Large herbivores and fire shape divergent woody assemblages in temperate wood-pasture

Experimental effects of large herbivores and fire on the survival of ten temperate woody species in southern Sweden

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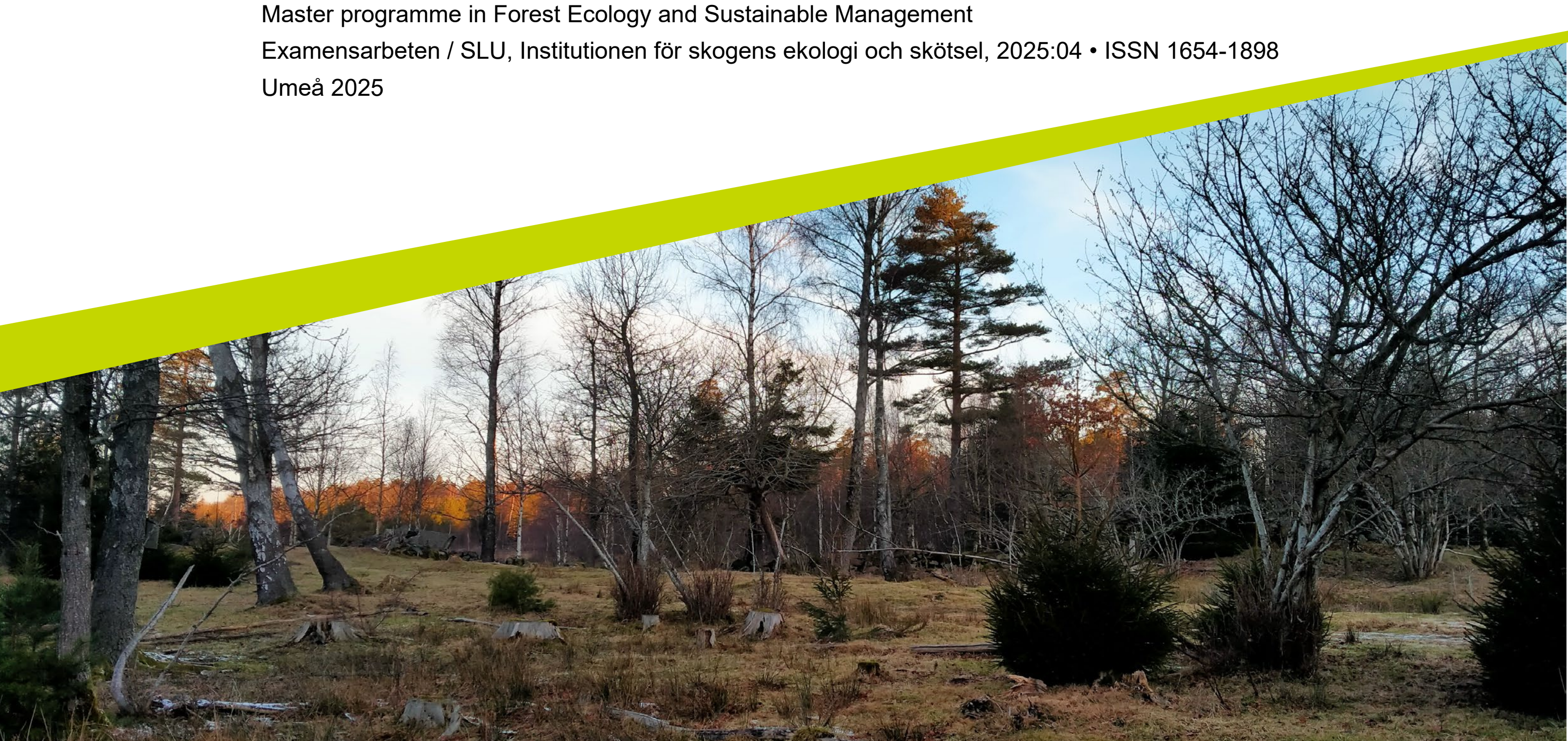

Large herbivores and fire shape divergent woody assemblages in temperate wood-pasture. Experimental effects of large herbivores and fire on the survival of ten temperate woody species in southern Sweden.

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Preface

Ever since I started my bachelor's degree in Forest and Nature Management in the Netherlands, I learned about how to remove topsoil, mow vegetation and remove woody species for the sake of biodiversity conservation. It seemed like the majority of species in temperate Europe could not maintain sustainable populations without anthropogenic intervention. Natural processes that drove ecosystem dynamics mainly occurred in remote and pristine areas, not in densely populated temperate Europe. Therefore, I wanted to learn more about what would happen when human intervention ceased in our parts of the world and decided to conduct research in the Dutch strict forest reserve programme. Although the forests were beautiful, all openness in the landscape had disappeared. Consequently, I soon realised that flowering plants, shrubs and pollinators were largely absent from the reserves. I noticed that saplings were being eaten by large herbivores, but no attention was paid to the effects of browsing on the young trees. Hence, I decided to study the effects of grazers such as European bison, horse and cattle on the establishment of woody species in a Dutch grassland mosaic. While some trees and shrubs managed to establish and survive in this grazed landscape, it was evident that the area remained largely open due to the activity of large herbivores. Now, everything finally fell into place. Human intervention such as removing woody species and mowing were not necessary to conserve biodiversity that depended on open conditions. Instead, large herbivores that once roamed Europe were able to create and maintain openness in temperate European ecosystems. Human intervention in semi-open nature reserves is mostly a substitute for the absence of these animals in our temperate ecosystems, where many species have co-evolved with large herbivores. From that point onwards, I was sure that I wanted to dedicate my career to the restoration of our ancient, grazed landscapes.

Therefore, I am deeply grateful to my supervisor Mats Niklasson that he was willing to offer me a chance to write my thesis on the effects of large herbivores on temperate woody species in Sweden. Additionally, he learned me a great deal about the role of fire as a driver of openness in temperate European ecosystems. Thanks for initiating this experiment, good conversations, valuable feedback, laughter and a chance to work at Nordens Ark during the summer. Even though I was quite late with my request and you already had a full agenda. Thereafter, I want to thank Vikki Bengtsson to put me in touch with Mats. Also, I want to thank Karin Amsten for laying the foundation for my research, providing me with everything I needed to carry out my fieldwork and for driving me around on a quad through the ecopark to check for errors in the field. Moreover, thanks to Sara Evaldsson for helping me out with the fieldwork and keeping me sharp. Further, I want to thank my former colleagues at ARK Rewilding the Netherlands for contributing to my understanding of grazing. Additionally, I want to thank John and Marita. You know that without your support, this work wouldn´t have been possible. Last but not least, I want to thank my partner, Ruby, for allowing me to pursue a master´s degree, always supporting me unconditionally and taking on the adventure of moving to Sweden together. Thank you for everything.

Abstract

In temperate Europe, the regrowth of open and semi-open habitats poses a threat to biodiversity, including the survival of light-demanding woody species. This study examines whether large herbivores and fire, individually and in combination, can reduce the survival of ten temperate woody species and thus create and maintain openness in the landscape. Additionally, it investigates whether woody species respond differently to large herbivores and fire regarding survival. Here, the survival rate of 4,800 planted saplings is evaluated in a full-factorial experiment. This study shows that the survival of nearly all tested trees and shrubs was significantly reduced by both large herbivores and fire, individually and in combination. The results indicate that large herbivores and fire not only may create and maintain openness but are also able to shape divergent woody species assemblages in temperate European ecosystems. Species with a significantly higher survival rate in the large herbivore treatment compared to the fire treatment are *Picea abies*, *Carpinus betulus*, *Fagus sylvatica* and *Prunus spinosa*. In contrast, *Betula pendula*, *Quercus robur*, *Tilia cordata*, *Corylus avellana* and *Viburnum opulus* have a significantly higher survival rate in the fire treatment. Hence, the survival rates between the two treatments significantly differed for all species except *Pinus sylvestris*. The results may also be compared to recent palaeoecological studies, which indicate that *Quercus robur* and *Corylus avellana* were also prevalent in the presumably large herbivore-driven last interglacial. This anomaly can be explained by the difference between planting saplings in the experiment and the natural recruitment process of these species in landscapes shaped by large herbivores. Consequently, the aforementioned species can also be a part of woody species assemblages in large herbivore dominated ecosystems. In conclusion, this study provides experimental understanding of how large herbivores and fire shape semi-open wood-pasture conditions, resulting in different woody species assemblages.

Keywords: large herbivores, fire, wood-pasture, survival of temperate woody species, Scandinavia, rewilding

Table of contents

List of figures

1. Introduction

Open and semi-open habitats host many species that demand light conditions to survive, but regrowth of formerly open habitats is a threat to the survival of these species in temperate Europe (Svenning 2002). In Sweden, wood-pastures and grasslands are among the most species-rich habitats and contain several red-listed species (Sandström et al. 2015). Within the scope of this study, it is important to note that light-demanding woody species such as hazel and oaks are dependent on semi-open and open conditions (Bobiec et al. 2018, Vera 2000).

Whether the natural vegetation of temperate Europe was dominated by closed canopy forest or semi-open and open conditions is subject to scientific debate (Mitchell 2005, Peterken 1996, Svenning 2002, Vera 2000). The perception that the monoclimax vegetation in temperate Europe is characterized by closed canopy forest, controlled by climatic factors and interspecies competition between woody species, is long held (Clements 1916, Ellenberg 1988). In this perceived closed canopy forest of temperate Europe, open conditions were seen as a result of agricultural practises such as livestock grazing and burning. However, Tansley (1935) partly rejected Clements´ theory by stating that livestock pasturing could lead to an alternative climax vegetation of grass- and heathlands. Nevertheless, Tansley (1935) stated that the effect of livestock had no natural equivalent.

Vera´s wood pasture hypothesis challenged this view (Vera 2000), where grazing by large herbivores like European wild horse (*Equus ferus*), aurochs (*Bos primigenius*) and European bison (*Bison bonasus*) is mentioned as a key process that sustained light-demanding woody species before the dawn of agriculture in Europe (Vera et al. 2006). In southern Sweden, wild horse, aurochs and European bison have also occurred during the Holocene (Sommer et al. 2011, Rosengren et al. 2024). In these dynamic open habitats and light woodlands, light-demanding woody species can develop viable populations. Without this dynamic nature of ecosystems, light-demanding woody species would be outcompeted by shade-tolerant species and gradually disappear from the landscape (Vera 2000). In addition to large herbivores, fire is mentioned as a driver of openness in temperate Europe that could probably maintain the diversity of light-demanding woody species, at least in upland forests (Svenning 2002).

Trees and shrubs that occur in ecosystems which are controlled by climatic factors and interspecies competition between woody species for resources were termed ´green world´ trees by Bond (2005). Additionally, ´brown´ and ´black world´ trees can be distinguished in ecosystems that are controlled by large herbivores and fire respectively (Bond 2005). Woody species in temperate Europe are traditionally regarded as green world trees, which aligns with the long-standing perception of closed canopy forests (Clements 1916, Ellenberg 1988). However, it is recently argued that the framework of brown world trees can be extended into temperate European ecosystems (Churski et al. 2017). Since alternative growth forms in European woody species can be activated in response to herbivory, enhancing survival when large herbivores are present, certain species that are traditionally regarded as green world trees may also function as brown world trees (Churski et al. 2024). Both chemical and structural defences such as spines, thorns and dense cage structures are traits of brown world trees that can increase the survival of woody species in ecosystems controlled by large herbivores (Charles-Dominique et al. 2017, Wigley et al. 2018). Much less is known about the effects of fire on temperate woody species and whether it can lead to black world ecosystems in temperate Europe. Although fire-related traits such as bark thickness and resprouting do exist in genera that occur in temperate Europe as well, for example in *Quercus* and *Pinus* (Keeley et al. 2011, Pausas 2015). In reality, ecosystems and the woody species within may exhibit components of both green, brown and black worlds (Bond 2005, Churski et al. 2017). Earlier experiments have indicated that the effects of both large herbivores and fire can lead to reduced survival in woody species in temperate Europe (Amsten et al. 2021). Especially in young or small-sized individuals that are located within the browse and fire traps (Staver et al. 2014, Knapp et al. 2022). However, plants have varying strategies to cope with large herbivores and fire.

Firstly, the avoidance strategy is employed to avoid the disturbances caused by large herbivores and fire. It is described as the ability to reduce being consumed by herbivores or fire, through for example low palatability and flammability (Hodgson & Illius 1996). Another example would be to invest in quick growth to avoid the browse and fire traps (Pearce et al. 2025). Secondly, traits are developed against large herbivores and fire if the resistance strategy is employed (Archibald et al. 2019). Here, plants can persist and reproduce in the presence of disturbances (Hodgson & Illius 1996). It is the ability of a plant to protect itself from large herbivores and fire and it ranges from preventing the loss of leaves to preventing death. Structural defences such as thick bark and spines are examples of resistance (Archibald et al. 2019). Additionally, the formation of cage structures can be viewed as resistance (Churski et al. 2024). Lastly, the tolerance strategy can be employed where species are able to recover after disturbances by developing new shoots from the base or stem (Archibald et al. 2019).

Europe has experienced extensive defaunation processes in the late Quaternary that were likely driven by modern humans (Davoli et al. 2024). However, from the Neolithic onwards, livestock partly substituted wild large herbivores (Pärtel et al. 2005). Primitive breeds of cattle and horse were even herded year-round until the Bronze Age in Sweden (Ekstam & Forshed 2000). Moreover, breeds such as the Gotland pony are still able to graze outside year-round without supplementary feeding in Sweden (Garrido et al. 2019). The practise of year-round grazing with large herbivores that have naturally occurred in Europe is known as trophic rewilding. The practice of rewilding is described as restoring the food web at all trophic levels and simultaneously minimize anthropogenic intervention (Carver et al. 2021). Rewilding with large herbivores can be an efficient approach to restore temperate wood-pasture, although grazing refuges are key for survival of woody saplings and thus for the emergence of wood-pasture (Smit et al. 2015). Large herbivore refuges might however be a more appropriate term since large herbivores impact the survival of woody species in more ways than merely through browsing or herbivory, namely by trampling and debarking (Cornelissen et al. 2014, Smit et al. 2015). Vera describes all of the woody species that are included in this study as being able to survive in wood-pasture, except Norway spruce (Vera, 2000). However, Norway spruce is able to survive in Fennoscandian wood-pasture (Oldén et al. 2017).

The effect of fire on temperate European ecosystems is largely unknown with the exception of conifer-dominated areas (Leys et al. 2018, Niklasson et al. 2010). Lightning-caused fire ignitions are part of the natural ecosystem in southern Sweden today, although occurring at a lower frequency than human-caused fire ignitions (Granström 1993). However, fire regimes in early to mid-Holocene temperate Europe are not well known and argued to be primarily linked to Mesolithic hunter-gatherers (Feurdean et al. 2019, Gauthier et al. 2021). Others state that fire is not a natural part of ecosystems in temperate Europe, including in grasslands (Ruprecht et al. 2013). Nevertheless, temperate European woody genera do react differently to fire and have therefore been divided into three classes of fire sensitivity. Here, *Pinus* and *Betula* are classified as fire adapted or favoured. Fire tolerant genera include *Fagus*, *Quercus*, *Corylus*, and *Carpinus*. Lastly, *Picea* and *Tilia* are deemed intolerant to fire (Molinari et al. 2020).

In a recent experiment, the combined effects of large herbivores and fire did not reduce survival further compared to large herbivores alone, indicating fuel load reduction (Amsten et al. 2021). Indeed, large herbivores are able to reduce fuel loads and even supress fires (Pringle et al. 2023, Rouet-Leduc et al. 2021). However, herbivory and fire combined differ from herbivory in the effect on stem reduction in temperate North American oak woodlands (Beebe et al. 2024).

Palaeoecological data can be used to gain insight into how large herbivores and fire, as driving forces of openness, affected the survival of temperate woody species in past ecosystems. Recent studies from the previous interglacial and the early to mid-Holocene, suggests that temperate Europe was dominated by open areas and light woodlands with abundant disturbance tolerating plants. Drivers of openness in the landscape were weakly related to climatic influences and stronger to disturbances, likely caused by large herbivores (Pearce et al. 2023). In the early to mid-Holocene, the combination of predominantly open habitats and light woodlands were more abundant in comparison with the last interglacial (Pearce et al 2023). Even though defaunation processes led to less disturbance and biomass consumption from large herbivores. It is therefore hypothesized that anthropogenic fire might explain the increased openness of early to mid-Holocene temperate ecosystems compared to the last interglacial, directly through fire ignition and indirectly through an increase in biomass due to defaunation processes (Pearce et al 2023, Gauthier et al. 2021). In support of this view, studies show that some fire-sensitive trees were almost twice as abundant in the last interglacial compared to early to mid-Holocene (Pearce et al. 2024). Additionally, no beetles were found with an adaptation to fire in the last interglacial in Great Britain. Whilst almost one out of ten beetle species in early Holocene Great Britain show an adaptation to fire (Sandom et al. 2014). Possibly, fire has driven the occurrence of fire-tolerant species such as oak, hazel and hornbeam in the early to mid-Holocene. However, they were less common compared to the previous interglacial (Pearce et al. 2023). Although the aforementioned species are tolerant to fire, they are not deemed adapted to fire (Molinari et al. 2020). Therefore, it is hypothesized that high levels of large herbivores resulted in a higher abundance of oak, hazel and hornbeam during the last interglacial compared to the early to mid-Holocene. The lower abundancy of these species in the Holocene might be explained by a higher fire occurrence (Pearce et al. 2023).

In earlier studies, the reconstruction of past temperate European wooded ecosystems based on pollen analysis is however met with criticism by Vera (2000). It is argued that correction factors of absolute tree pollen are drawn up and interpreted in a way that confirm the theory that temperate Europe was covered by closed canopy forests (Vera 2000). The effects of large herbivores and fire on the survival of temperate European woody species can therefore not be understood directly by pollen analysis. However, full-factorial experiments can offer insights. Although experiments are very few in temperate European conditions, some woody species in our experiment have been part of such experiments. Even so, one such experiment only includes the effects of large herbivores and is tested in closed forests and gaps, as opposed to in wood-pasture (Churski et al. 2017).

The following ten woody species are included in this study: silver birch (*Betula pendula*), Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), pedunculate oak (*Quercus robur*), small-leaved lime (*Tilia cordata*), common hornbeam (*Carpinus betulus*), common beech (*Fagus sylvatica*), hazel (*Corylus avellana*), blackthorn (*Prunus spinosa*) and Guelder rose (*Viburnum opulus*). Hereafter, these species are referred to by their genus name only. In Amsten et al. 2021, the survival rates of *Betula*, *Pinus*, *Picea*, *Quercus* and *Tilia* in wood-pasture are only recorded in the first three years after planting. Due to ongoing impact by large herbivores and fire, the results after a ten-year period might differ considerably. Moreover, it is unknown how large herbivores and fire affect the survival of *Carpinus*, *Corylus*, *Fagus*, *Viburnum* and *Prunus* in wood-pasture regardless.

2. Aim of study

This study aims to examine how saplings of ten woody species that occur in temperate Sweden are affected by large herbivores, fire and the combination of large herbivores and fire in terms of survival. Thereby, insights can be gained in how large herbivores and fire act as drivers of openness by reducing the survival of ten woody species in temperate wood-pasture. The saplings in the large herbivore treatment are impacted by cattle and extant wild herbivores, which extends beyond herbivory and also includes trampling and debarking. Saplings in the fire treatment are subject to prescribed burning in grass-dominated wood-pasture conditions. Lastly, the combined treatment is subject to both large herbivores and fire. The effects of large herbivores, fire and the combination on the survival of the first set of species are examined after 10 years and includes *Betula*, *Pinus*, *Picea*, *Quercus* and *Tilia*. The second set of species is examined after 7 years and includes *Carpinus*, *Corylus*, *Fagus*, *Viburnum* and *Prunus*. The research questions are:

I. Do large herbivores, fire and the combination of large herbivores and fire reduce the survival of woody species in a temperate wood-pasture?

II. Does the survival of woody species vary between treatments: large herbivores, fire and the combination of large herbivores and fire in a temperate wood-pasture?

III. Does the survival of *Betula*, *Pinus*, *Picea*, *Quercus* and *Tilia* vary within each of the four treatments: control, large herbivores, fire and the combination of fire and large herbivores in a temperate wood-pasture after 10 years?

IV. Does the survival of *Carpinus*, *Corylus*, *Fagus*, *Viburnum* and *Prunus* vary within each of the four treatments: control, large herbivores, fire and the combination of fire and large herbivores in a temperate wood-pasture after 7 years?

3. Materials and methods

3.1 Study area

The Ecopark of Nordens Ark (ENA) belonged to Åby manor and is located in the historical landscape of Bohuslän, part of the county of Västra Götaland. ENA is situated along the Åby fjord on the Swedish Westcoast (58°27′N 11°25′E), between Göteborg and Oslo (Figure 1). The total area of ENA covers 400 ha, whereof 100 ha of spruce plantations were cleared and restored to create wood-pasture in 2011 and 2012 (Amsten et al. 2021). The wood-pasture within ENA comprises four different corrals (Figure 1). These corrals are grazed by three different breeds of cattle, namely Fjällnära, Rödkulla and Herefordshire in densities varying from 1 to 2,5 individuals per hectare in the first year of the experiment. Similar densities were maintained throughout the experiment. However, limited variation in densities did occur due to practicalities of herd management such as sick individuals. The cattle are present in the corrals from May-June until September-October. Occasionally, low densities of sheep, goats and horses were present as well (Amsten et al. 2024). Additionally, extant free-living herbivores in the study area include roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), European elk (*Alces alces*), wild boar (*Sus scrofa*) and mouflon (*Ovis aries musimon*) (Amsten et al. 2021).

The site lies within the temperate region of Sweden and the average annual mean temperature in Bohuslän for the period between 1991-2020 is 8.0 °C. Whereof the warmest month is July with an average mean temperature of 17.1 °C and the coldest month is February with an average mean temperature of -0.1 °C (Sveriges meteorologiska och hydrologiska institut 2021a). The average annual mean precipitation in Bohuslän between 1991-2020 is 897 millimetres (Sveriges meteorologiska och hydrologiska institut 2021b). In the study area, acidic granite bedrock, more specifically Bohusgranite, is dominant and reaches the surface locally (Sveriges geologiska undersökning 2023a). Moraines do occur as well. Additional soil types that occur within the corrals are clay-silt and to a minor extent postglacial sand (Sveriges geologiska undersökning 2023b). Besides, estimated soil depths in the corrals varies from 0 metres on the bedrock to 20-30 metres in valleys (Sveriges geologiska undersökning 2023c).

Humans have been present in the study area for thousands of years, as indicated by the megaliths dating back to Neolithic times (Bradley & Philips 2008). The landscape was largely barren until the 19th century, including the rocky outcrops that are forested today (Fries 1958). Barren heathlands are still present in Southwestern Sweden today as well as former heathlands that were converted into conifer plantations. Livestock grazing, burning and tree removal have maintained these heathlands in historical times (Lindholm et al. 2019).

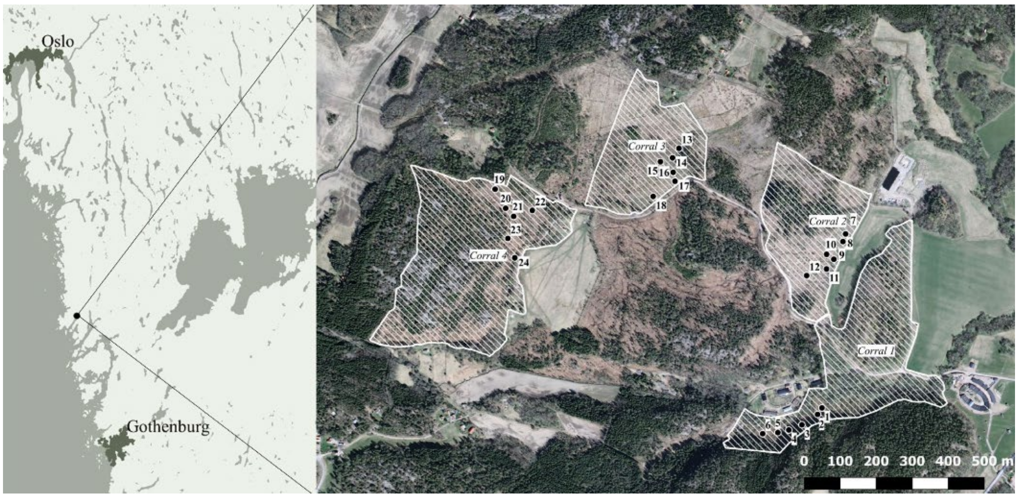

Figure 1. Location of study area in Sweden (left) and positions of corrals 1-4 and plots 1-24 in ENA (right). Modified from (Amsten et al. 2021:4106).

3.2 Experimental design

Two sets of species are part of the experiment. The first set is planted in 2015 and includes *Betula*, *Picea*, *Pinus*, *Quercus* and *Tilia*. The second set is planted in 2018 and consists of *Carpinus*, *Corylus*, *Fagus*, *Prunus* and *Viburnum*. Hence, the saplings within the first set have been subject to the experiment for ten growing seasons and the second set of species for seven growing seasons. The species of the first set had an average height that ranged from 20,9 centimetres for pine to 68,8 centimetres for birch during planting and were one to two years old during planting (Amsten et al. 2021). Height data were not published for the second set, but the species were the same age. For each of the two sets of species, 24 plots of 14 x 14 metres were randomly chosen. This equals 48 plots in total. All of these plots contain four subplots of 7 x 7 metres with different treatments (Figure 2): control – no fire and no herbivores (C), herbivores – no fire and herbivores (H), fire – fire and no herbivores (F) and fire & herbivores – fire and herbivores (FH). The control and fire treatment were fenced with a 2-metre-high fence, excluding all herbivores. In each subplot, all five species of a given set were planted in rows on random positions in equal numbers. Every subplot is planted with 25 saplings (Figure 2), which equals 4,800 planted individuals in total.

Natural regeneration of woody species was removed before the planting of saplings took place but was not continued after planting. Also, the fire and fire-herbivores treatments were subject to prescribed burning before planting in 2015 and 2018. Consequently, both sets of species were not subject to fire during the first year of planting. Drip torches are used to create low-intensity surface fires over the full length of these subplots. When the first line failed to ignite due to an insufficient fuel load, the process was repeated five times at a one metre interval. In contrast to the large herbivores, prescribed burning was not carried out consistently on an annual basis. The first set of species was not burned during 2021, 2022 and 2023 whilst the second set was not burned in 2024 and will not be burned in 2025 and 2026. This section is partly derived from (Amsten et al. 2021).

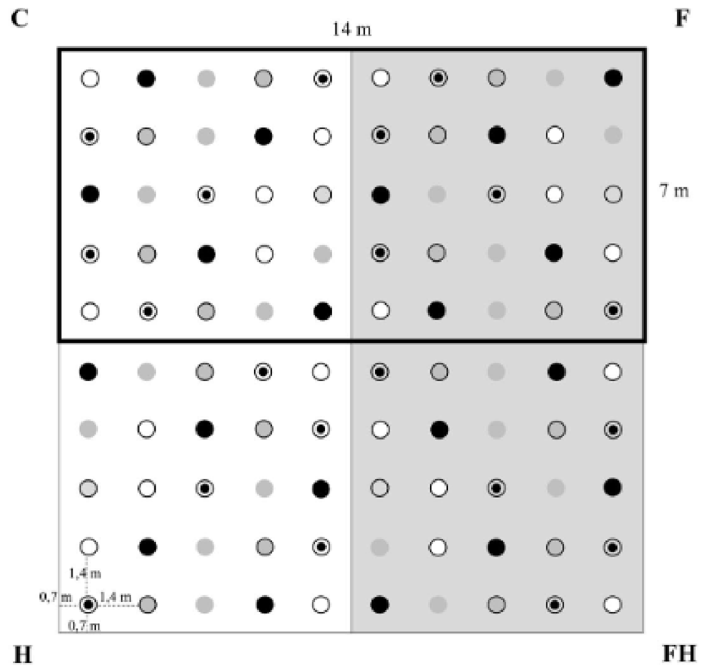

Figure 2. All 24 plot locations consist of two of the above pictured plots, situated at least partly against each other. One plot includes Betula, Picea, Pinus, Quercus and Tilia. The other plot includes Carpinus, Corylus, Fagus, Prunus and Viburnum. Every plot consists of four subplots: Control (C), Herbivores (H), Fire (F) and Fire Herbivores (FH). Saplings are positioned at 1.4 metres apart from each other. Modified from (Amsten et al. 2021:4106).

3.3 Data collection

The parameter status in relation to survival is recorded for all 4,800 planted saplings in the experiment. Three different categories could be chosen: alive, dead or gone. Saplings were granted the status alive when above-ground parts such as stems and buds were alive, even if only partly. The status dead was assigned to individuals when all above-ground parts were dead without signs of living buds and stems. If there were no traces of the individual to be found, the status gone applies. Large herbivores can trample saplings and pull saplings out of the soil, which can lead to the status gone. Saplings can also be destroyed by fire. Additionally, saplings can simply decay after mortality or become unrecognisable. Even so, individuals with the status gone were treated as dead in the analysis.

All rows where saplings have been planted were walked on to increase the chance of successfully detecting all individuals. The collection of data in the field is carried out on paper. Prepared field forms with the position of each sapling in a row were used during the fieldwork. The data is entered into Excel manually.

3.4 Data analysis

The data on survival was analysed by using Microsoft Excel 365 MSO version 2503. Subsequently, the Analysis Toolpak was downloaded via the Add-inns function in Excel. This allowed for the calculation of p-values by making use of the chi-square (χ^2) equation (Pandis 2016). The equation below has been performed in Excel to calculate the χ^2 value:

$$\chi^2 = \sum \frac{(O - E)^2}{E}$$

In this equation, the O stands for the observed value and the E for the expected value. Here, the expected value is calculated by the row total*column total/overall total (Pandis 2016). The χ^2 value and degrees of freedom (*df*) are thereafter used to calculate the p-value by using the CHISQ.DIST.RT function in Excel. The degrees of freedom were simply calculated by using the following formula: (r-1*c-1), where r stands for the number of rows and c for the number of columns (Pandis 2016). The variance in survival between treatments was analysed for all ten species: *Betula*, *Picea*, *Pinus*, *Quercus*, *Tilia*, *Carpinus*, *Corylus*, *Fagus*, *Prunus* and *Viburnum*. Additionally, the variance in survival between species was analysed within each of the four different treatments: control – no fire and no herbivores (C), herbivores – no fire and herbivores (H), fire – fire and no herbivores (F) and fire & herbivores – fire and herbivores (FH). This was done for the first and the second set of species separately, since the first set has been in the experiment for 10 years and the second set for 7 years. Therefore, the species cannot be compared to each other directly. This equals to 18 chi-square tests in total. For these tests, confidence levels of 95% were used ($p < 0.05$).

When the outcomes were significant, which all were, pairwise comparison post-hoc tests were performed to test for within group variance (Agbangba et al. 2024). The chi-square test was used for all post-hoc tests whenever possible. However, when expected values were below 5, post-hoc testing by using the chi-square test does not suffice and the Fisher´s exact test should be used instead (Kim 2017). Here, the Fisher´s exact test was used for 12 post-hoc tests with an expected value below 5. This included *Quercus* FH-H, *Tilia* FH-H and *Corylus* FH-H. In addition to *Betula-Pinus, Betula-Quercus, Betula-Tilia, Pinus-Quercus, Pinus-Tilia, Quercus-Tilia* in the fire & herbivore (FH) treatment of the first set of species. As well for *Quercus-Tilia* in the herbivory (H) treatment of the first set of species and *Carpinus-Corylus* and *Corylus-Viburnum* in the fire & herbivore (FH) treatment of the second set. Because Fisher´s exact test cannot be added into Excel, GraphPad was used instead (GraphPad 2025). Thereafter, the Holm-Bonferroni method was used to correct for the problem of multiple comparisons and thus to reduce type I errors or false-positives (Agbangba 2024).

4. Results

4.1 Survival of *Betula*, *Picea*, *Pinus*, *Quercus* and *Tilia* between treatments

The survival on species level for *Betula*, *Picea*, *Pinus*, *Quercus* and *Tilia* differed significantly between the four treatments: control (C), herbivores (H), fire (F) and fire & herbivores (FH) after 10 years (Table 1). Therefore, all species and treatment combinations were subject to post-hoc testing (Appendix 1).

Table 1. Differences in survival between treatments (Control, Herbivores, Fire, and Fire-Herbivores) for Betula, Picea, Pinus, Quercus and Tilia after 10 years. Results based on chi-square tests.

Species	χ^2	*df*	*p*-value
Betula	185.4259753	3	<0.001
Picea	125.745554	3	<0.001
Pinus	154.0558173	3	<0.001
Quercus	173.2580038	3	<0.001
Tilia	120.96	3	<0.001

Each of the three treatments herbivores (H), fire (F) and the combination of fire & herbivores (FH) significantly reduced the survival of all five woody species in comparison with the control (C) treatment (Figure 3).

As for the variation between treatments, *Picea* was the only species with a significantly higher survival in the herbivore (H) treatment compared to the fire (F) treatment. In contrast, all of the three deciduous species *Betula*, *Quercus* and *Tilia* had a significantly higher survival in the fire (F) treatment compared to the herbivore (H) treatment. The only exception was *Pinus*, where herbivores (H), fire (F) and the combination of fire & herbivores (FH) did not significantly differ from each other. Moreover, the fire & herbivores (FH) treatment did have an additional effect on the survival of the deciduous species in comparison with fire (F) and herbivores (H) as separate treatments. Whilst fire & herbivores (FH) had an additional significant reducing effect on the survival of *Betula*, *Quercus* and *Tilia* compared to fire (F) as a separate treatment, it only significantly reduced the survival of *Betula* and *Tilia* compared to herbivores (H) as a separate treatment (Figure 3).

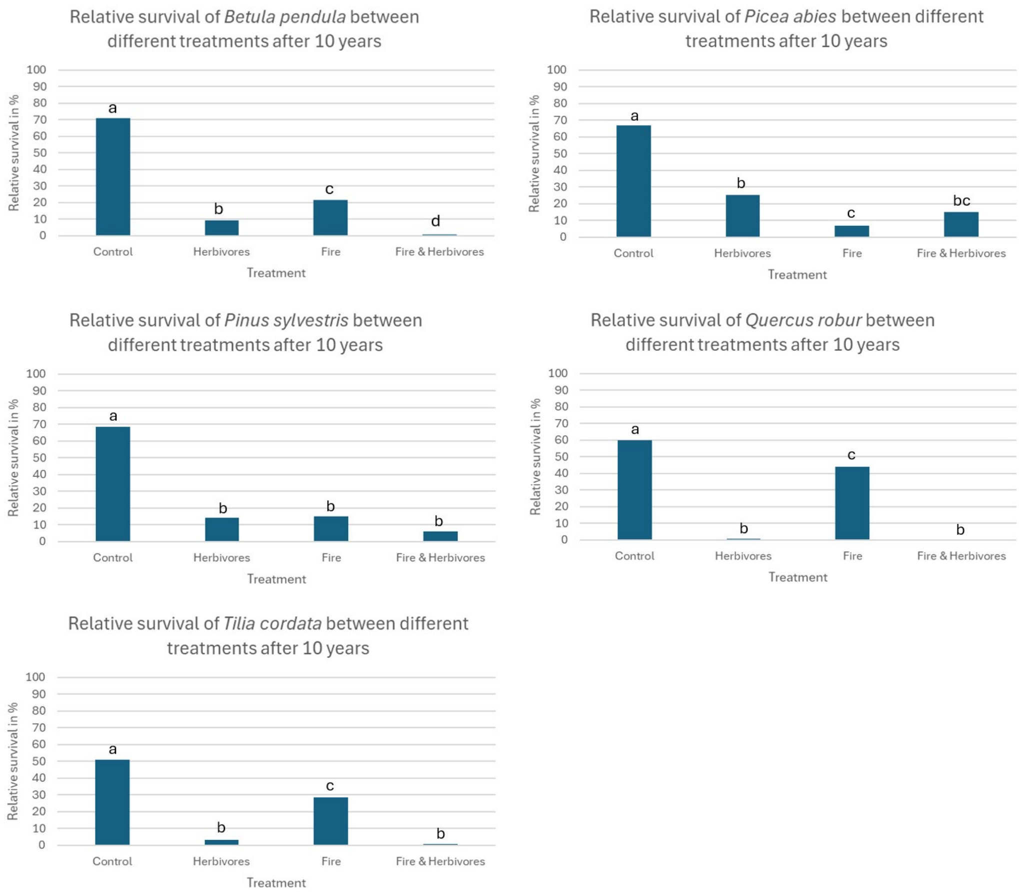

Figure 3. Relative survival between different treatments for Betula pendula, Pinus sylvestris, Picea abies, Quercus robur and Tilia cordata after 10 years (n = 120 individuals per species per treatment). Different letters represent significant differences.

4.2 Survival of *Carpinus*, *Corylus*, *Fagus*, *Prunus* and *Viburnum* between treatments

The survival on species level for *Carpinus*, *Corylus*, *Fagus*, *Prunus* and *Viburnum* differed significantly between the four treatments: control (C), herbivores (H), fire (F) and fire & herbivores (FH) after 7 years (Table 2). Hence, all species and treatment combinations were subject to post-hoc testing (Appendix 2).

Table 2. Differences in survival between treatments (Control, Herbivores, Fire and Fire-Herbivores) for Carpinus, Corylus, Fagus, Prunus and Viburnum after 7 years. Results based on chi-square tests.

Species	χ^2	*df*	*p*-value
Carpinus	56.57775026	3	<0.001
Corylus	163.0326994	3	<0.001
Fagus	90.81081081	3	<0.001
Prunus	48.70484784	3	<0.001
Viburnum	161.2155745	3	<0.001

With the exception of *Corylus*, all of the three treatments: herbivores (H), fire (F) and the combination of fire & herbivores (FH), significantly reduced the survival of all woody species in comparison with the control treatment (C). As for *Corylus*, the fire (F) treatment did not differ significantly from the control (C) treatment (Figure 4).

Regarding the difference between treatments, *Carpinus*, *Fagus* and *Prunus* had a significantly higher survival in the herbivore (H) treatment compared to the fire (F) treatment. On the contrary, *Corylus* and *Viburnum* showed a significantly higher survival in the fire (F) treatment compared to the herbivore (H) treatment. Additionally, fire & herbivores (FH) significantly reduced the survival of woody species in comparison with herbivores (H) and fire (F) separately. For *Viburnum*, fire & herbivores (FH) had an additional significant reducing effect on survival compared to both herbivores (H) and fire (F) individually. Moreover, fire & herbivores (FH) had an additional significant reducing effect on the survival of *Corylus* compared to fire (F) as a separate treatment, it significantly reduced the survival of both *Carpinus* and *Fagus* compared to herbivores (H) alone (Figure 4).

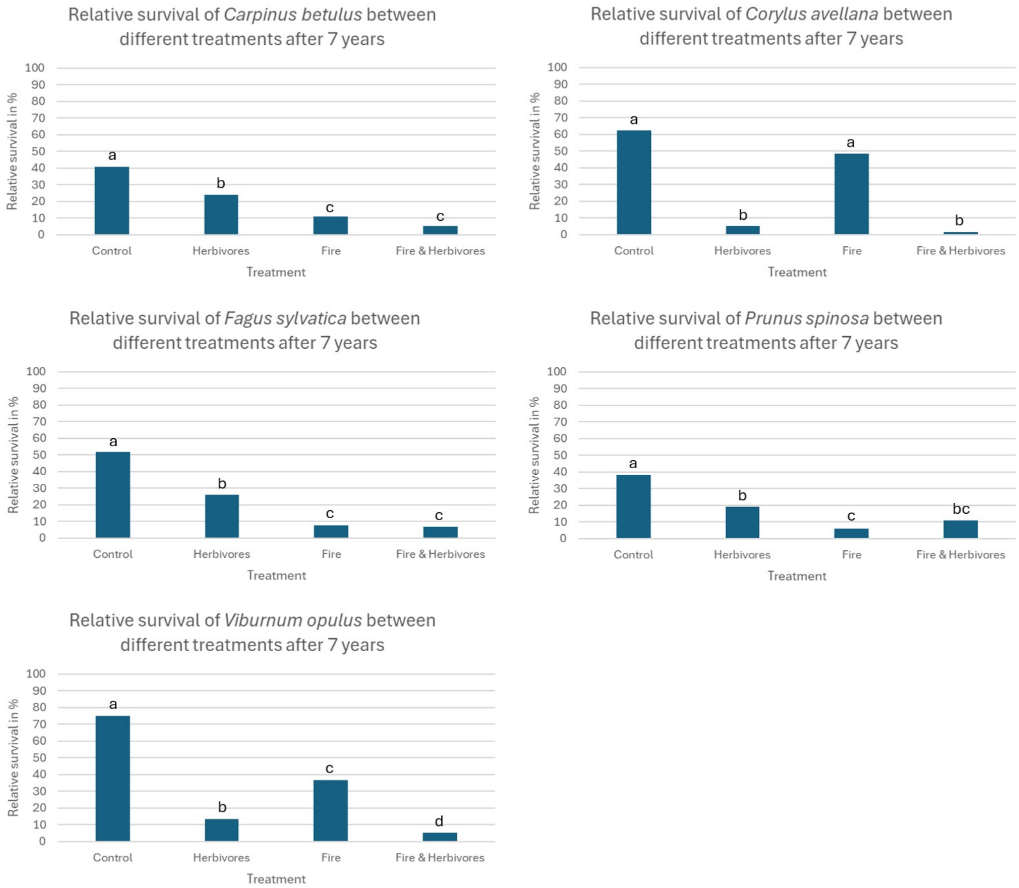

Figure 4. Relative survival between treatments for Carpinus betulus, Corylus avellana, Fagus sylvatica, Prunus spinosa and Viburnum opulus after 7 years (n = 120 individuals per species per treatment). Different letters represent significant differences.

4.3 Survival of *Betula*, *Picea*, *Pinus*, *Quercus* and *Tilia* within treatments

The survival on treatment level for *Betula*, *Picea*, *Pinus*, *Quercus* and *Tilia* differed significantly within the four treatments: control (C), herbivores (H), fire (F) and fire & herbivores (FH) after 10 years (Table 3). Thus, all species and treatment combinations were subject to post-hoc testing (Appendix 3).

Table 3. Differences in survival between species (Betula, Picea, Pinus, Quercus and Tilia) within the Fire-Herbivores, Herbivores, Fire and Control treatments after 10 years. Results based on chi-square tests.

Treatment	χ^2	*df*	*p*-value
Fire-Herbivores	44.44444444	4	<0.001
Herbivores	47.28207857	4	<0.001
Fire	54.5326862	4	<0.001
Control	13.42105	4	0.009392

The only significant difference within the control (C) treatment is observed between *Betula* and *Tilia*, where *Betula* has the highest survival rate and *Tilia* the lowest of all five species. While the survival of *Picea*, *Pinus* and *Quercus* did not differ significantly from both *Betula* and *Tilia* (Figure 5). Within the fire (F) treatment, *Quercus* had the highest survival, but did not differ significantly from *Tilia*. Simultaneously, *Tilia* showed no significant difference from both *Betula* and *Pinus*. Of all five species, *Picea* had the lowest survival rate. However, no significant difference was observed between *Picea* and *Pinus* (Figure 5). On the contrary, *Picea* had the highest survival rate in the herbivores (H) treatment and did not differ from *Pinus* here also. Further, no significant differences were observed between *Pinus* and *Betula* as well as between *Betula* and *Tilia*. The lowest survival rate is observed in *Quercus*, but did not significantly differ from *Tilia* (Figure 5). Lastly, the highest survival rate in the fire & herbivores (FH) treatment was observed in *Picea*. Here, *Picea* differed significantly from all deciduous trees. Whilst *Pinus* did not differ significantly from all other species within this set (Figure 5).

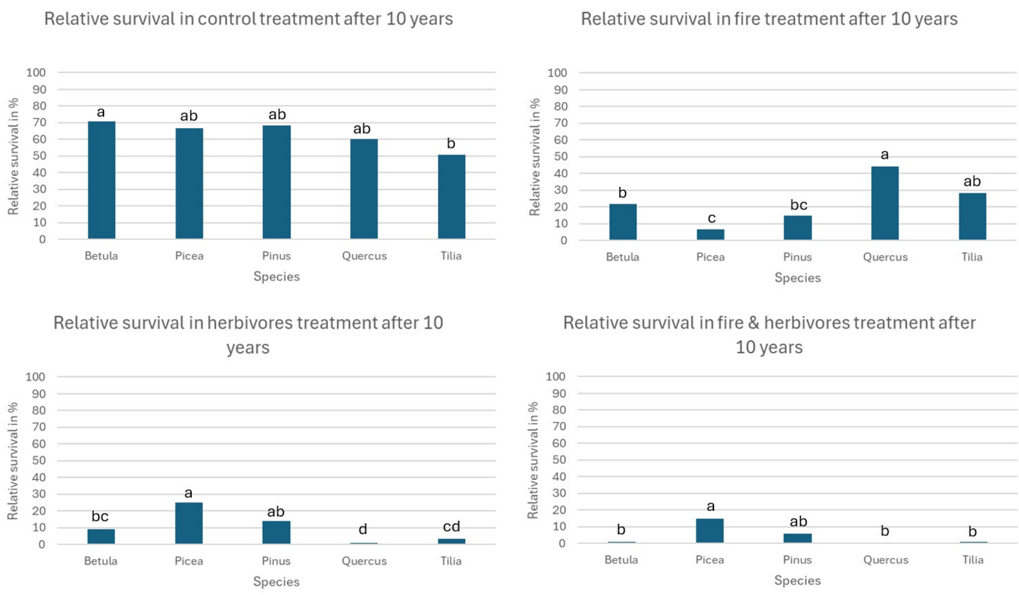

Figure 5. Relative survival within treatments for Betula pendula, Pinus sylvestris, Picea abies, Quercus robur, and Tilia cordata after 10 years (n = 120 individuals per treatment per species). Different letters represent significant differences.

4.4 Survival of *Carpinus*, *Corylus*, *Fagus*, *Prunus* and *Viburnum* within treatments

The survival on treatment level for *Carpinus*, *Corylus*, *Fagus*, *Prunus* and *Viburnum* differed significantly within the four treatments: control (C), herbivores (H), fire (F) and fire & herbivores (FH) after 7 years (Table 4). Consequently, all species and treatment combinations were subject to post-hoc testing (Appendix 4).

Table 4. Differences in survival between species (Carpinus, Corylus, Fagus, Prunus and Viburnum) within the Fire-Herbivores, Herbivores, Fire and Control treatments after 10 years. Results based on chi-square tests.

Treatment	χ^2	*df*	*p*-value
Fire-Herbivores	9.709229	4	0.045621
Herbivores	24.12698413	4	<0.001
Fire	105.8025033	4	<0.001
Control	45.21649761	4	<0.001

The control (C) treatment of the second set showed more differences between the species. Here, *Viburnum* had the highest survival rate but did not differ significantly from *Corylus*. Additionally, there was no significant difference in survival between *Corylus* and *Fagus*. The lowest survival has been observed in both *Carpinus* and *Prunus*, but they did not significantly differ from *Fagus* (Figure 6). No statistical difference was observed between *Corylus* and *Viburnum* in the fire (F) treatment as well, where *Corylus* had the highest survival rate. Both

Corylus and *Viburnum* did differ significantly from each of the other three species. Here, no significant differences were found between *Carpinus*, *Fagus* and *Prunus* (Figure 6). In contrast, the species with the lowest survival in the fire (F) treatment had the highest survival in the herbivores (H) treatment. Namely, *Carpinus*, *Fagus* and *Prunus*. Here, no significant differences were observed between *Carpinus*, *Fagus*, *Prunus* and *Viburnum.* Whilst a significant difference was found between *Corylus* on the one hand and *Carpinus*, *Fagus* and *Prunus* on the other, *Corylus* and *Viburnum* did not differ significantly (Figure 6). Lastly, *Prunus* had the highest survival rate in the fire & herbivores (FH) treatment. However, *Prunus* only differed significantly from *Corylus* which had the lowest survival rate within the treatment. Each of the other three species: *Carpinus*, *Fagus* and *Viburnum* did not differ significantly from both *Prunus* and *Corylus* (Figure 6).

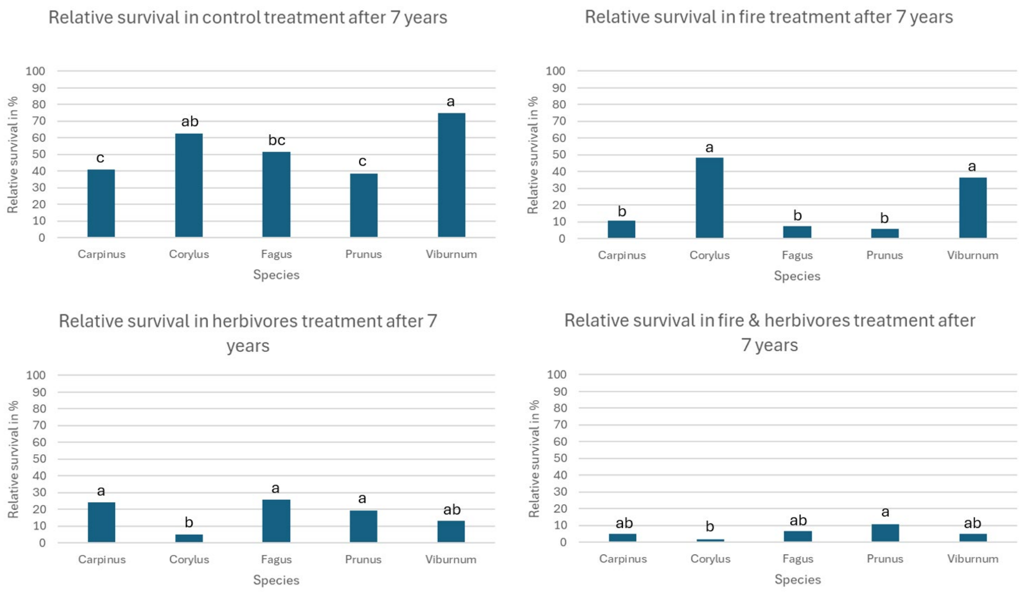

Figure 6. Relative survival within treatments for Carpinus betulus, Corylus avellana, Fagus sylvatica, Prunus spinosa and Viburnum opulus after 7 years (n = 120 individuals per treatment per species). Different letters represent significant differences.

5. Discussion

Large herbivores and fire are important drivers that affect the survival of woody species in ecosystems on a near-global scale, resulting in the emergence of brown and black world trees (Bond 2005). Arguably, the framework of large herbivore-driven brown world trees can be extended into temperate European ecosystems (Churski et al. 2017, Churski et al. 2024). Whether fire can lead to a dominance of black world trees in temperate European ecosystems is largely unknown (Leys et al 2018). However, it has been shown that fire dynamics have shaped temperate *Pinus*-dominated forests in Europe (Niklasson et al. 2010). Also, it has been suggested that the survival of European temperate woody species differs in response to fire (Molinari et al. 2020). Additionally, it is hypothesized that large herbivores and fire have affected temperate woody species assemblages differently in different time periods. Whereas the previous interglacial is hypothesized to be primarily shaped by large herbivores, the early to mid-Holocene is thought to be predominantly shaped by fire (Pearce et al. 2023, Pearce et al. 2024). However, experimental data to supports this hypothesis is limited. This study shows that both large herbivores and fire reduce the survival of virtually all woody species in the experiment, thereby enabling the establishment of temperate wood-pasture conditions. Furthermore, it reveals that large herbivores and fire shape divergent woody species assemblages by impacting the survival of virtually all woody species differently (Figure 4 and 5). Therefore, the results indicate that the framework of both brown and black world trees can be extended into both past and present temperate European ecosystems.

5.1 Divergent effects of large herbivores and fire on the survival of woody species

Species with a significantly higher survival rate in the treatment with large herbivores compared to with fire were *Picea*, *Carpinus*, *Fagus* and *Prunus*. On the other hand, *Betula*, *Quercus*, *Tilia*, *Corylus* and *Viburnum* had a significantly higher survival rate in the treatment with fire compared to with large herbivores. The only exception was *Pinus*, with a similar survival rate in both treatments (Figure 4 and 5).

The lower survival rate of *Betula* in the large herbivore treatment corresponds to other studies, also in Fennoscandian wood-pasture, where seedlings of *Betula* are negatively affected by large herbivores (Atkinson 1992, Oldén et al. 2017). In contrast, *Betula* had a higher survival rate in the fire treatment. This aligns with other authors, which describe Betula as a fire adapted or favoured species due to its ability to resprout from basal buds (Kauppi et al. 1987, Molinari et al. 2020).

As for *Picea*, saplings have a high density in grazed Fennoscandian wood-pasture (Oldén et al. 2017), but density is nevertheless reduced when grazing by cattle is compared to the control without cattle (Hjeljord et al. 2014). These findings correspond to the results in this study, where large herbivores reduced the survival of saplings compared to the control but not as severe as in the fire treatment. In contrast, the findings in this study showed a lower survival rate of *Picea* in the fire treatment. Indeed, *Picea* is deemed a fire intolerant species due to its thin bark and shallow root system (Molinari et al. 2020, Pennanen 2002).

Saplings of *Pinus* are often browsed in Fennoscandian wood-pasture as well (Oldén et al. 2017). Whilst some authors found no reducing effect of large herbivores on survival, others found a significant reduction in the density of *Pinus* when cattle were present (Hjeljord et al. 2014, Lyly et al. 2014). As for fire, different authors describe *Pinus* as adapted or resistant to fire (Fernandes et al. 2008, Molinari et al. 2020). *Pinus* was the only species without a significant difference in survival between the large herbivores and fire treatment in this experiment, which means that *Pinus* can be perceived as adapted or resistant to large herbivores as well.

Quercus is described as having a high ability to resprout after large herbivore impact (Bobiec et al. 2018). This is however not observed in this experiment, where the survival of *Quercus* is low in the large herbivore treatment. This is line with other studies, where *Quercus* survival is negatively affected or even non-existing in combination with large herbivores (Jensen et al. 2020, Smit et al. 2015). Additionally, it is observed that *Quercus* saplings can survive mowing one time per year for four years in a row before mortality occurs (Mellanby, 1968). This might explain the relatively high survival of *Quercus* after three years in the herbivore treatment in the same experiment as this study (Amsten et al. 2021). On the contrary, *Quercus* survival in the fire treatment was very high in this study. Indeed, Quercus is described as a fire tolerant species with a high resprouting capacity after the occurrence of fire (Jones 1958, Molinari et al. 2020).

Tilia had a very low survival rate in the large herbivore treatment in this study. This is in line with other findings, where the survival of *Tilia* was higher in unfenced areas compared fenced areas, due to its vulnerability to browsing by cattle (Hasstedt & Annighöfer 2020). Interestingly, in contrast to the large herbivore treatment, *Tilia* had a very high survival rate in the fire treatment in this experiment. This was unexpected, since other authors describe *Tilia* as fire intolerant and even at risk of local extinction after fire (Clear et al. 2015, Molinari et al. 2020).

In accordance with this study, others state that *Carpinus* is one of the few temperate European woody species with a high survival rate in systems with large herbivores due to its ability to alternate between growth forms (Churski et al. 2024). This is especially true in high light conditions, as is the case in this study, where *Carpinus* is able to withstand browsing from large herbivores (Bezacinsky 1971, Churski et al. 2017). On the contrary, *Carpinus* had a significantly lower survival rate in the fire treatment compared to in the large herbivore treatment. In contrast, other authors state that *Carpinus* is tolerant towards fire (Molinari et al. 2020, Shafiei et al. 2010).

As for *Corylus*, it is suggested that the species is able to persist in areas with large herbivores without the protection of thorny shrubs due to its high ability to produce new shoots (Coppins et al. 2002). However, this study indicates that *Corylus* has a very low survival rate in the large herbivore treatment. This corresponds to other studies which state that mortality is greater with high levels of large herbivores (Laborde & Thompson 2009), as is the case in this study. In contrast, *Corylus* had a very high survival rate in this study and was the only species with no significant differences in survival between the control and fire treatment. This is line with other studies, which affirm that *Corylus* is a fire tolerant species (Huntley 1993, Molinari et al. 2020).

In response to large herbivores, *Fagus* is another European woody species that is able to form a cage structure (Churski et al, 2024). Moreover, *Fagus* is able to regenerate and survive as a so-called pasture-beech in grasslands with relatively low densities of large herbivores by producing multiple stems (Schwabe & Kratochwil 1986). The aforementioned corresponds with this study, where *Fagus* has a higher survival rate in the large herbivore treatment. Here, the survival rate of *Fagus* in the fire treatment is low but does not significantly differ from *Carpinus*. Whilst others state that *Fagus* is affected more by fire than *Carpinus*, even though this concerns the similarly thin-barked oriental beech (*Fagus orientalis*). However, *Fagus* is also regarded as tolerant to fire (Molinari et al. 2020).

In this study, *Prunus* is yet another species with a higher survival rate in the large herbivore treatment. It is generally regarded as a species resistant to browsing but large herbivores can hamper the expansion of *Prunus*, and it can only expand when browsing is stopped or of low intensity (Laborde et al. 2013, Smit et al. 2010, Tansley 1922). Although it possesses thorns to resist large herbivores, it is still impacted by large herbivores such as cattle because new shoots lack thorny defences (Buttenschoen & Buttenschoen 1978, Vera 2000). Furthermore, *Prunus* has a significantly lower survival rate compared to other shrubs like hawthorn (*Crataegus monogyna*) when cut (Michielsen et al. 2017). In relation to fire, *Prunus* has a lower survival rate compared to species like hawthorn as well (Michielsen et al. 2017).

As for *Viburnum*, it has a lower survival rate in the large herbivore treatment compared to in the fire treatment in this study. Due to a weak root system, large herbivores uproot it easily and thereby prevent resprouting. Additionally, *Viburnum* has a low capability to survive after browsing occurs and mortality is thus higher in areas with large herbivores (Laborde 2005). Overall, its palatability is considered high, and it is a preferred food source for large herbivores (Kollman & Grubb 2002). In this study, the survival of *Viburnum* was very high in the fire treatment and no statistical difference compared to *Corylus* were observed. Indeed, others show that *Viburnum* has a high abundance in burned plots as well (Bowles et al. 2007).

Intriguingly, an additional significant effect of the fire & herbivore (FH) treatment, compared to the herbivore treatment (H) alone, on the survival of certain woody species was observed in this study. This was unexpected, since large herbivores are thought to reduce fuel loads and even subdue fires (Pringle et al. 2023, Rouet-Leduc et al. 2021). Also, no additional effect of fire and herbivores on the survival of woody species was observed in the same experiment as in this study after three years (Amsten et al. 2021). Here, the survival of *Betula*, *Carpinus*, *Fagus* and *Viburnum* was however significantly reduced in the fire & herbivores treatment compared to in the herbivore treatment. Although others found that fire and large herbivores, compared to large herbivores alone, had an additional negative effect on the survival of *Quercus* in North America (Beebe et al. 2024). However, no such additional effect was found for *Quercus* in this study.

5.2 Comparison with palaeoecological data from temperate Europe

As discussed earlier, the previous interglacial was likely predominantly shaped by large herbivores whereas the early to mid-Holocene was primarily shaped by fire due to the anthropogenic processes of defaunation and direct fire ignition (Davoli et al. 2023, Gauthier et al. 2021, Pearce et al. 2023, Pearce et al. 2024). As a consequence, human influence on the vegetation composition is substantial in the early to mid-Holocene. Therefore, the last interglacial could be a more suitable reference state due to the absence of modern humans. Nevertheless, drivers of openness were weakly correlated to climate and stronger to internal disturbances (Pearce et al. 2023). Possibly, fire has driven the occurrence of tolerant species such as *Carpinus*, *Corylus* and *Quercus* (Pearce et al. 2023). However, all of the aforementioned species are tolerant and not adapted to fire (Molinari et al. 2020). Additionally, *Carpinus* had a low survival rate in the fire treatment in this study. Moreover, these species were less common in the Holocene compared to in the last interglacial (Pearce et al. 2023). Hence, it is assumed that higher levels of large herbivores explain the greater abundance of *Carpinus*, *Corylus* and *Quercus* in the last interglacial while the lower abundancy of these species in the early to mid-Holocene might be explained by anthropogenic fire (Pearce et al. 2023, Pearce et al. 2024). In this study however, and in contrast to *Carpinus*, both *Corylus* and *Quercus* have low survival rates with large herbivores as opposed to fire.

In order to compare the results in this study with the possibly more suitable reference state of the last interglacial, it is important to note that phase I and II differed from eachother. Here, phase I was characterised by a warmer climate with more seasonality while phase II had decreasing seasonality with cooler summer temperatures (Katrantsiotis et al. 2021). In temperate Europe, the proportion of the combination of open and light woodlands was 79% in phase I but only 51% in phase II. Both phases were characterised by an abundance of *Quercus* and *Corylus* in open and light woodland. Only in Phase II did *Carpinus* expand into temperate Europe and became more dominant, which might be explained by the effects of large herbivores (Pearce et al. 2023). As both *Carpinus* and *Tilia* are among the few temperate trees that are able to develop cage structures to withstand large herbivores in light conditions (Churski et al. 2017, Churski et al 2024). The findings in this study support the presence of high light conditions that could enable *Carpinus* to survive and dominate in ecosystems shaped by large herbivores, but not for *Tilia* due to its low survival rate.

In the middle of the last interglacial, palaeoecological data in temperate and southern Sweden indicates wetlands, surrounded by light woodlands and mixed-*Picea* woodlands. Here, *Betula*, *Picea* and *Pinus* occurred alongside more open vegetation with *Corylus* and *Quercus* (Lemdahl et al. 2013). If this species assemblage is to be compared to the results in this study, the presence of *Picea* might exclude fire whereas the presence of *Corylus* and *Quercus* might exclude large herbivores. However, *Picea* could have survived in damp or wet areas within the landscape that are less prone to fire ignition. In temperate Europe generally, the woody genera of *Corylus*, *Pinus* and *Quercus* had the highest coverages in the last interglacial (Pearce et al. 2025). This study demonstrates that no significant difference in terms of survival between treatments with large herbivores and with fire for *Pinus*, while *Corylus* and *Quercus* had a higher survival rate in the fire treatment. Other palaeoecological results from temperate Europe in the last interglacial show that *Prunus* and other thorny shrubs such as hawthorn were well represented, as well as *Fagus*, *Corylus* and *Taxus* (Jolly-Sand & Dabkowski 2021). Many of these species had high survival rates in the large herbivore treatment but low survival rates in the fire treatment in this study, except for *Corylus* and *Quercus*. Possibly, this is an indication that large herbivores predominantly shaped the species assemblage during the last interglacial as opposed to fire.

When *Corylus* and *Quercus* are compared between the last interglacial and the early to mid-Holocene, the mean cover of *Corylus* is lower in the Holocene while there is no difference between the two periods for *Quercus*. Additionally, the fire intolerant yew (*Taxus baccata*) had a higher coverage in the last interglacial compared to in the Holocene. Therefore, it is hypothesised that *Corylus* and *Taxus* are more likely to occur in areas with disturbances created by large herbivores whereas *Quercus* is more influenced by climatic factors (Pearce et al. 2024). In this study, both *Corylus* and *Quercus* had a low capacity to resprout in treatments with large herbivores but a high capacity in treatments with fire. These results deviate from others, which state that the two species have a high ability to resprout after browsing by large herbivores (Bobiec et al. 2018, Coppins et al. 2002, Jones 1958). However, this deviation for *Corylus* and *Quercus* might be explained by their ability to survive in wood-pasture due to the protection of thorny shrubs (Vera et al. 2006).

5.3 Oak, hazel, thorns and birds

In present temperate European wood-pasture, *Corylus* and *Quercus* occur commonly when large herbivores are present (Rackham 2003, Vera 2000, Vera et al. 2006). Additionally, they are dominant woody species in temperate Europe in the predominantly large herbivore-driven last interglacial as well as in the predominantly fire-driven early to mid-Holocene (Pearce et al. 2024). Meanwhile, they occur together with fire sensitive or intolerant species such as *Fagus*, *Picea*, *Prunus* and *Taxus* (Jollysand & Dabkowski 2021, Lemdahl et al. 2013, Pearce et al. 2023, Pearce et al. 2024). However, in this study, both *Corylus* and *Quercus* have very low survival rates in the large herbivore treatment.

This anomaly can be explained by the relationship between *Corylus*, *Quercus*, thorny shrubs and birds in present and past temperate European wood-pasture. When large herbivores disappear from wood-pasture, so do *Corylus* and *Quercus* (Vera 2000). These light-demanding and palatable species do survive in wood-pasture with large herbivores due to the co-evolution with and protection of thorny shrubs (Bobiec et al. 2018, Milewski et al. 1991, Salek et al. 2019, Smit et al. 2015, Vera et al. 2006). Even though shade-tolerant species occur in wood-pasture, the light-demanding *Quercus* is more common (Rackham 2003).

Since these species have vectors that spread their seed, they can occur more commonly in wood-pastures in combination with the protection of thorny shrubs. The Eurasian jay (*Garrulus glandarius*) is an important vector of *Quercus*. It prefers open areas to hide acorns and thereby select places with short grass at the fringe of thorny shrub such as *Prunus* (Bossema 1978). Most shade-tolerant species lack such a vector. Although beech nuts are collected by mice over short distances, the higher establishment of *Quercus* in thorny shrubs close to *Fagus* forests indicate an advantage of *Quercus* over *Fagus* in wood-pasture (Tansley 1922, Watt 1925). As for *Corylus*, it also survives in open conditions when protected by thorny shrubs (Sanderson 1958). Its vector is the Eurasian nuthatch (*Sitta europaea)*. It hides hazelnuts in thorny shrubs, where seedlings can survive (Sanderson 1958, Vera et al. 2006). In this study, *Corylus* had a low survival rate with large herbivores. Whilst others state that *Corylus* can survive in the presence of large herbivores without thorny shrubs (Coppins et al. 2002).

The low survival rate of both *Corylus* and *Quercus* with large herbivores in this study can thus be explained by the fact that the species were planted individually, without the protection of thorny shrubs. Consequently, a crucial process of natural establishment and survival of these species in temperate wood-pasture was bypassed. Namely, that they have co-evolved with the protection of thorny shrubs and birds as vectors (Bobiec et al. 2018, Bossema 1978, Milewski et al. 1991, Salek et al 2019, Sanderson 1958, Vera et al. 2006). Therefore, it can be argued that *Corylus* and *Quercus* potentially have high survival rates and thus belong in temperate wood-pasture that is shaped by large herbivores and not only by fire.

5.4 Experimental limitations and the survival of temperate woody species

Several experimental limitations may have influenced the survival rate of woody species in this study. Ideally, larger subplots should have been utilized in this experiment to counteract the edge effects. An important limitation in relation to the edge effects in small subplots is the intensity of fire. One edge effect that may have more influence as the size of subplots decreases is powerful wind (Bradstock 2010). As a result, areas with high fuel loads on the edges may not burn because of unexpected changes in wind (Parkins et al. 2018). On the other hand, edges may also not burn due to insufficient fuel loads and safeguarding watering measures during the prescribed burning. Here, drip torches over the length of the subplot were used and this process was repeated five times at a one-meter interval if ignition failed, leaving one outer edge unburned. The small size and ignition pattern may have hindered the behaviour of fire to fully develop spread rate in relation to the wind. Therefore, the survival of woody species in the fire treatment is likely higher around the edges due to the small size of subplots compared to the effects of fire in the core of the subplot or at the landscape level.

Obviously, the woody species in this experiment were planted and not sown from seed or naturally regenerated. The size of the one- to three-year-old planted saplings was larger compared to the size of saplings when they would have germinated from seed. Therefore, the survival rate of planted saplings in this experiment may have been higher compared to small-sized seedlings germinating from sown seeds. Additionally, seed predation is a substantial bottleneck for temperate trees that would further reduce the survival rate to a large extent (Garcia et al. 2005, Vera 2000). This process is avoided in the experiment by planting saplings. Thus, the potential effect of both large herbivores and fire on the survival of woody species may have been underestimated in this study. On the other hand, the process of planting might have further reduced the survival for some woody species in the large herbivore treatment in comparison to establishment in regular wood-pasture conditions. It is argued that light-demanding and palatable woody species such as *Corylus* and *Quercus* are dependent on the protection of thorny shrubs to establish and survive in ecosystems that are shaped by large herbivores (Bobiec et al. 2018, Milewski et al. 1991, Salek et al 2019, Vera et al. 2006). Also, their seeds would normally be distributed by birds. The foremost vector species of *Quercus*, the Eurasian jay, even has a preference to hide acorns at the edge of protective thorny shrubs (Bossema 1978). This natural process, which would normally affect survival positively, is bypassed in this experiment by planting saplings.

Yet another possible limitation is the high density at which individuals were planted in grass-dominated wood-pasture conditions. In this experiment, 25 saplings were planted on 49 m^2, which corresponds to over 5,000 saplings per hectare. Normally, the establishment of woody species would be restricted to less palatable species, cage-forming species and the establishment of species in thorny shrubs within semi-open ecosystems that are shaped by large herbivores (Churski et al. 2017, Churski et al. 2021, Oldén et al. 2017, Schwabe & Kratochwil 1986, Smit et al. 2015, Vera et al. 2006). In this experiment, all species were planted at equal distances from each other, randomly positioned and planted at high densities. As a result, interspecies competition could have led to the reduced survival of light-demanding, slow-growing or short-statured species as opposed to shade-tolerant, fast-growing and tall-statured species. Additionally, natural regeneration of woody species was not removed after planting and could have contributed to an increased interspecies competition.

6. Conclusions

By assessing the long-term survival of planted saplings, this thesis aimed to analyse how large herbivores and fire, individually and in combination, affects the survival rate of ten temperate European woody species with various ecological traits in a full-factorial experiment at Nordens Ark´s Ecopark.

Both large herbivores and fire, individually and in combination, significantly reduced the survival rates of nearly all species and thereby shaped semi-open wood-pasture conditions. Survival rates of virtually all species significantly differed between treatments with large herbivores and fire. Species with a higher survival rate in the large herbivore treatment were *Picea*, *Carpinus*, *Fagus* and *Prunus*. In contrast, a higher survival rate in the fire treatment was observed for *Betula*, *Quercus*, *Tilia*, *Corylus* and *Viburnum*. Thus, survival rates between the two treatments differed for all species except *Pinus*. I suggest that, based on this experiment, large herbivores and fire have the potential to shape divergent woody species assemblages in temperate European wood-pasture. Interestingly, even though large herbivores reduce fuel loads, the combined effects of large herbivores and fire, as opposed to large herbivores individually, did result in a reduced survival rate for *Betula*, *Carpinus*, *Fagus* and *Viburnum.*

The results of this experimental study showed that large herbivores and fire are able to shape semi-open and open conditions by reducing the survival of woody species in temperate Europe, which is of importance since many species, including light-demanding woody species, are dependent on such conditions. Additionally, this thesis demonstrated that the framework of brown and black world trees might be extended into temperate European ecosystems because both large herbivores and fire shape divergent woody assemblages in temperate European wood-pasture. Moreover, it has contributed to the ongoing debate on past temperate European ecosystems by comparing the survival of woody species in the large herbivore and fire treatments to recent palaeoecological data from the hypothesised large herbivore-driven last interglacial and fire-driven early to mid-Holocene to evaluate how survival rates in this experiment relate to the occurrence of species in the past.

However, future research should seek to reduce edge effects and replace planting with sowing to incorporate the recruitment phase of woody species. To improve our understanding of open landscapes in temperate Europe, similar experiments should be initiated in other regions. Additionally, large herbivores, that have naturally occurred in temperate Europe, should be grazing year-round in such experiments to mimic the presence of large herbivores in past landscapes.

Lastly, the results indicate that fire and large herbivores should be included into restoration efforts on a wider scale to promote openness and halt the ongoing biodiversity loss in semi-open and open temperate European ecosystems.

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Popular science summary

In European regions with a mild climate, formerly open environments that turn into forests are a threat to biodiversity, including tree and shrub species that need light conditions to survive. This study looks into whether large plant-eating mammals and fire, alone and in combination, can reduce the survival of ten tree and shrub species that can be found in mild climates and therefore if they can maintain a mostly open landscape. Also, it investigates if tree and shrub species respond differently to large plant-eating mammals and fire when we talk about survival. In this study, the number of young trees and shrubs that survived out of a total of 4,800 planted individuals is evaluated in an experiment. The results show that both large plant-eating mammals and fire, alone and in combination, reduce the number of young trees and shrubs of almost all species in this experiment and thereby help to create mostly open environments with only a few trees and shrubs. Besides, the results suggest that large plant-eating mammals and fire create different communities of tree and shrub species in European ecosystems with a mild climate. Species with a higher amount of young trees and shrubs that survive with large plant-eating mammals compared to with fire are Norway spruce, hornbeam, beech and blackthorn. On the other hand, silver birch, pedunculate oak, small-leaved lime, hazel and Guelder rose have a higher survival rate with fire compared to with large plant-eating mammals. So, the amount of trees and shrubs that survive when the effects of large plant-eating mammals are compared to the effects of fire is different for all species in the experiment except for Scots pine. However, recent studies on pollen analysis indicate that pedunculate oak and hazel were also common in the last interglacial, when large plant-eating mammals probably created open environments. This deviation can be explained by the difference between how young trees and shrubs are planted in the experiment and how these species would normally establish and survive in landscapes where large plant-eating mammals are present. As a consequence, the above-mentioned species can also be a part of tree and shrub communities in ecosystems that are dominated by large plant-eating mammals. In conclusion, this study provides experimental understanding of how large plant-eating mammals and fire create mostly open environments with only a few trees and shrubs, resulting in different communities of tree and shrub species.

Appendix 1

Multiple pairwise comparison chi-square tests and Fisher´s exact tests of survival between treatments (Control (C), Herbivores (H), Fire (F), and Fire-Herbivores (FH)) for *Betula*, *Picea*, *Pinus*, *Quercus* and *Tilia* after 10 years. See chapter 3.4 for details on the test used.

Species	Treatment combination	p-value	Holm-Bonferroni threshold	Significant
Betula	FH - C	<0.001	0.0083	yes
	H - C	<0.001	0.01	yes
	F - C	<0.001	0.0125	yes
	FH - F	<0.001	0.0167	yes
	FH - H	0.003059	0.025	yes
	H - F	0.007333	0.05	yes
Picea	F - C	<0.001	0.0083	yes
	FH - C	<0.001	0.01	yes
	H - C	<0.001	0.0125	yes
	H - F	<0.001	0.0167	yes
	FH - F	0.037812	0.025	no
	FH - H	0.052808	0.05	no
Pinus	FH - C	<0.001	0.0083	yes
	H - C	<0.001	0.01	yes
	F - C	<0.001	0.0125	yes
	FH - F	0.020105	0.0167	no
	FH - H	0.031424	0.025	no
	H - F	0.854883	0.05	no
Quercus	FH - C	<0.001	0.0083	yes
	H - C	<0.001	0.01	yes
	FH - F	<0.001	0.0125	yes
	H - F	<0.001	0.0167	yes
	F - C	0.014088	0.025	yes
	FH - H	1	0.05	no
Tilia	FH - C	<0.001	0.0083	yes
	H - C	<0.001	0.01	yes
	FH - F	<0.001	0.0125	yes
	H - F	<0.001	0.0167	yes
	F - C	<0.001	0.025	yes
	FH - H	0.3697	0.05	no

Appendix 2

Multiple pairwise comparison chi-square tests and Fisher´s exact tests of survival between treatments (Control (C), Herbivores (H), Fire (F), and Fire-Herbivores (FH)) for *Carpinus*, *Corylus*, *Fagus*, *Prunus* and *Viburnum* after 7 years. See chapter 3.4 for details on the test used.

Species	Treatment combination	p-value	Holm-Bonferroni threshold	Significant
Carpinus	FH - C	<0.001	0.0083	yes
	F - C	<0.001	0.01	yes
	FH - H	<0.001	0.0125	yes
	H - C	0.005845	0.0167	yes
	H - F	0.006565	0.025	yes
	FH - F	0.094225	0.05	no
Corylus	FH - C	<0.001	0.0083	yes
	H - C	<0.001	0.01	yes
	FH - F	<0.001	0.0125	yes
	H - F	<0.001	0.0167	yes
	F - C	0.027266	0.025	no
	FH - H	0.2807	0.05	no
Fagus	FH - C	<0.001	0.0083	yes
	F - C	<0.001	0.01	yes
	H - C	<0.001	0.0125	yes
	FH - H	<0.001	0.0167	yes
	H - F	<0.001	0.025	yes
	FH - F	0.801342	0.05	no
Prunus	F - C	<0.001	0.0083	yes
	FH - C	<0.001	0.01	yes
	H - C	0.001037	0.0125	yes
	H - F	0.001791	0.0167	yes
	FH - H	0.070645	0.025	no
	FH - F	0.161125	0.05	no
Viburnum	FH - C	<0.001	0.0083	yes
	H - C	<0.001	0.01	yes
	FH - F	<0.001	0.0125	yes
	F - C	<0.001	0.0167	yes
	H - F	<0.001	0.025	yes
	FH - H	0.025286	0.05	yes

Appendix 3

Multiple pairwise comparison chi-square tests and Fisher´s exact tests of survival between species (*Betula*, *Picea*, *Pinus*, *Quercus* and *Tilia*) within each of the four treatments after 10 years. See chapter 3.4 for details on the test used.

Treatment	Species combination	p-value	Holm-Bonferroni threshold	Significant
Fire-Herbivores	Picea - Quercus	<0.001	0.005	yes
	Betula - Picea	<0.001	0.005556	yes
	Picea - Tilia	<0.001	0.00625	yes
	Pinus - Quercus	0.0143	0.007143	no
	Picea - Pinus	0.02010458	0.008333	no
	Betula - Pinus	0.0658	0.01	no
	Pinus - Tilia	0.0658	0.0125	no
	Betula - Quercus	1	0.016667	no
	Betula - Tilia	1	0.025	no
	Quercus - Tilia	1	0.05	no
Herbivores	Picea - Quercus	<0.001	0.005	yes
	Picea - Tilia	<0.001	0.005556	yes
	Pinus - Quercus	<0.001	0.00625	yes
	Betula - Picea	0.001119347	0.007143	yes
	Pinus - Tilia	0.002980596	0.008333	yes
	Betula - Quercus	0.003059016	0.01	yes
	Picea - Pinus	0.034466894	0.0125	no
	Betula - Tilia	0.061948151	0.016667	no
	Betula - Pinus	0.227643388	0.025	no
	Quercus - Tilia	0.3697	0.05	no
Fire	Picea - Quercus	<0.001	0.005	yes
	Pinus - Quercus	<0.001	0.005556	yes
	Picea - Tilia	<0.001	0.00625	yes
	Betula - Quercus	<0.001	0.007143	yes
	Betula - Picea	<0.001	0.008333	yes
	Quercus - Tilia	0.010734	0.01	no
	Pinus - Tilia	0.012178	0.0125	no
	Picea - Pinus	0.037812	0.016667	no
	Betula - Pinus	0.182017	0.025	no
	Betula - Tilia	0.233038	0.05	no
Control	Betula - Tilia	0.001504689	0.005	yes
	Pinus - Tilia	0.005739551	0.005556	no
	Picea - Tilia	0.012726419	0.00625	no
	Betula - Quercus	0.077689915	0.007143	no
	Quercus - Tilia	0.153147662	0.008333	no
	Pinus - Quercus	0.178251569	0.01	no
	Picea - Quercus	0.283899985	0.0125	no
	Betula - Picea	0.486234321	0.016667	no
	Betula - Pinus	0.673808087	0.025	no
	Picea - Pinus	0.782830158	0.05	no

Appendix 4

Multiple pairwise comparison chi-square tests and Fisher´s exact tests of survival between species (*Carpinus*, *Corylus*, *Fagus*, *Prunus* and *Viburnum*) within each of the four treatments after 7 years. See chapter 3.4 for details on the test used.

Treatment	Species combination	p-value	Holm-Bonferroni threshold	Significant
Fire-Herbivores	Corylus - Prunus	0.003353436	0.005	yes
	Corylus - Fagus	0.052601894	0.005556	no
	Carpinus - Prunus	0.094225112	0.00625	no
	Prunus - Viburnum	0.094225112	0.007143	no
	Fagus - Prunus	0.253368967	0.008333	no
	Carpinus - Corylus	0.2807	0.01	no
	Corylus - Viburnum	0.2807	0.0125	no
	Carpinus - Fagus	0.581750396	0.016667	no
	Fagus - Viburnum	0.581750396	0.025	no
	Carpinus - Viburnum	1	0.05	no
Herbivores	Corylus - Fagus	<0.001	0.005	yes
	Carpinus - Corylus	<0.001	0.005556	yes
	Corylus - Prunus	<0.001	0.00625	yes
	Fagus - Viburnum	0.014691952	0.007143	no
	Corylus - Viburnum	0.025286323	0.008333	no
	Carpinus - Viburnum	0.031560325	0.01	no
	Fagus - Prunus	0.216221857	0.0125	no
	Prunus - Viburnum	0.220641922	0.016667	no
	Carpinus - Prunus	0.347163802	0.025	no
	Carpinus - Fagus	0.765594484	0.05	no
Fire	Corylus - Prunus	<0.001	0.005	yes
	Corylus - Fagus	<0.001	0.005556	yes
	Carpinus - Corylus	<0.001	0.00625	yes
	Prunus - Viburnum	<0.001	0.007143	yes
	Fagus - Viburnum	<0.001	0.008333	yes
	Carpinus - Viburnum	<0.001	0.01	yes
	Corylus - Viburnum	0.067538285	0.0125	no
	Carpinus - Prunus	0.161124949	0.016667	no
	Carpinus - Fagus	0.370893956	0.025	no
	Fagus - Prunus	0.604772854	0.05	no
Control	Prunus - Viburnum	<0.001	0.005	yes
	Carpinus - Viburnum	<0.001	0.005556	yes
	Fagus - Viburnum	<0.001	0.00625	yes
	Corylus - Prunus	<0.001	0.007143	yes
	Carpinus - Corylus	<0.001	0.008333	yes
	Corylus - Viburnum	0.036713856	0.01	no
	Fagus - Prunus	0.037894211	0.0125	no
	Corylus - Fagus	0.090001121	0.016667	no
	Carpinus - Fagus	0.092368705	0.025	no
	Carpinus - Prunus	0.692114522	0.05	no

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