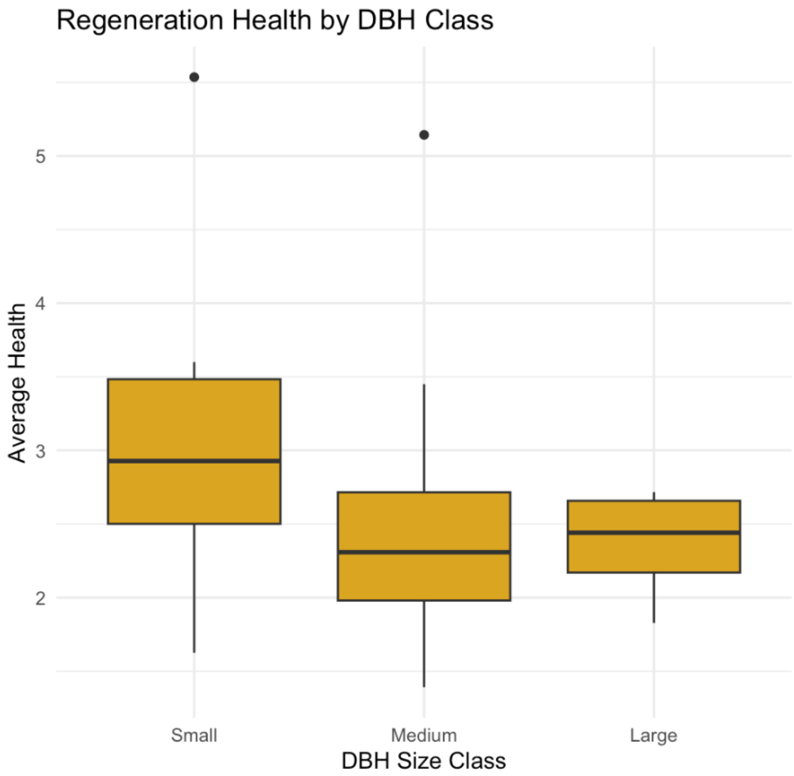

Figure 9 Effect of Diameter at breast height class on Average health of the regeneration

3.6 Forest type

No significant relationship was revealed between forest type and average health of regeneration. Although some variation was observed among types (see Fig. 10), no specific forest category consistently supported healthier regeneration

Grouping forest types into 'wetland' vs. 'non-wetland; did not improve model significance, neither did categorizing it by 'broadleaved' and 'deciduous'. Overall, forest type alone was not a strong predictor of regeneration health.

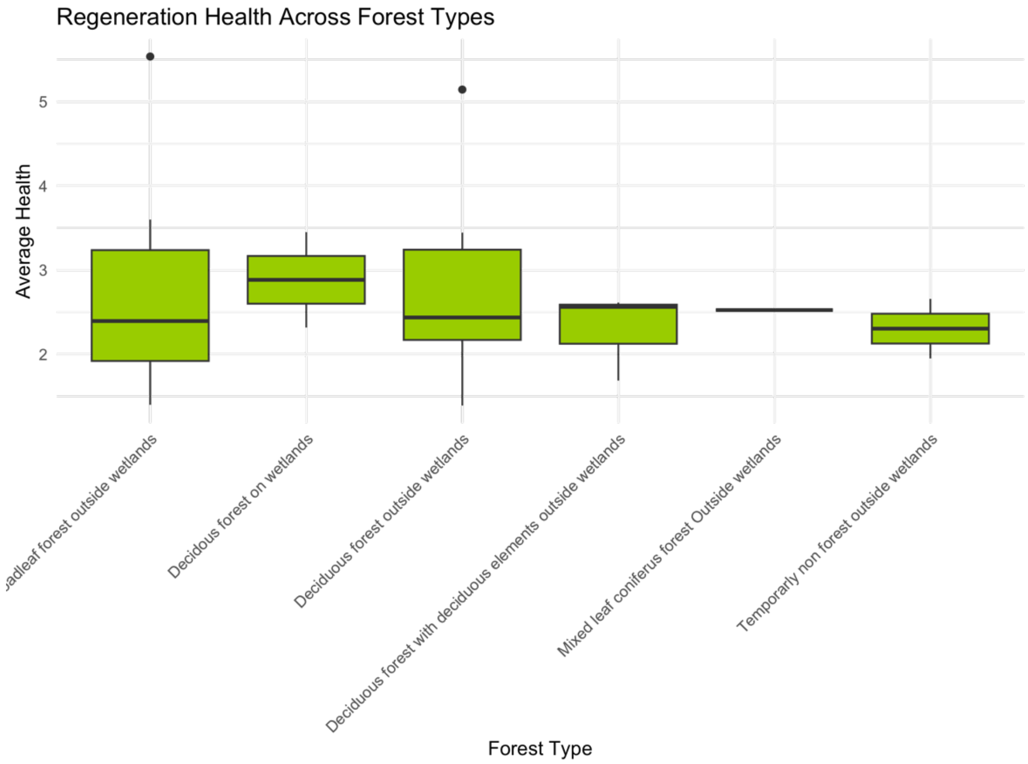

Figure 10 The average health of all ash regeneration across all recorded forest types

3.7 Soil moisture

In a ANOVA soil moisture class was not significantly associated with regeneration health. Slight trends suggested that mesic-moist soils might be linked with marginally worse seedling health than mesic sites (Figure 11), but the differences were not statistically meaningful**.** Soil moisture alone may not strongly influence regeneration health in this dataset.

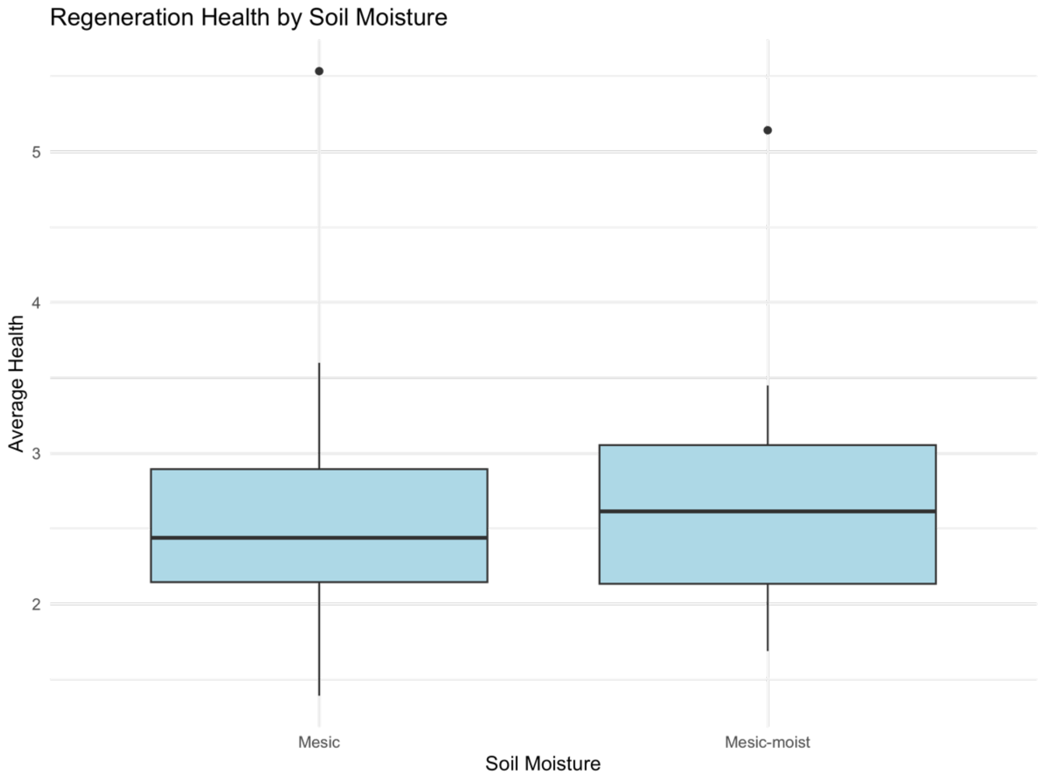

Figure 11 Average regeneration health across observed moisture categories

3.8 Soil type

An ANOVA did not reveal any significant relationships between average health (see Table 4) and soil type. A linear model was then used to assess the effect of soil type on the average health of ash regeneration. The model explained approximately 27% of the variation in health scores ($R^2 = 0.27$), and the overall model was not statistically significant ($F(4, 22) = 2.05$, $p = 0.122$).

Among the soil types, regeneration growing on postglacial sand and gravel was associated with significantly worse health ($\beta = 1.54$, $p = 0.047$) compared to the reference category (bedrock). Regeneration on other soil types, including moraine, moraine clay, and peat (torv), showed no statistically significant differences in health status (see Fig. 12).

Table 7 Average values for the health of the regeneration for soils with listed soil types alongside the number of observations of each group.

Soil type	Average health	No. of plots
Bedrock	2.537365	7
Postglacial sand--grus	4.074585	2
Morain	2.809572	12
Morain clay	2.066476	5
Peat	1.828000	1

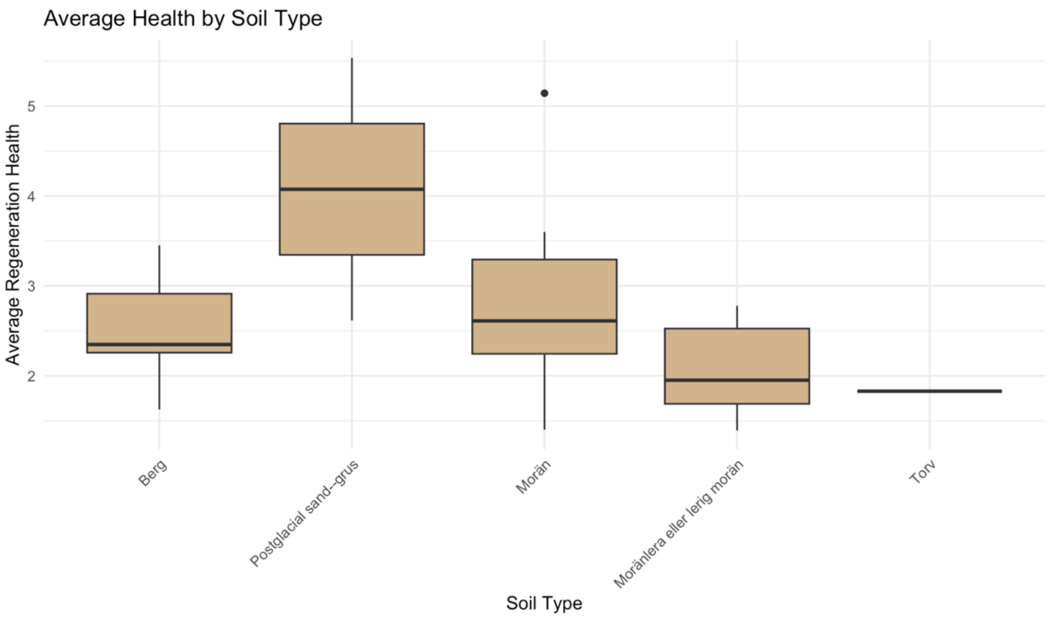

Figure 12 Average regeneration health across the observed soil types arranged with their increasing water holding capacities from the left (Irrigation New Zealand, n.d.)

To assess the combined effects of soil type and soil moisture on ash regeneration health, a linear model with interaction terms was fitted. The model explained approximately 58% of the variation in average health scores (adjusted $R^2 = 0.39$) and was statistically significant ($F(8, 18) = 3.06$, $p = 0.023$).

Plots on postglacial sand and gravel soils had significantly worse average regeneration health ($\beta = 3.14$, $p = 0.002$) under mesic conditions. However, this effect was significantly reduced in mesic-moist conditions (interaction $\beta = -3.41$, $p = 0.015$), suggesting that improved soil moisture may mitigate the negative effect. No other soil types or interactions were found to be statistically significant.

3.1 Nitrophyllic species (Urtica dioica, Anemone nemorosa)

Models found no significant relationship between the presence of nitrophilic species and regeneration health (Figure 13) . While presence indicated nutrient-enriched sites, it did not correlate with worse health in regenerating ash.

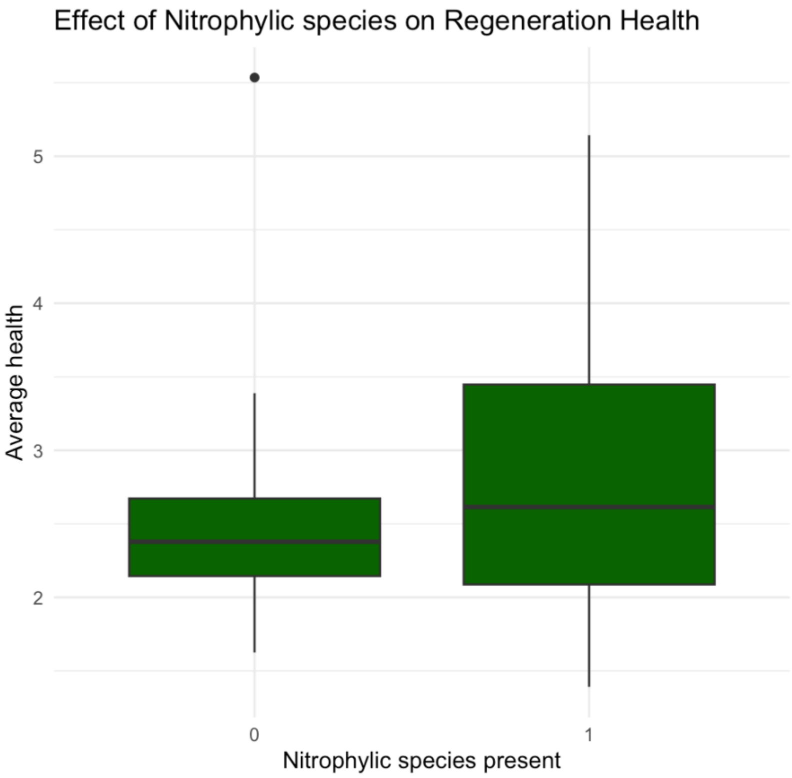

Figure 13 Average health with presence (1) and absence (0) of nitrophyllic species

3.2 Foreign species (Acer pseudoplatanus, Amelanchier spp., Impatiens glandulifera)

No significant effect of invasive species presence on health was found. Regeneration on sites with foreign plants showed slightly worse average health, but the difference was not significant. Foreign species presence had no effect on the regeneration abundance either. While a weak trend suggested lower regeneration counts where invasives were present, it was not statistically supported.

3.3 Naturally occurring competition of woody tree species

The linear model used revealed a weak, non-significant trend toward better ash regeneration health (lower scores, Figure 14) in areas with lower competition (expressed in percentage of woody plants observations that were not the European ash), but the effect was small and statistically insignificant. On average, saplings in high-competition plots had a health score of 2.82 (ranging from 1.39 to 5.53), while those in low-competition plots averaged 2.53 (range: 1.69–3.60). Slightly lower abundance was noted with increasing competition (Figure 15), but it was not statistically significant ($p \sim 0.1$).

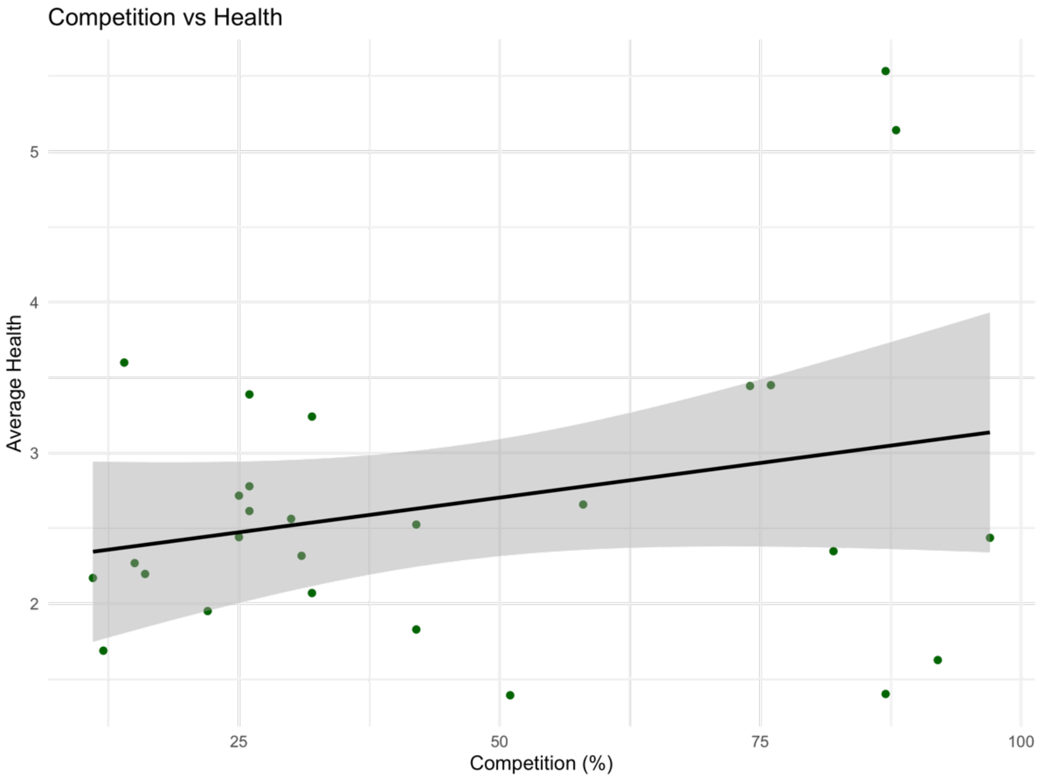

Figure 14 The effect of increasing competition on the average health of natural regeneration of ash

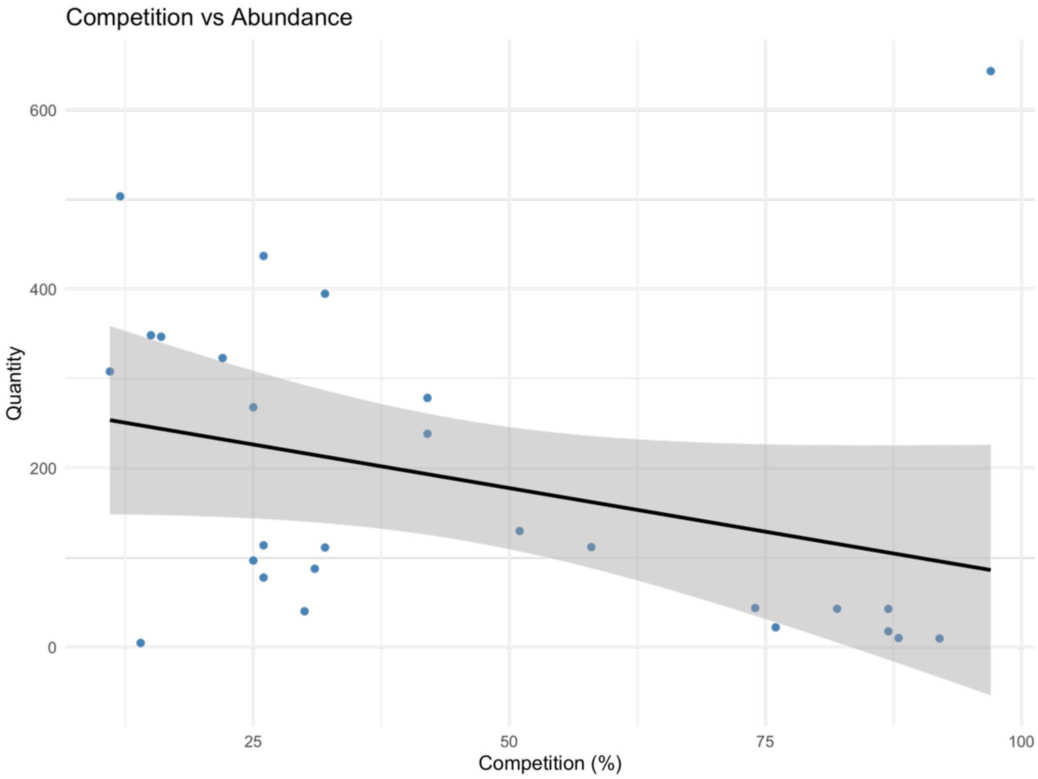

Figure 15 The effect of increasing competition on the abundance of natural regeneration of ash

3.4 Combined environmental factors

A multivariate model incorporating environmental variables (average temperature, precipitation, soil type and moisture, and forest group) explained a moderate portion of the variance in regeneration health ($R^2 = 0.37$), but the model was not statistically significant overall ($p = 0.30$). Neither average precipitation nor average temperature had measurable effects, and forest group or soil moisture did not show significant influence.

4. Discussion

This study examined the influence of various factors and site properties on the health and abundance of natural regeneration of European ash surrounding mature ash` trees selected for tolerance to the pathogen *H. fraxineus*. Relationships were found between among others height of the sapligns, stem form as well as significant differences were observed between different sites

Strong correlation was observed between the height of the saplings and their health, suggesting that longer exposure to the pathogen could result in higher mortality and more severe symptoms. This finding is consistent with previous research indicating that larger trees, due to prolonged exposure, may experience higher disease severity (Turczański et al. 2022; Havrdova at al. 2017).

The analysis revealed relationships between the stem form of the regeneration and its average health. The result is might be caused by the fact that the presence of forking is often a result of damage to the top shoot (Drénou et al. 2020) and one of the criteria of classifying the trees into health classes was necrosis of the top shoot. It is no wonder then that co-dominant stems will occur in the health categories where a necrosis of the top shoot is observed but the crown vitality is sufficient for observation, in this case Health Classes 2, 3 and 4. An interesting direction would be to see how long multiple stems can be identified in a tree after *H. fraxineus* causes topshoot dieback.

Site has been found to have a significant influence on both abundance and health of the natural regeneration. In this dataset however, we were not yet able to determine specific site conditions underlying this diversity. The environmental factors such as temperature and precipitation were found not to have significant influence on the regenerations health and abundance in this dataset. The values were sourced from an online database which in itself might not be precise enough to reveal the factual state of the site and the relationship between the plants and their growing conditions.

Interactios could be observed between the soil type and moisture. Regeneration occurring on postglacial sand-gravel had poorer health compared to other soil types. However, this negative effect was mitigated at moister sites where larger and more abundant regeneration was observed. This pattern suggests that the high drainage capacity of sandy soils may reduce moisture availability for the plants, and diminish their capacity to response effectively to infection. This observation aligns with previous sutides indicating that ash dieback severity is often associated with site moisture conditions (Havrdova at al. 2017; Keßler et al., 2012; Koltay et al., 2012). Due to the limited sample size and representation of this specific soil in the dataset, this relation needs to be investigated closer.

It's important to note that the soil data utilized in this study were derived from an online database rather than on-site measurements, which may not capture the fine-scale variability necessary for detailed analyses. Earlier mentioned limitations such as the facy that there were only a few observations for each soil type, as well as, there there was no data about the humus layer which could significantly influence the water retention and the moisture availability to the pathogen on fallen rachises from the previous year in the leaf litter. Future research should incorporate direct soil sampling and assessments of organic layer depth to better understand these dynamics. Nevertheless, this method still serves as a useful tool for broad-scale planning and site assessment purposes.

Contrary to expectations, soil moisture alone had a small effect on sapling health in this study. This may be attributed to the limited gradient of moisture within the dataset, which included only mesic or mesic-moist sites. The subtle differences between these categories, such as the presence of standing water all year versus standing water periodically, may not have been sufficient to detect significant effects. Expanding the number of sites to include a bigger gradient in soil types and moisture categories might produce better insights.

Conclusion

Natural regeneration around healthy, disease-tolerant ash trees may serve as a possible option for restoring ash in the landscape. While the there is large potential in the natural regeneration, this study highlights that environmental and site factors may well affect the success and health of natural regeneration under the pressure of ash dieback.

The results of this study point to several promising directions for future research. For example: soil water holding capacity, assessing the effect of the length of the vegetative period (using more detailed temperature data), the presence of late frost, browsing by herbivores, insect damage, as well as competition form understory that could influence the development of ash dieback in the natural regeneration.

Collectively, these findings offer us a glimpse into the complexity of the interactions between abiotic conditions and disease dynamics which are a part of every forest disease epidemic. The actuality of it only highlights forest ecosystems and their multitude of dependencies. Furthering the knowledge and filling the gaps in that area will be crucial to developing effective forest restoration strategies and preserving Europe’s biological diversity

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Popular science summary

The European ash (*Fraxinus excelsior*) is a tree of significant cultural and biological importance in Europe. In past years, its population has been declining due to a disease known as ash dieback. It is caused by a fungus from Asia, *Hymenoscyphus fraxineus*, which causes the shoots of the trees to wilt and often leads to the death of the entire plant. For that reason, the stability and existence of ash in the landscape of Europe are in danger.

In this study, we inventoried 27 sites from an existing database of 1300 trees that show signs of resistance, so to put it simply, are less sick than their neighbours. The selection was based on the presence of at least one tree showing signs of resistance to the disease and its distribution in Sweden. Around each selected tree, we established eight circular sample plots of 2,78 m with centres located 8 and 20 meters away in the cardinal directions. In each plot, we counted the number of naturally regenerated seedlings, higher than 25 cm, and categorised them into three size strata, six health classes (from no symptoms of disease to dead) and three stem forms. Later data about the site properties was extracted from online databases.

The purpose of the study was to analyse the status of the potential offspring of ash trees showing signs of tolerance. It is done to consider their potential for tolerance, as well as to get a better understanding of the joint effects of the disease and other environmental and site factors on ash natural regeneration under the pressure of the disease.

It was found that the natural regeneration surrounding ash trees selected for tolerance showed differences between sites. The disease severity of the three size strata differed from each other, with trees higher than 4m exhibiting significantly worse health. The stem form, so the number of dominant topshoots, on the examined trees was found to be influenced by the disease severity.

These findings offer us a glimpse into the complexity of the interactions of the disease development and site conditions in the field. Pointing to how complex the mechanisms and processes of resistance are and how much more knowledge is needed to introduce successful programs of restoration for the ash population.

Appendix 1

Table 8 List of recorded species on all the established plots with percentage of woody species to ash marked as competition

No.	Location	Tree species	Understory species	Competition [%]*
12	Björnhult	*Alnus spp., Prunus padus, Betula pubescens, Corylus avellana, Acer platanoides, Quercus spp., Sorbus acuparia, Betula pendula, Sorbus intermedia, Picea abies, Prunus avium, Acer pseudoplatanus, Salix caprea*	*Oxalis acetostella, Fragaria vesca, Rubus idaeus, ,Geum urbanum , Anemone nemorosa, Equisetum arvensis*	32
10	Bondberget naturreservat	*Populus tremula, Prunus padus, Betula pubescens, Ulmus spp., Sambucus racemosa, Sorbus acuparia, Betula pendula, Picea abies, Prunus avium*	*Rubus idaeus, Anemone nemorosa*,	74
25	Bornholm Östra Sörby 5:2	*Populus tremula, Prunus avium, Salix caprea, Alnus incana, Corylus avellana, Acer platanoides, Quercus spp., Sorbus*	*Rubus idaeaus, Rubus fruticosus ,Filipendula ulmaria, Euonymus europaeus, Prunus padus*	15

		acuparia, Betula pendula		
8	Halmstad Stjärnap	*Corylus avellana, Prunus padus, Fagus sylvatica, Tilia cordata, Quercus spp., Alnus spp., Sambucus nigra, Ulmus spp., Prunus padus, Sorbus acuparia, Frangula alnus, Acer platanoides*	*Rubus idaeus, Geum urbanum, Impatiems glandulifera*Ribes nigrum, *Juncus effuscus, Aegopodium podagraria*	42
22	Höganäs	*Prunus padus, Sambucus nigra, Ulmus spp., Corylus avellana, Acer pseudoplatanus*	*Impatiens parviflora, Urtica dioica, Geum urbanum, Granuim robertianum, Fragaria vesca, Ribes nigrum,ribes uva-crispa, Rubus idaeus*	87
3	Hörby Rugerup 1-4	*Populus tremula, Fagus sylvatica, Grey Alder, Crataegus spp., Quercus spp., Sorbus acuparia, Picea abies*	*Pteridium, rubus idaeus,Geum urbanum, Oxalis acetostella, Anemone nemorosa,Filipendula ulmaria*	82
23	Hörby Skäpperöd	*Fagus sylvatica, Betula pubescens, Sambucus nigra, Quercus spp., Sorbus acuparia, Betula pendula, Picea abies*	*Impatiens parviflora, Gallopsis tetrahit, ferns, Geranium robertianum,Urtica dioica, Galium aparinum, Filipendula ulmaria*	76
6	Hörby viggarum 1:2	*Betula pendula, Prunus spinosa, Quercus spp.,*	*Juncus effuscus,Oxalis acetostella, Anemone*	88

		Sambucus racemosa, Sorbus acuparia, Picea abies	*nemorosa,Lysimachia europaea Rubus idaeus, Aegopodium podagraria, Geranium robertianum, Vaccinium myrtillius, Geum urbanum, Urtica dioica Ferns ,galium odoratum , Equisetum sylvaticum, Veronica oficinalis*	
16	Hösås Reserve	*Alnus spp., Crataegus spp., Corylus avellana, Acer platanoides, Sorbus acuparia, Salix caprea, Betula pendula, Picea abies,*	*Viburnum opulus, Paris quadrifolia, Filipendula ulmaria*	12
24	Ivösjön	*Sambucus nigra, Ulmus spp., Alnus incana, Crataegus spp., Corylus avellana, Betula pendula*	*Geum urbanum, Geranium robertianum, Rubus ideaeus, Aliari petiolata,glechoma hederacea, Ribes uva-crispa, Stachys sylvatica*	32
13	Kungsgälv Torsby 1:8	*Alnus spp., Ulmus spp., Sorbus acuparia, Betula pendula*	*Filipendula ulmaria, Urtica dioica, Geum urbanum*	26
5	Kävlinge 34:19	*Sambucus nigra, Carpinus betulus, Acer platanoides, Prunus avium,*	*Cornus mas, Cornus sanguinea, Ribes nigrum, Geum urbanum*	92
7	Laholm Uddekulla 1:1	*Betula pendula, Prunus padus, Betula pubescens, Alnus incana, Corylus avellana,*	*Anemone nemorosa, Ribes nigrum,Juncus effuscus, Oxalis acetostella, Rubus idaeus*	51

		Quercus spp., Sorbus acuparia, Prunus avium, Acer pseudoplatanus		
18	Lönnskog Smedjebacken	*Populus tremula, Prunus padus, Juniperus communis, Acer platanoides, Sorbus acuparia, Picea abies*	*Rosa canina*	30
1/2	LUND DALBY 60:33	*Ulmus spp., Crataegus spp., Corylus avellana, Fagus sylvatica, Carpinus betulus, Acer platanoides*	-	25
1/2	LUND DALBY 60:33	*Ulmus spp., Crataegus spp., Corylus avellana, Fagus sylvatica, Carpinus betulus, Acer platanoides*	-	25
27	Mörbylånga LillaVickleby 4:1	*Crataegus spp., Corylus avellana, Quercus spp., Sorbus acuparia, Betula pendula*	*Viburnum opulus, Viola reichenbachiana, Euonymus europaeus*	26
11	Nyköping Svarta gård 2:1	*Ash, Betula pendula, Prunus spinosa, Crataegus spp., Quercus spp., Sorbus acuparia, Picea abies*	*Prunus spionsa bushes, Fragaria vesca, Dehampsia flexuosa, Dactylis glomerata, Peucedanum oreoselinum, Campanula persicifolia, Geum*	16

			urbanum, Rosa canina	
4	Ortofta	*Sambucus nigra, Ulmus spp., Corylus avellana, Acer platanoides,*	*Aegopodium podagraria, Rubus idaeus*	11
17	Säffle gillberga-torp 1:14	*Alnus spp., Populus tremula, Betula pubescens, Ulmus spp., Crataegus spp., Corylus avellana, Salix caprea, Betula pendula, Picea abies*	*Frangula alnus, Pteridium aquilinus, Geum urbanum, Rubus idaeus, Paris quadrifolia*	58
14	Tidaholm strakaskogen 1:1	*Alnus spp., Populus tremula, Prunus padus, Betula pubescens, Corylus avellana, Tilia cordata, Tillia platyphyllos, Acer platanoides, Quercus spp., Sorbus acuparia, Picea abies, Sorbus intermedia, Prunus avium*	*Aegopodium podagraria, Paris cuatrifolia, Geum urbanum,Rubus idaeaus, Cirsium oleraceum*	26
19	Uppsala Enköping	*Populus tremula, Prunus padus, Betula pubescens, Amelanchier spp., Acer platanoides, Quercus spp., Poplar, Sorbus acuparia, Betula pendula, Picea abies, Salix alba*	*Rubus idaeus, Filipendula ulmaria, Fragaria vesca, Geum urbanum, Galium aparine*	42

21	Uppsala Tämnaren	*Prunus padus, Betula pubescens, Ulmus spp., Alnus incana, Acer platanoides, Quercus spp., Sorbus acuparia, Picea abies*	*Fragaria vesca, Rubus idaeus, Dryopteris ferns, Frangula alnus, Oxalis acetostella, Cardamine impatiems, Paris quadrifolia*	22
20	Uppsala Vildökens	*Populus tremula, Prunus padus, Corylus avellana, Acer platanoides, Quercus spp., Sorbus acuparia, Picea abies*	*Filipendula ulmaria, Lonicera xylostemum, Rubus idaeus, Ribes alpinum, Viburnum opulus*	31
26	Värnamo Svensbygd 1:3	*Populus tremula, Prunus padus, Betula pubescens, Ulmus spp., Salix caprea, Corylus avellana, Acer platanoides, Quercus spp., Betula pendula, Picea abies, Prunus avium*	*Anemone nemorosa, Fragaria vesca*	97
9	Vaxjo Borlanda 5:13	*Populus tremula, Prunus padus, Sambucus nigra, Corylus avellana, Acer platanoides, Quercus spp., Sorbus acuparia, Pyrus pyraster*	*Urtica dioica, Geum urbanum, Dryopteris spp., Rubus idaeus, Polypodium vulgare*	14
15	Örebro Vintrosa	*Prunus padus, Ulmus spp., Betula pendula*	No species presesnt	87

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