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Fire and herbivory – key drivers of temperate open ecosystems

Effects of consumer control on woody and herbaceous plant communities in temperate wood-pastures

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Abstract

The decline of open and semi-open habitats is an important reason behind the ongoing worldwide loss of biodiversity. Understanding the drivers of habitat openness is an important key for preventing the continued loss of these ancient ecosystems. In other continents, fire and herbivory are well-studied and identified as important processes in preventing open habitats from turning into closed forests. The aim of this thesis is to apply the established concept of *consumer control* in a new context: the northern areas of temperate Europe. In a large field experiment in a Swedish wood-pasture, we first studied how two consumers, prescribed grass fire and grazing by cattle, alone or in combination, affected the survival and growth of planted tree saplings (**I**). The tree species demonstrated different strategies to resist fire or herbivory. Either they survived by re-sprouting or they quickly grew out of reach of the consumers. In addition, we studied the effect of the two consumers on the establishment and reproduction of sowed open habitat forbs (**II**). Herbivory improved the conditions for the establishment of forbs, but fire promoted the production of inflorescences. A release of grazing pressure increased the number of remaining flowers at the end of the growing season, confirming the importance of variation in herbivory intensity over time for the persistence of forbs. In a third study, we studied the interaction between fire and cattle grazing (**III**). We followed the foraging behaviour of cattle with camera traps and found that when a larger proportion of an area was burned, the cattle preferred to graze in the newly burned areas. This led to a reduction in fuel, altering the future fire pattern. In a final study, we evaluated the long-term effects of fire and herbivory by comparing the biomass of woody and herbaceous vegetation (**IV**). Without fire and herbivory, trees out-shaded grasses and forbs, leading to conversion from an open grassy ecosystem to a tree-dominated forest. In conclusion, herbivores and potentially also fire can be important drivers of openness, also in temperate Northern Europe, but further research is needed to understand the effect of different fire and grazing regimes.

Keywords: consumer control, fire, grassland, grazing, herbivory, open ecosystem, savanna, vegetation structure, wood-pasture

Brand och bete – nyckelfaktorer för tempererade öppna ekosystem: Effekter av brand och bete på ved- och örtartade växter

Sammanfattning

Tillbakagången av öppna och halvöppna livsmiljöer är en viktig och bidragande orsak till den pågående globala förlusten av biologisk mångfald. Att förstå processerna som håller dessa landskap öppna är en viktig del i att förhindra fortsatt förlust av dessa ekosystem. På andra kontinenter är effekterna av brand och bete välstuderade och har identifierats som nyckelprocesser för att bevara öppna livsmiljöer från igenväxning. Syftet med denna avhandling är att använda och applicera denna kunskap i ett nytt sammanhang, nämligen de norra delarna av tempererade Europa. I ett jämförande experiment studerade vi först hur gräsbränder och bete med nötkreatur påverkade överlevnaden och tillväxten av planterade trädplantor (**I**). Trädarterna uppvisade stor variation i överlevnad och hade olika strategier för att överleva brand och bete, antingen genom att återkommande sätta nya skott eller genom att snabb växa förbi brand- och/eller betesnivån. Vidare studerade vi brandens och betets effekt på etablering och reproduktion av sådda ängsblommor (**II**). Bete förbättrade förutsättningarna för etablering medan eld främjade produktionen av blommor. Ett uppehåll i betet ledde till fler kvarvarande blomställningar i slutet av säsongen, vilket bekräftar betydelsen av en variation i brand- och betesintensitet över tid. I en tredje studie studerade vi interaktionen mellan brand och bete (**III**). Med kamerafällor följde vi nötkreaturens födosöksbeteende och fann att när större områden brändes så föredrog nötkreaturen att beta på de nybrända områdena. Detta ledde i sin tur till en minskning av bränslet vilket förändrade framtida brandmönster. I en sista studie utvärderade vi den långsiktiga effekten av brand och bete genom att jämföra biomassan av ved- och örtartad vegetation (**IV**). Utan vare sig bete eller brand skuggade träden ut gräs och örter, vilket ledde till igenväxning av den öppna gräsmarken. Sammanfattningsvis kan bete, och eventuellt även brand, utgöra viktiga drivkrafter för öppna landskap, även i norra tempererade Europa. Ytterligare forskning behövs för att förstå effekten av varierande brand- och betesregimer.

Nyckelord: bete, skogsbetesmark, brand, gräsmarker, savann, vegetationsstruktur, öppna ekosystem

Dedication

To my family: Martin, Vilda, and Lova.

And also to You, Mom, who never got to see this.

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by bold Roman numerals in the text:

- **I.** Amsten, K., Cromsigt, J. P. G. M., Kuijper, D. P. J., Loberg, J. M., Churski, M., & Niklasson, M. (2021). Fire-and herbivory-driven consumer control in a savanna-like temperate wood-pasture: An experimental approach. *Journal of Ecology*, 109, 4103–4114. https://doi.org/10.1111/1365-2745.13783

- **II.** Amsten, K., Cromsigt, J. P. G. M., Kuijper, D. P. J., Ivarsson, F., Jakobsson, A., Churski, M., & Niklasson, M. Forb recruitment in relation to fire and herbivory in a temperate savanna experiment (manuscript)

- **III.** Amsten, K., Cromsigt, J. P. G. M., Kuijper, D. P. J., Loberg, J. M., Jung, J., Strömgren, M., Niklasson, M., & Churski, M. Pyric herbivory in a temperate European wood-pasture system (In review, *Journal of Applied Ecology*)

- **IV.** Amsten, K., Loberg, J. M., Hedwall, P. O., Cromsigt, J. P. G. M., Kuijper, D. P. J., Niklasson, M., & Churski, M. Tree-grass coexistence in a temperate savanna experimentally created by fire and large grazers (manuscript)

Paper **I** is reproduced with the permission of the publisher.

The contribution of Karin Amsten to the papers included in this thesis was as follows:

I. KA developed the research idea together with JPGMC, DPJK, MC and MN. KA performed the field work and also conducted the statistical analyses together with JML and MC. KA wrote the manuscript in collaboration with the co-authors.

II. KA participated in planning and performing fieldwork together with JPGMC, DPJK, FI, AJ, MC, and MN. KA conducted the statistical analyses together with MC. KA, MC and MN wrote the manuscript in collaboration with the co-authors.

III. KA developed the research idea together with JPGMC, DPJK, MN and MC. KA performed the field work together with JJ, MS, and students. KA also conducted the statistical analyses together with JML. KA wrote the manuscript in collaboration with the co-authors.

IV. KA developed the research idea together with POH, JPGMC, DPJK, MN and MC. KA performed the major part of the field work and conducted the statistical analyses together with JML and POH. KA wrote the manuscript in collaboration with the co-authors.

Karin Amsten (KA), Joris P. G. M. Cromsigt (JPGMC), Dries P. J. Kuijper (DPJK), Marcin Churski (MC), Mats Niklasson (MN), Jenny M. Loberg (JML), Felicia Ivarsson (FI), Anna Jakobsson (AJ), Jens Jung (JJ), My Strömgren (MS), Per-Ola Hedwall (POH).

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1. Introduction

Biodiversity is highly dependent on the continuity of different natural ecological processes (Archibald et al., 2005; Archibald & Hempson, 2016; Bond, 2005; Canals, 2019; Keeley et al., 2011). Fire and large mammalian herbivores are two natural factors that play a key role in the creation and maintenance of open and semi-open habitats, such as savannas, which are important for many different kinds of species (Bond, 2021; Dengler et al., 2020). In Europe, where these natural open habitats now make up a very small proportion of their original extent and have been replaced by agricultural areas or forests (Bakker & Berendse, 1999; Bond, 2019; Bond & Parr, 2010; Hartel et al., 2013; Plieninger et al., 2015), we see a decline in open habitat specialists of vascular plants but also fauna, such as species of insects as well as birds (Dengler et al., 2020; Sutcliffe et al., 2015). The hypothesis that these species are a heritage of prehistoric presence of fire and herbivory has been confirmed in many studies (Bakker et al., 2016; Hejcman et al., 2013). Protected open areas are therefore more important than ever for these organisms, since modern agricultural and silvicultural land use provides less and less suitable habitats (Bond, 2019; Bond & Parr, 2010). To improve the management and restoration of open habitats in Europe, we can learn from other ecosystems, such as African and Australian savannas and American prairies, where fire and mammalian herbivory still act as key processes (Allred et al., 2011; Archibald, 2008; Reid et al., 2023). The focus of this thesis is the effect of these two important natural processes on vegetation in a temperate Northern European landscape, and how they interact with each other.

1.1 Open ecosystems

The natural open habitats of the world are some of the most biodiversity rich ecosystems (Bond & Parr, 2010; Petermann & Buzhdygan, 2021). The evolution and maintenance of these habitats have been well studied in tropical savannas in Africa (Archibald & Hempson, 2016; Charles-Dominique et al., 2015), but also in temperate areas such as in temperate prairies of North and South American (Anderson, 2006; Briggs et al., 2002; Veach et al., 2014) and Australian savannas (Bowman et al., 2021; Kirkpatrick et al., 2016). However, studies on the origin and functioning of temperate open ecosystems in Europe are rare.

For a long time, many open habitats have been seen as successional stages on the way to a closed forest (Odum, 2014). This view is based on classical successional models (see, e.g., Clements, 1936), which imply that vegetation development is driven by the competition for resources (Bond, 2005; Connell & Slatyer, 1977; Van Andel et al., 1993). Many efforts have also been made to divide the earth into vegetation zones, based on factors such as temperature, precipitation, altitude, and longitude, which determine the expected vegetation type in a certain area (see, e.g., Holdridge, 1947). However, during the last decades, these views have been challenged. In 1969, Lewontin suggested the *Alternative Stable State theory*, which describes the ability of an ecosystem to have different stable vegetational states, depending on which ecological processes that dominate (Lewontin, 1969; May, 1977; Pausas & Bond, 2020). Simultaneously, Whittaker (1975) presented the *Ecosystem Uncertain Climate Zones*, which are areas of the world where two or more stable states can co-occur, often including open or semi-open states, under the same climate conditions. This implies that open ecosystems are not just successional stages on the way to become forests, but are in fact ancient stable ecosystems, comparable to forests (Bond, 2019). These theories are strengthened by the fact that open ecosystems are some of the world´s most biodiverse habitats with substantial speciation of species, which would only be possible if these habitats have been persistent and stable for a sufficient amount of time (Bond, 2019).

Natural open habitats are defined by the complex coexistence of trees and grasses, where grasses often are the dominant vegetation type, and tree abundance ranges from a few scattered trees to small groves (Archibald & Hempson, 2016; Bond & Parr, 2010; Greve, 2013; Sankaran et al., 2004). Indeed, competition for resources, such as light, water, and nutrients, is an important driver of these ecosystems (Lehmann et al., 2011; Riginos, 2009; Scholes & Archer, 1997). However, today there is a great consensus that fire and herbivory by large mammalian herbivores (hereafter 'herbivores'), also play a key role and that they are important drivers of vegetation structure (Archibald & Hempson, 2016; Bond et al., 2005; Bond, 2008; Higgins et al., 2000; Keeley et al., 2011; Veldman et al., 2015). Fire and herbivory are often considered natural disturbances. However, they differ from other physical disturbances, such as earthquakes, because not only do they affect the ecosystem, but the ecosystem can also affect the conditions for fire and herbivory, e.g., by more or less flammable or palatable vegetation (Bond, 2019; Bowman et al., 2016).

The main effect from fire and herbivory on an ecosystem is the consumption of vegetation biomass (Archibald & Hempson, 2016). However, these two 'consumers' differ in the way they consume biomass (Archibald & Hempson, 2016). Herbivores prefer fresh vegetation high in nutrients (Owen-Smith & Novellie, 1982), while fires 'select' (*sensu* Archibald & Hempson, 2016) for dry vegetation, high in fiber (Schwilk, 2015). The two processes also differ in time and space, with herbivory being a more continuous process but spatially heterogeneous, and fires occurring less frequently but are often more spatially uniform (Archibald & Hempson, 2016).

Despite the differences, by consuming both herbaceous and woody vegetation to different degrees, fire and herbivory can control tree recruitment and prevent them from growing into adult trees (Archibald et al., 2005; Bond, 2005; Staver et al., 2009). The controlling effect of fire and herbivory can keep the woody vegetation in so-called *fire-* and *browse traps* (LaMalfa et al., 2019; Sankaran et al., 2013; Staver & Bond, 2014). The only chance for the trees to become adults in this situation is a relaxation of the control from fire and/or herbivory, which enables an escape of the trees from the trap (Higgins et al., 2000; Sankaran et al., 2013). However, if the relaxation continues for a long time or if the consumers disappear completely, the escaping trees will eventually grow into a closed canopy, i.e., a forest, with the potential to out-shade the herbaceous vegetation (Scholes and Archer 1997, Charles-Dominique et al. 2018, Bond 2021).

There are many studies on the effects of fire and herbivory in open habitats, especially on woody vegetation. Simulations have shown that without fire, the area of closed forests would increase substantially in all of the world (Bond et al., 2005). N'Dri et al. (2022) found that dry season fire reduced the tree density in a West African savanna. In a study from the African savanna, native ungulates prevented woody expansion (Sankaran et al., 2013) and Capozzelli et al. (2020) showed that introducing both fire and herbivory into the landscape decreased the woody encroachment on grasslands in central North America. Similar results were found in studies in the African savanna (Ngugi et al., 2022; Staver et al., 2009). All of these studies show that fire and herbivores are important factors that can control woody vegetation.

1.2 Fire and herbivory create heterogeneity

The strong effects of fire and herbivory have led to the evolution of plant traits to persist in their presence. According to Archibald et al. (2019), there are three different types of traits to persist in the presence of fire and herbivory. *Avoidance* traits act before consumption, by plants being non-flammable or unpalatable (Archibald et al., 2019). *Resistance* traits act during consumption, by protecting certain parts of the plant by e.g., thick bark or a cage structure (Archibald et al., 2019). *Tolerance* traits act after consumption, by plants being able to re-sprout or germinate after fire or herbivory (Archibald et al., 2019). Although this was shown for grasses primarily, this framework seems to be also relevant for trees (Archibald et al., 2019). However, plants themselves can also alter the fire and herbivory regimes by, e.g., increasing the occurrence of fire by being flammable and/or attracting herbivores by being palatable and thereby reduce the competition from other fire- or herbivory-sensitive species (Archibald et al., 2019; Bond & Midgley, 1995; Hempson et al., 2019). In this case, the plant is not an avoider, but must instead have traits for resistance or tolerance (Adie & Lawes, 2022; Churski et al., 2022; Coughenour, 1985; Schwilk & Ackerly, 2001).

The presence or absence of fire and herbivory ultimately drives the plant species composition and abundance and creates different communities of species (Bond, 2005; Charles-Dominique et al., 2015; Hoffmann et al., 2012; Keeley et al., 2011; Ratnam et al., 2019). Bond (2005) named these communities *green*, *brown,* and *black worlds*, which states that the presence or absence of consumers of plant biomass, i.e., fire and herbivory, drives the development of these ecosystems (*consumer control*). The green world is driven by competition for resources, without the impact of the consumers present. The brown world is mainly driven by herbivory, and in the black world, fire is the main driver of vegetation structure (Bond, 2005).

Fire and herbivory, as separate processes, can have a great effect on vegetation structure and thereby, the heterogeneity in an ecosystem (Bakker et al., 2004; Cingolani et al., 2005; Vera, 2000). Furthermore, the interaction between fire and herbivory can have an even greater effect on the ecosystem than the two processes separately (Bernardi et al., 2019; Collins & Smith, 2006; Holdo et al., 2009; Nieman et al., 2022; Royo et al., 2010). To capture these interactive effects, the term *pyric herbivory* was first introduced in 2009 by Fuhlendorf et al., defined as 'herbivory driven by fire'. Pyric herbivory conceptualises the process of spatiotemporal interaction between fire and herbivory, which happens when herbivores are attracted to newly burned vegetation (Fuhlendorf et al., 2009). When herbivores prefer to graze and browse on the nutrient rich vegetation on newly burned patches, they reject other patches, with an accumulation of fuel on these patches as a result (Allred et al., 2011; Archibald et al., 2005; Donaldson et al., 2018; Kramer et al., 2003; Leverkus et al., 2018). This alters the probability of future fires and, in the end, creates a shifting mosaic in the landscape with a great variation in both space and time (Figure 1; van Langevelde et al. 2003, Fuhlendorf and Engle 2004, Starns et al. 2019, Young et al. 2022). This process creates more heterogeneity, both at fine and at landscape scale, than when the two consumers act as two separate forces (Fuhlendorf & Engle, 2004; Fuhlendorf et al., 2009; McGranahan et al., 2012; Olff et al., 1999).

1.2.1 The use of fire and herbivory in nature conservation

Fire and herbivory are widespread grassland management tools, mainly in the Southern Hemisphere and North America (Bond, 2005; Bowman et al., 2011; Gillson et al., 2019; Kirkpatrick et al., 2011; Reid et al., 2023). In North America, fire has been introduced to improve livestock production, but also to restore natural processes (Scasta et al., 2015), and in Africa both fire and herbivory are used to manage shrublands (Johansson & Granström, 2014). However, in Europe traditional management methods are usually costly, such as using machines for mowing and tree cutting, and fire is rarely used (Bonari et al., 2017; Török et al., 2011). Furthermore, until now, conservation management practices have been focusing on managing for an 'intermediate state', where large areas are exposed to intermediate levels of management, creating homogenised ecosystems (Bonari et al., 2017; Briske et al., 2003; Fuhlendorf & Engle, 2001). Unfortunately, these methods ignore the spatiotemporal differences in vegetation structure that are created when both fire and herbivory are present and interact (Briske et al., 2003; Fuhlendorf & Engle, 2001). Reintroducing the interaction of fire and herbivory in management has therefore been suggested to increase the heterogeneity of the European open ecosystems (Múgica et al., 2021; Smit & Coetsee, 2019).

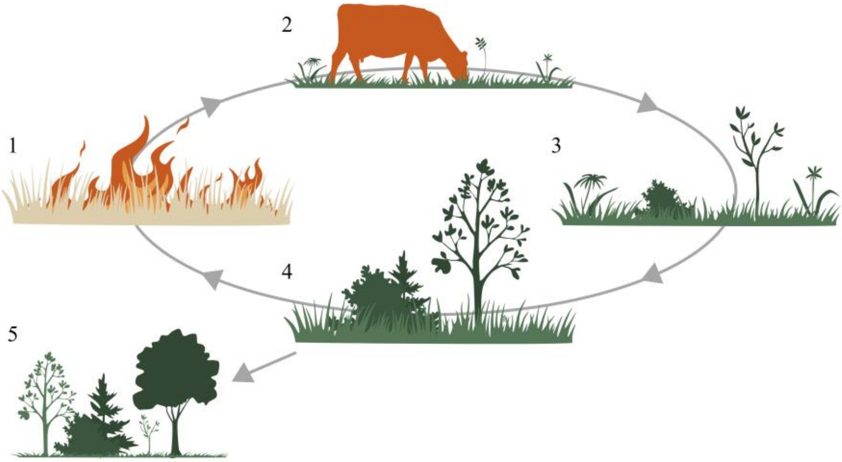

Figure 1. Conceptual model of the effect of and interaction between fire and herbivory, termed pyric herbivory (Fuhlendorf et al., 2009). Fire consumes grass litter, inducing re-sprouting of vegetation (1); herbivores consume the highly nutritional re-sprouting vegetation (2); herbivores move to more recently burned areas, leading to a relaxation in consumption in the previously grazed area (3); vegetation accumulation with some trees outgrowing the fire-/browse trap (4); the accumulation of vegetation fuels a new fire, which kills or inhibit smaller trees (1); alternatively, the fire is inhibited and the herbivores are absent, resulting in woody vegetation growing into a closed canopy which out-shades the herbaceous vegetation (5).

1.3 The temperate European view

Despite existing knowledge about the important effects of fire and herbivory as drivers in open ecosystem on other continents, few studies have been conducted in Europe, especially in the temperate northern part of the continent. For long, the general view has been that the few existing open areas in temperate Europe are anthropogenic remnants of prescribed fires and livestock management and that the ‘natural’ ecological state is a dense forest cover (Leuschner & Ellenberg, 2017; Mitchell, 2005). The reason for the lag in recognizing the natural origin of open habitats in temperate Europe is the rareness of undisturbed open ecosystems in this region (Estes et al., 2011). Temperate European grasslands have, in comparison with tropical grasslands, experienced a greater loss of megaherbivores (Estes et al., 2011) and have a largely unknown fire history (Leys et al., 2018). Furthermore, human impact, such as conversion to arable land, has been much greater in Europe than in other continents (Bond, 2019; Bond & Parr, 2010).

The alternative view of a semi-open landscape in temperate Europe was first proposed by Vera (2000) and Svenning (2002). Both suggested that large parts of Europe were prehistorically covered with open vegetation, shaped by a diverse fauna of now mostly extinct large wild herbivores and also natural fires. Many studies have followed in their footsteps (see, e.g., Birks, 2005; Bobek et al., 2017; Bond, 2005; Feurdean et al., 2018; Scheffer et al., 2012). Many ecologists and paleoecologists now claim that savanna-like open and semi-open ecosystems were naturally present in many parts of Europe in the early Holocene (Bradshaw et al., 2003; Feurdean et al., 2018; Hejcman et al., 2013; Pokorný et al., 2015; Svenning, 2002). The theories are based on paleoecological studies on subfossil remains of extinct megaherbivores (Bakker et al., 2016; Hejcman et al., 2013; Malhi et al., 2016; Mitchell, 2005) and dendrochronology studies (Bond & Keeley, 2005; Carcaillet et al., 2009; Zin et al., 2015). These studies confirm the presence of large mammalian herbivores and natural wildfires earlier than the entry of human impact. This presence would probably have had the same effect and led to the same processes that are still ongoing in some African, American, and Australian ecosystems. It has been suggested that Neolithic livestock grazing and anthropogenic fires were rather a replacement for ancient processes than the origin of open ecosystems in Europe (Bocherens, 2018; Feurdean et al., 2018; Pokorný et al., 2015; Vera, 2000).

These findings suggest that both fire and herbivory probably have also been important drivers of processes shaping plant traits and ecosystems in many parts of temperate Europe (Churski et al., 2017, 2022; Erdős et al., 2022). and that these processes should be considered in the management and conservation of open habitats in this region. However, the lack of knowledge on how fire and herbivory, both separately and simultaneously, affect temperate European ecosystems calls for more research based on knowledge from other continents. With a loss of more than 90% of European grasslands in recent centuries, resulting in highly negative consequences for biodiversity (Bullock et al., 2011; Cousins & Eriksson, 2008; Dengler et al., 2020; Pärtel et al., 2005; Plieninger et al., 2015), we need a better understanding of how different management methods affect the temperate open ecosystems of Europe.

2. Thesis aim

The overall aim of this thesis is to examine how fire and herbivory (alone and interactively) affect landscape openness in a temperate Northern European context. For this we conducted a full-factorial field experiment in a wood-pasture with prescribed grass fires and grazing by cattle, both separately and in combination. We studied both the effects of fire and herbivory on different types of vegetation, such as trees, forbs, and grasses (**I, II,** and **IV**), and also the interactive effects that these two processes have on each other (**III**).

The following research questions are addressed in the papers included in this thesis:

I Can fire and herbivory induce consumer control (in terms of reduced tree sapling survival and growth) in a temperate ecosystem, and do the responses to fire and herbivory vary among different temperate tree species?

II How do fire and grazing affect the establishment and reproductive success of temperate forbs?

III Does fire affect the grazing behaviour of cattle in a temperate ecosystem in similar ways that have been shown in other grassy ecosystems, and can this in turn affect the fuel load for future fires?

IV Can fire and grazing by cattle alter the tree-grass ratio in a temperate Northern European ecosystem?

3. Methods

All the papers in this thesis are based on one ecological field experiment. Below, I briefly summarise the experimental setup, while more detailed descriptions concerning each specific study can be found in the individual papers.

3.1 Study area

The experiment was carried out in the Ecopark of Nordens Ark (ENA, Figure 2), located on the west coast of Sweden (58°27'N 11°25'E). ENA is located next to the Åby fjord with acid granites dominating the bedrock (Berglund, 1988). There is a high variation in soil layers with deep clay layers in valleys and rocky outcrops on the higher lying areas (Blomgren & Falk, 2011), and also accumulations of clamshells from the ice age enriching the soils (Hallberg, 1971).The Atlantic has a strong influence on the climate, leading to mild winters and cool summers (Wastenson et al., 2004), with a mean annual temperature of 8-9 °C and an average annual precipitation of 800-900 mm (www.smhi.se/kunskapsbanken/klimat/normaler/normalperioden-1991-2020-1.166930, 2023-09-18).

The area has had a long history of anthropogenic fires, with burning of *Calluna* heathlands and spring grass burning as common management methods (Atlestam, 1942; Lindholm, 2019; Weimarck, 1979), as well as natural fires (Högbom, 1934). The experimental site has also a long history of grazing by livestock until the early 1900s, when the area was planted with conifer production forest (Figure 3; Ernby 2010). In 2011, the ENA was established, including a restoration program that converted 100 ha of conifer plantation into wood-pastures with several large corrals suitable for cattle, sheep, goats, and horses.

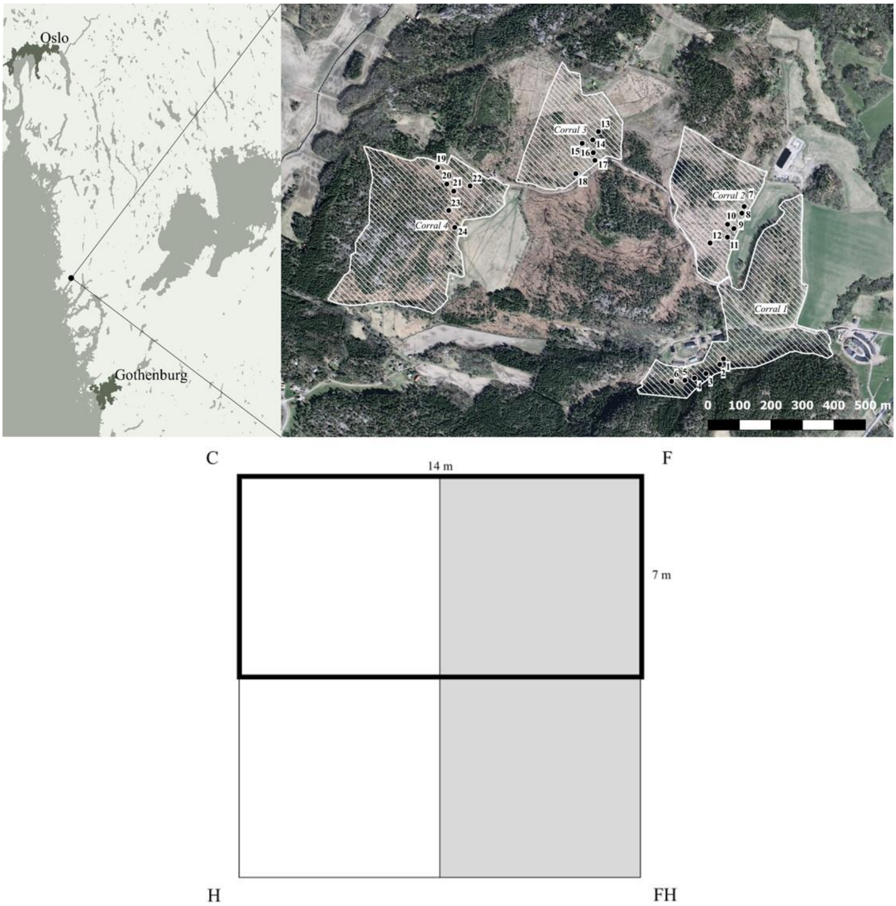

Figure 2. Upper left: Location of the study area on the Swedish west coast. Upper right: Position of the 24 study plots in the Ecopark Nordens Ark. Lower: Design of the study plots (14x14 m). The study plots were divided into four subplots (7x7 m), with two fenced (bold line) and two burned (grey colour) subplots leading to four treatment combinations: FH=*fire+herbivory*, H=*herbivory*, F=*fire*, and C=*control*. Each number in the figure represents two adjacent study plots (established 2015 and 2017; modified from Amsten et al., 2021).

Since then, the area has undergone a drastic transformation from shady forest conditions with little herbaceous vegetation to early successional species, such as raspberry *Rubus idaeus*, and later to open and semi-open grasslands with some naturally regenerated woody species also in the grazed areas (Figure 3; Hedlund 2019).

Figure 3. A dead European oak *Quercus robur* in Corral 2 before the forest was felled (left) and after felling in 2011 (right).

3.2 Experimental setup

In spring 2015, we established 24 study plots (hereafter ‘plot’), in four of the corrals in ENA, each plot measuring 14x14 m (Figure 2). Randomly chosen, one half of the plot was fenced with a 2 m high mesh wire and one transverse half was randomly chosen for fire treatment. This design gave us four different treatment combinations in all plots: *control* (no fire and no herbivory), *fire* (fire but no herbivory), *herbivory* (herbivory but no fire) and *fire+herbivory* (fire and herbivory; Figure 2). In 2017, we replicated each plot in direct connection to the existing one, to double the study area. These are hereafter called ‘2017-plots’ and the original plots are called ‘2015-plots’.

The initial prescribed burning of the *fire* and *fire+herbivory* subplots in the 2015-plots was conducted in spring 2015. We continued with annual burnings in early spring, and from 2018 we also burned the 2017-plots each year. All subplots were burned with the same technique, using a drip torch in six parallel lines across the subplot (Figure 4). In 2022 we collected detailed fire behaviour data for some plots, which can be found in Table 1 as an indicator of the fire regime. The 2015-plots were burned until spring 2020, and the 2017-plots were burned until spring 2023.

Table 1. Example of fire behaviour data from the *fire* subplot, collected in six plots in 2022. A similar fire regime was applied throughout the whole experiment.

Plot	**Rate of spread ($m*min^{-1}$)**	**Flame height (cm)**	**Temperature (ºC)***	**Tailwind ($m*s^{-1}$)**
7	1.7	37	-	1.9
8	2.1	12	-	1.4
9	3.3	40	-	1.9
10	1.5	40	96	0.3
11	2.4	40	124	0.7
12	1.2	36	80	0.7

*****Temperature measured with a plate thermometer. Missing values indicates failed measurements.

During the experiment, the main herbivores in the corrals were cattle (*Bos taurus*) of different breeds, mainly old native Swedish breeds (Figure 4). There were also horses, sheep, and goats during shorter periods. The grazing period began in May-June and ended in October-November each year (see Table 2 for grazing data from the first grazing season). Wild herbivores were also present in the area, such as moose *Alces alces* and roe deer *Capreolus capreolus*, although in small numbers.

Table 2. Grazing period and animal density during the first grazing season (2015) in the four corrals. A similar grazing regime was applied throughout the whole experiment.

Corral	**Plot ID**	**Grazing period**	**CD***	**Breed****
Corral 1 (12.6 ha)	1-6	15/5-30/10	875	RK, HF
Corral 2 (8.5 ha)	7-12	14/5-22/10	1349	RK, HF
Corral 3 (7.9 ha)	13-18	28/5-31/10	1648	RK, FN, HF
Corral 4 (16.8 ha)	19-24	2/6-3/9	1344	HF

* CD=Cattle-days (Number of cattle*number of grazing days)

** RK=Rödkulla, FN=Fjällnära, HF=Hereford

Figure 4. The two main treatments in the study, prescribed burning (left) and grazing by cattle (right).

In 2015, after the first burning, we planted 2400 saplings of the five temperate tree species Scots pine *Pinus sylvestris*, Norway spruce *Picea abies*, European oak *Quercus robur*, silver birch *Betula pendula*, and small-leaved lime *Tilia cordata* in the 2015-plots. In each subplot, we planted 25 saplings, 1-2 years old (Figure 5A). These trees were studied in Paper **I**. In 2018 we repeated the planting in the 2017-plots with five new species: European beech *Fagus sylvatica*, hornbeam *Carpinus betulus*, hazel *Corylus avellana*, guelder rose *Viburnum opulus*, and blackthorn *Prunus spinosa*. However, these trees were not included in any analysis in this thesis.

In 2016 and 2017, we sowed five species of open habitat forbs in the 2015-plots. In two randomly selected spots (one sowed in 2016 and one in 2017) in each subplot, we used a 45x60 cm sowing grid with grids forming 12 squares (one square per species, one control, and six buffer squares; Figure 5B). In the whole sowing grid, we cut the vegetation to 3 cm and lightly raked the soil. The five species used, selected for their differences in response to herbivory according to Ekstam & Forshed (1992), were common whitlowgrass *Draba verna*, brown knapweed *Centaurea jacea*, oxeye daisy *Leucanthemum vulgare*, cowslip *Primula veris*, and devil's-bit scabious *Succisa pratensis*. In 2022, we put up cages around the sown forbs in the grazed subplots in half of the plots, to protect them from herbivory, and thereby test how herbivory affects flower abundance. Both sowings were studied in Paper **II**.

During the first season of the experiment (2015), we used camera traps in all the plots to record the behaviour and grazing preference of the cattle. The cameras were placed to capture as much of the unfenced part of the plots as possible, and were activated by the movements of the cattle and recorded a 1-minute video each time the cow visited the plot (Figure 5C). The videos were used in Paper **III**.

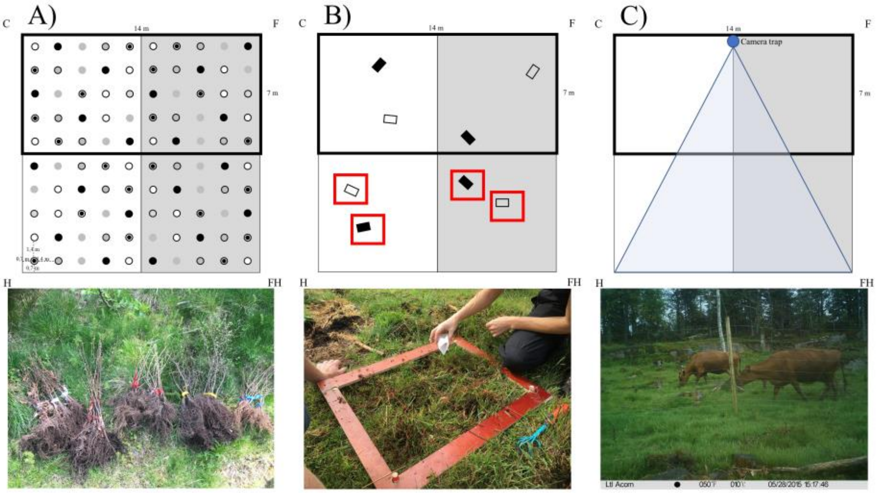

Figure 5. Different study setups in the experiment. (A) Upper left: 25 tree saplings were planted in each subplot of five different species (here represented by different dots), and each row (here horizontal) containing one sapling of each species planted in random order (**I**). Lower left: The tree saplings were 1-2 years old; (B) Upper middle: Example of the positions of the sowing grid within the subplots. One sowing was carried out in 2016 (white rectangles) and one in 2017 (black rectangles). The red surrounding rectangles indicate the cages built in 2022 in half of the plots (**II**). Lower middle: When sowing we used a frame with grid forming 12 squares; (C) Upper right: Position of the camera trap in the plots in 2015. The blue triangle indicates the view of the camera trap, covering ca. 75% of the grazed subplots **(III**). Lower right: The view of the camera traps (modified from Amsten et al., 2021).

3.3 Data collection

For the first paper (**I**), we recorded the survival and height increment of the tree saplings planted in 2015, during spring 2018, after three seasons of treatment. Survival was classified into three classes (live/dead/gone) and sapling height was measured on the stretched main top.

The sowed forbs, studied in the second paper (**II**), were surveyed with regard to establishment (defined as the development of a rosette with mature leaves), production of inflorescences (defined as the production of a flower stalk) and the remaining inflorescences after caging. The survey was conducted annually until 2020, except for 2019.

In the third paper (**III**), we used the videos from the camera traps to analyse the time the cattle spent visiting the plots and the time they spent grazing. In total we had over 4000 visitations and over 2000 grazing events. We estimated the grazing time as the mean time in seconds per 1-minute videos. As an indicator for fire intensity we made a visual assessment of the proportion of each subplot that was burned, and as an indicator of fuel load we measured the pre-fire grass height before the burning took place each year. We also surveyed the vegetation composition in two 45x60 cm quadrants in each subplot with regard to cover of individual species and life-forms according to Kattge et al. (2020; hemicryptophyte graminoids, hemicryptophyte forbs, hemicryptophyte ferns, phanerophytes and chamaephytes).

For the final paper (**IV**), we surveyed all plots for woody and herbaceous biomass in January-March 2023. We measured the diameter at breast height of all tress taller than 130 cm, and for trees below 130 cm we recorded the root collar diameter and the sapling height. To calculate woody biomass per square metre, we used Marklund's (1988) equations for trees taller than 130 cm and the general equations from Menéndez-Miguélez et al. (2022) for trees shorter than 130 cm. The herbaceous biomass (graminoids and forbs) was first estimated for cover in nine quadrants (50x50 cm) in each subplot. We then cut all the graminoids and forbs (live and dead) in two randomly chosen quadrants. This material was then dried and weighed. The biomass weight was related to the cover and this relation could then be used to predict the weights for all nine quadrants with estimated cover in each subplot. From these predicted values, we calculated the total herbaceous biomass per square metre.

4. Main results and discussion

4.1 Temperate trees have different adaptations to fire and herbivory (I)

In this study, we examined the effect of fire and herbivory on the survival and height increment of saplings of five different temperate tree species, three years after planting. Herbivory had an overall reducing effect on sapling survival and height increment, but the strength of the effect varied between species (Figure 6). Herbivory significantly decreased the survival of all species (Figure 6A), but height increment was only reduced by herbivory for *P. sylvestris*, *Q. robur,* and *B. pendula* (Figure 6B). Important to consider is that the reduction in tree sapling survival and height by herbivory is not only the result of direct foraging but is also a consequence of other effects of the presence of herbivores, such as trampling (Van Uytvanck & Hoffmann, 2009). Fire had a significant reducing effect on the survival of all species, except for *Q. robur* (Figure 6A), but only reduced the height increment of the surviving saplings of *B. pendula* (Figure 6B). A possible explanation for the lack of effect on height increment in our study is the relatively low flame height, which never reached the top of the saplings (see Paper **III**).

As expected, we found an interaction between fire and herbivory, where fire did not have an additional effect when added to herbivory treatment. Previous studies have shown that herbivory can reduce the amount of fuel and thus reduce the intensity and effect of fire (Archibald & Hempson, 2016; Hierro et al., 2011; Kimuyu et al., 2014; Leonard et al., 2010). Herbivory thereby controls fire or can even completely exclude it (Archibald & Hempson, 2016; Staver & Bond, 2014). In our experiment, the subplots with herbivory rarely had sufficient vegetation acting as fuel to support a self-spread fire (see Paper **III**).

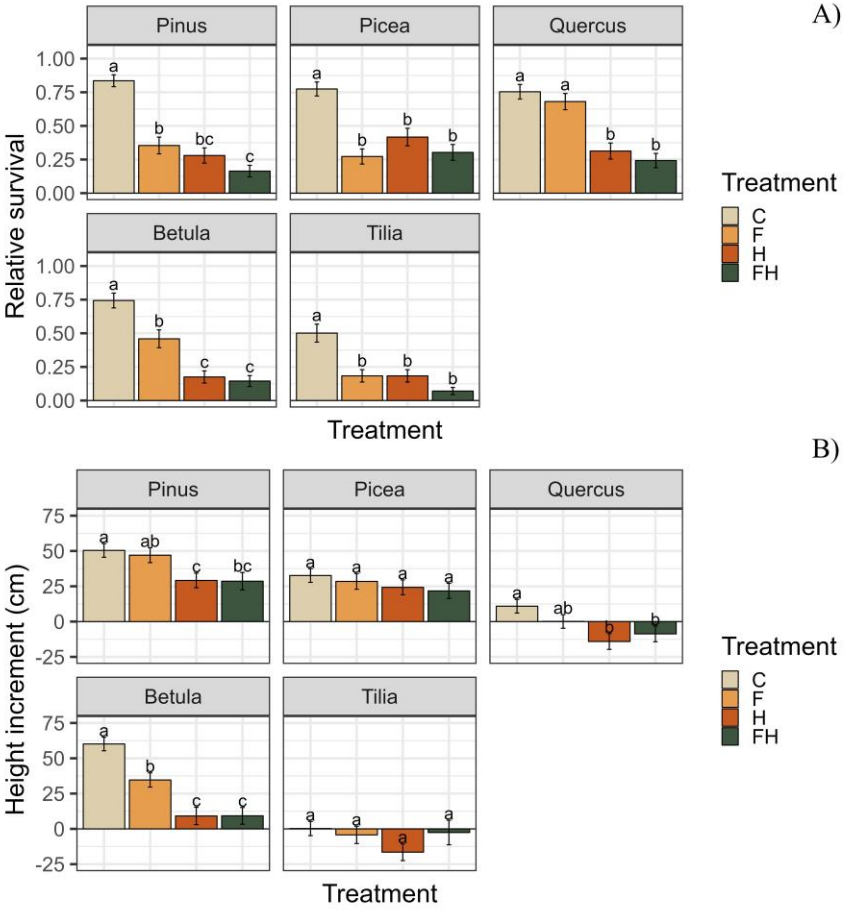

Figure 6. Relative survival (A) and average height increment (B) of tree saplings per species and treatment, three years after planting (error bars represent ±1 SE). 100 tree saplings of each species per treatment were included in the analysis, resulting in a total of 2000 individual saplings of which 806 saplings were alive after three years and were further measured for height increment. Significance within each species is indicated with letters (P<0.05). Species as appearing in figure: Pinus *Pinus sylvestris*, Picea *Picea abies*, Quercus *Quercus robur*, Betula *Betula pendula*, and Tilia *Tilia cordata* (Amsten et al., 2021). Treatments as appearing in figure: FH=*fire+herbivory*, H=*herbivory*, F=*fire,* and C=*control*.

The three best surviving species in our experiment, *Q. robur, B. pendula,* and *P. sylvestris,* have all previously been shown to be strong survivors in fire (Bond & Midgley, 2012; Carcaillet et al., 2009; Fréjaville et al., 2018; Niklasson et al., 2010; Richardson, 2000; Spînu et al., 2020). However, their observed differences in height increment suggest that they possess different strategies to persist fire. *B. pendula* and *P. sylvestris* were both the tallest in the burned treatment after three years, indicating that they escaped the flame zone by investing in height growth (LaMalfa et al., 2019; Skowno et al., 1999). *Q. robur*, on the other hand, showed almost no height increment following fire, indicating investment in other mechanisms. Fire resistance through re-sprouting has previously been shown in the *Quercus* genus (Abrams, 1992; McEwan et al., 2011; Petersson et al., 2020; Ziobro et al., 2016) and is the reason for the high survival of *Q. robur* in our study. An important factor, which determines the efficiency of a strategy to persist in the presence of consumers, is the life stage of the tree (Barton & Koricheva, 2010; Linder et al., 1998). Bark thickness, which is a trait in many tree species that increases fire resistance, is strongly dependent on the age of the tree, since it takes time to develop thick bark (Bär & Mayr, 2020; Fernandes et al., 2008; Pausas, 2015; Zin et al., 2015). The three-year time frame in our study was probably not sufficient for the saplings to develop the thick bark needed to resist fire. Therefore, the saplings instead depended on traits such as rapid height growth and re-sprouting.

The high survival rates of, and relatively low effect on height increment in the two conifers in the presence of herbivores correspond to previous studies showing that conifer species are the dominant tree type in herbivory due to low preference in herbivores (Lorentzen Kolstad et al., 2018; Pastor et al., 1988; Speed et al., 2013). Among the deciduous trees, *Q. robur* showed the highest survival under herbivory, although it showed a decrease in height after three years. This is again a result of the re-sprouting ability in *Q. robur*, which provides the strongest tolerance to herbivory among the tested deciduous trees.

As seen in our study, high survival in response to the two consumers tested did not always imply a large height increment. This confirms the existence of species-specific strategies to persist under fires and herbivory. Belsky et al. (1993) and Rosenthal & Kotanen (1994) suggested two highly contrasting plant strategies. The *tolerance strategy* implies that a plant can tolerate and survive a consumer but at the cost of height growth, such as the response of *Q. robur*, while the *avoidance strategy* implies avoiding the consumer by investing in fast growth or a defence, such as *B. pendula* and *P. sylvestris* in our experiment (Belsky et al., 1993; Rosenthal & Kotanen, 1994).

4.2 Forbs need open habitats to germinate and a relaxation of herbivory for reproductive success (II)

In this study, we examined the effect of fire and herbivory on the establishment and reproductive success of five temperate grassland forbs. Herbivory had a positive effect on the establishment of individual plants compared to treatment with neither fire nor herbivory (Figure 7A). Adding fire to herbivory did not increase the effect. However, fire alone had a positive effect, though not as large as herbivory. These results confirm previous findings that the coexistence of different types of species in open ecosystems is driven by the reduced competition from grasses by the removal of biomass by herbivores (Borer et al., 2014; Elson & Hartnett, 2017; Segre et al., 2016). Removal of grass litter increases light availability for shade-intolerant forbs (Borer et al., 2014; Foster & Gross, 1998). However, in addition to removing competition, the impact from herbivores may also include other processes, such as soil disturbance, which creates suitable conditions for germination (Pakeman et al., 2002). Additionally, seed dispersal and redistribution of nutrients are important consequences of herbivory (Le Roux et al., 2020; Pakeman et al., 2002).

In similar ways as herbivory, fire may also provide release from competition and may therefore be an important driver of species coexistence, but there are some fundamental differences. Fire only consumes dead dry material, while herbivores prefer fresh material (Archibald & Hempson, 2016). Fire also acts differently in spatial and temporal aspects; fire affects spatially uniform areas and occurs more rarely while herbivory is considered more continuous in time but more patchy in space (Archibald & Hempson, 2016). Furthermore, fire is restricted to periods when the vegetation is flammable, and the release of competition also has a shorter duration than under constant herbivory (Sjöström & Granström, 2023). As you move northward towards colder climates and increasing seasonality, the flammable periods become shorter and less frequent (Sjöström & Granström, 2023). In the temperate region of this study, flammability is often restricted to previous-year grass litter and for a short period in early spring (Sjöström & Granström, 2023). This is a likely reason for the weaker effect of fire than of herbivory in our study. Nevertheless, fire had a positive effect on establishment, with a higher number of established rosettes in *fire* than in *control*.

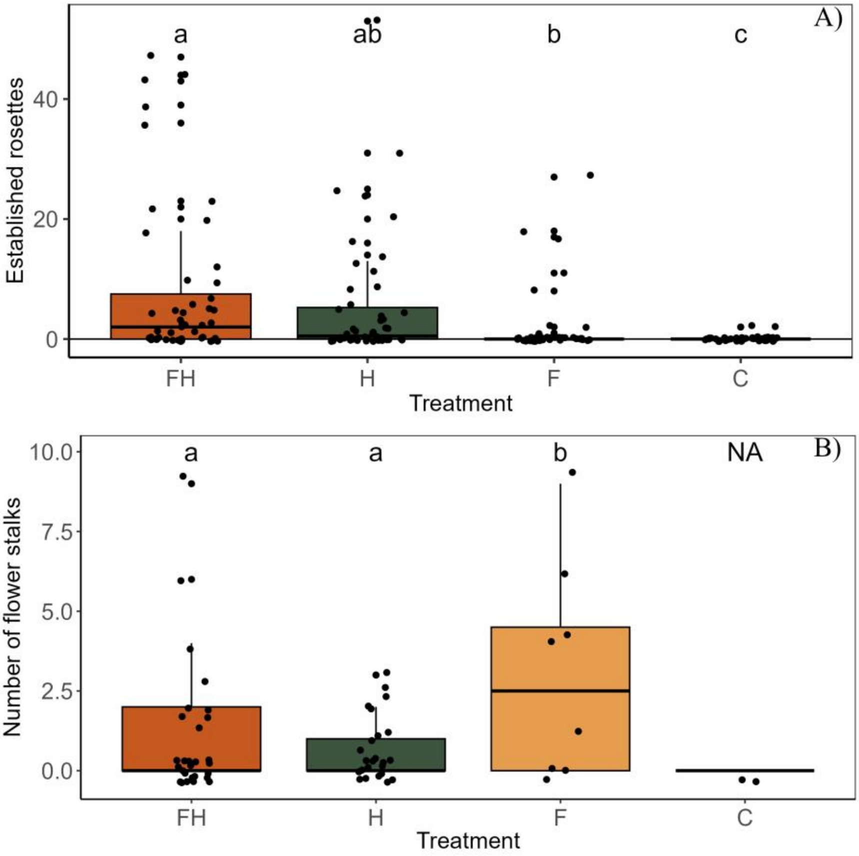

Figure 7. Established rosettes in 192 sowing grids (A) and number of stalks in 60 sowing grids with established rosettes (B) per treatment in fall 2020 (2016- and 2017-grids; all species combined). The *control* was not included in the analysis of the flower stalks due to zero establishment ('NA'=Not Analysed). Significance is indicated with letters (*P*<0.05). Treatments as appearing in figure: FH=*fire+herbivory*, H=*herbivory*, F=*fire*, and C=*control*.

Once the plants were established, the treatment with fire had the highest relative production of flower stalks (Figure 7B). Without a release from competition by neither fire nor herbivory, none of the few remaining individual plants produces flower stalks. Further, for the flowers to remain until the end of the reproduction season in the presence of herbivory, a relaxation in the herbivory pressure increased the probability of flowers remaining throughout the reproductive season (Figure 8).

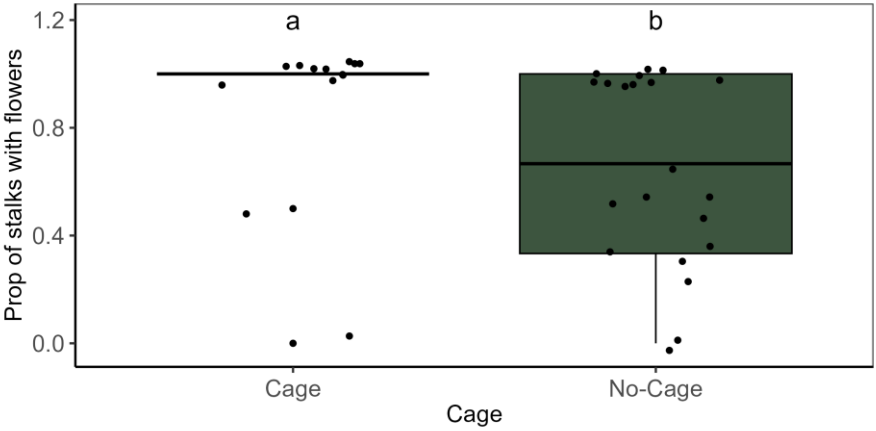

Figure 8. Proportion of stalks with remaining flowers with and without cages by the end of summer 2022 (2016- and 2017-grids; all species combined) in a total of 34 sowing grids (13 with cages and 21 without). Significance is indicated with letters (*P*<0.05).

To conclude, our results clearly indicate that grassland forbs strongly depend on the removal of competition induced by herbivory and/or fire both to establish and to produce flower stalks. At the same time, herbivores can also prohibit reproduction by removing flowers (Hempson et al., 2015). At high herbivory pressure, sensitive forbs can even disappear (Vázquez & Simberloff, 2004; Yoshihara et al., 2008). The reproductive success and thereby long-term persistence of forbs are therefore dependent on time windows of releases in herbivory pressure (Bonari et al., 2017; Larkin & Stanley, 2021; Nakahama et al., 2016; Uchida & Kamura, 2020; Vessby et al., 2002). However, since different species have different phenology, the timing and duration of this release will have varying effects on individual species.

4.3 Fire controls grazing preference in cattle and grazing controls future fires (III)

In this study, we examined the process of pyric herbivory in a temperate Northern European context. We found that cattle were attracted to the burned subplots, but only in the corral with the highest proportion of the subplots burned (Corral 1; Figure 9). The connection between burn size and strength in attraction after burning have also been shown by (Archibald & Bond, 2004). Furthermore, we also connected the proportion of the subplot that burned with the amount of fuel before the fire and found similar results to Augustine and Derner (2014). They suggested that productivity (in our case indicated by pre-fire grass height) has a positive effect on the attraction of herbivores to recently burned areas, due to the increase in fire size and intensity. In our study, the difference in productivity between the corrals can probably be explained by soil conditions and water availability, which have also been described as important factors affecting the strength of pyric herbivory (Sankaran et al., 2005; Staver et al., 2011). There are also other aspects, such as grazing pressure and cattle group composition, that need to be considered, however, they were not examined in detail this study.

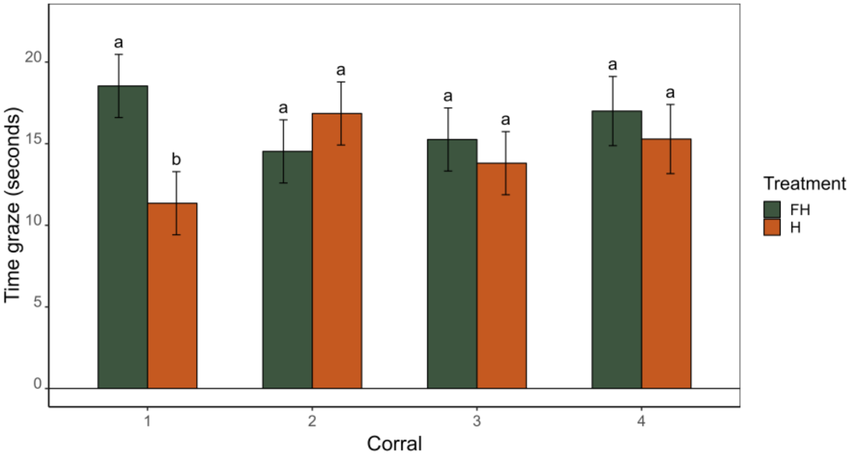

Figure 9. Mean time in seconds spent on grazing per treatment and corral during the grazing period in 2015 (error bars represent ±1 SE). Significance within each corral is indicated with letters (P<0.05). Treatments as appearing in figure: FH=*fire+herbivory* and H=*herbivory.*

After five years of fire and herbivory treatment, there was a decrease in grass height in Corral 1, with a greater reduction in the burned and grazed treatment (*fire+herbivory*) than in the only grazed (*herbivory*). This is probably a direct effect of the attraction after fire, i.e., pyric herbivory, and corresponds to previous studies (Fuhlendorf et al., 2009; Starns et al., 2019; Young et al., 2022). As predicted, the decrease in grass height also led to a decrease in proportion of a subplot burned in in Corral 1 (Figure 10). Five years of repeated burning and grazing decreased the mean proportion of the *fire+herbivory* subplots that burned in Corral 1 from almost 70% to less than 20%.

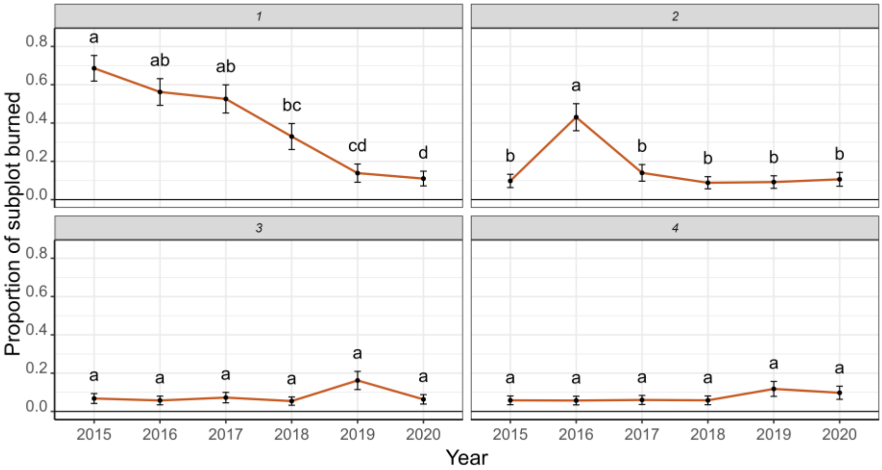

Figure 10. Proportion of subplot burned in *fire+herbivory* per corral over five years of treatment (error bars represent ±1 SE). Significance between years within each corral is indicated with letters (*P*<0.05).

Fire and herbivory also had an effect on plant species composition with a difference in species composition between the grazed and the ungrazed treatments after six seasons of treatment (2020), while fire had no effect. There was also a difference in the composition of life-forms. Herbivory promoted hemicryptophyte graminoids and inhibited chamaephytes (shrubs: *Rubus idaeus* and *Rubus fruticosus*; Figure 11). Fire also promoted graminoids, but interestingly, it did not inhibit shrubs, as shown in other studies (see, e.g., Pekin et al. 2012), probably due to the high re-sprouting ability of the main shrubs in our study, *Rubus idaeus* and *Rubus fruticosus* (Ainsworth & Mahr, 2004).

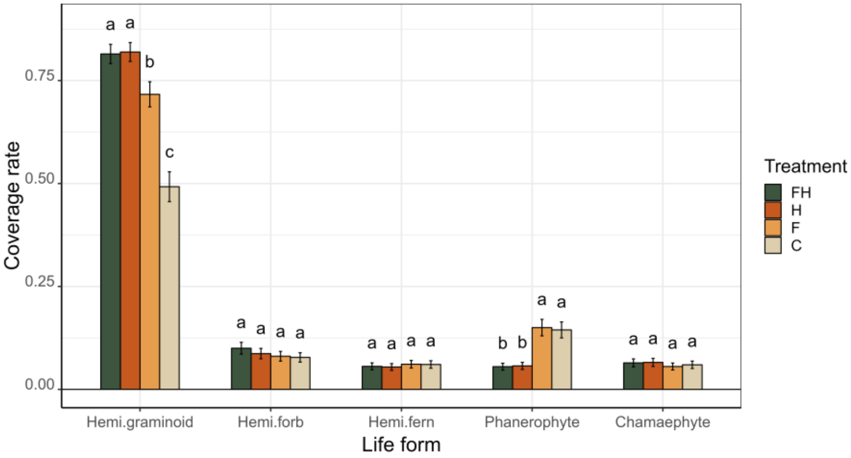

Figure 11. Coverage rate of five different plant life-forms per treatment in fall September 2020 (error bars represent ±1 SE). Significance within each life-form is indicated with letters ($P<0.05$). Treatments as appearing in figure: FH=*fire+herbivory*, H=*herbivory*, F=*fire*, and C=*control*.

Our study showed that if we add fire to management regimes of open habitats that includes herbivory, it will lead to an interaction between fire and herbivores, i.e., herbivores following fires and altering the fuel load for future fires. This likely leads to a shifting mosaic landscape with varying species and life-form composition (Collins, 1992; Fuhlendorf & Smeins, 1999).

Patch-burn grazing is a method that incorporates the concept of pyric herbivory in the management of open ecosystems (Fuhlendorf & Engle, 2004; Fuhlendorf & Engle, 2001), which has been used to increase heterogeneity in vegetation structure and plant functional groups, which promotes species richness (Leis et al., 2013; McGranahan et al., 2012; McGranahan, Raicovich, et al., 2013; Starns et al., 2020). However, this is the first time the concept has been studied in a temperate Northern European ecosystem. The common conservation management practices have, so far, included intermediate levels of management, applied uniformly to large areas, which creates homogenised ecosystems (Briske et al., 2003; Fuhlendorf & Engle, 2001). Hence, these methods do not result in the same spatiotemporal variation and pattern as pyric herbivory (Briske et al., 2003; Fuhlendorf & Engle, 2001).

In this study, we did not use a rotational fire regime, but burned the same subplots every year, and we also only used one type of herbivore, i.e., cattle. Nevertheless, we showed that after the first season, the cattle preferred to graze on burned subplots, and that the species and life-form composition differed among the treatments after six years, which is an indication that pyric herbivory can be an effective tool to promote heterogeneity also in a temperate ecosystem.

4.4 Fire and herbivory suppress tree recruitment and promote grasses (IV)

In this study, we examined the effect of fire and herbivory on the tree-grass ratio. The results show that there exists a clear reducing effect on tree biomass from both fire and herbivory and, reversely, an increasing effect on grasses and forbs. The highest levels of tree biomass were found in the *control* without fire or herbivory (Figure 12A). This is in line with previous studies, e.g., from South America, where Durigan et al. (2022) found that without cattle grazing, savannas can experience undesired woody encroachment. Similarly, in a study using satellite imagery, Venter et al. (2018) could show that with a decline in burned areas in African savannas, woody encroachment would increase.

Fire reduced tree biomass, in comparison with no treatment, but not as much as herbivory, and promoted grasses and forbs (Figure 12A). This is in contrast to other studies, which have found that fire reduces tree biomass more than herbivory (see, e.g., Staver et al. 2009). However, it is difficult to compare these results with our results because of differences in fire frequency and grazing pressure. Staver et al. (2009) used a two-year fire interval, while we burned every year which could result in differences in fuel loads and fire behaviour. Furthermore, grazing pressure was higher in our study, with at least four times the animal density compared to Staver et al. (2009; >400 kg/ha in our study compared to 116 kg/ha in the study by Staver et al. 2009).

Herbivory had the largest reducing effect on tree biomass (Figure 12A). This contradicts earlier findings that herbivores would promote woody vegetation by removing grasses and reducing competition (Bernardi et al., 2019; Briggs et al., 2002; Davies et al., 2021). An explanation to these contradicting results can be the high grazing pressure in our study, and that trampling can have an important effect on tree establishment and recruitment (Van Uytvanck & Hoffmann, 2009). This was also suggested in Paper **I** as an important factor for mortality on the planted tree saplings in the experiment.

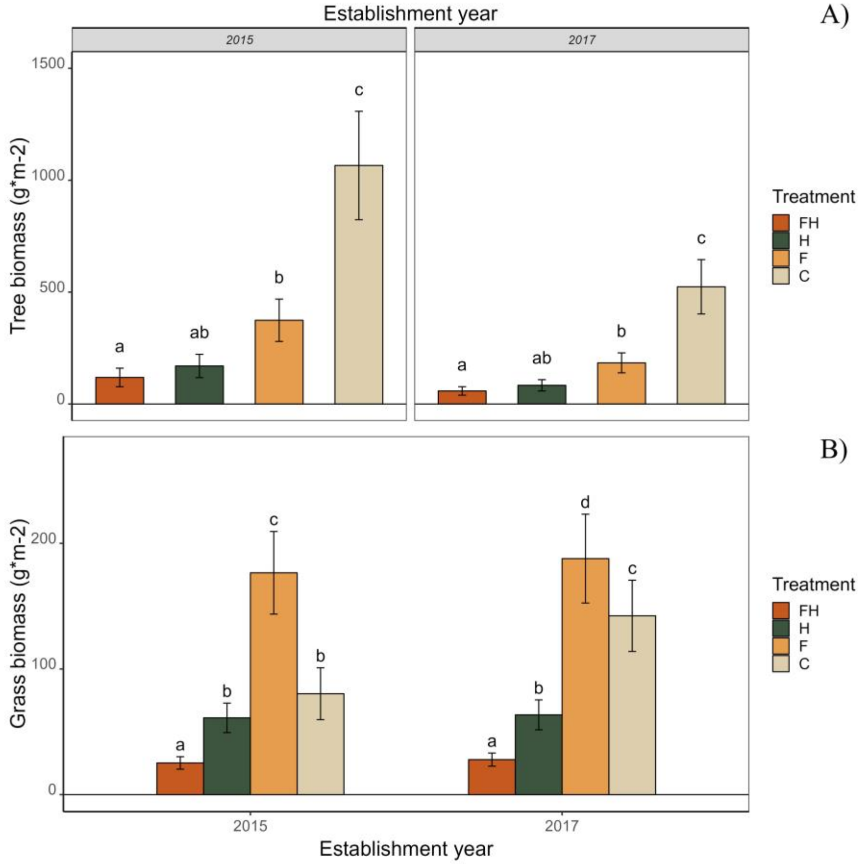

Figure 12. Tree (A) and grass (B) biomass in g*m^{-2} for each treatment and establishment year (error bars represent ±1 SE). Significance within establishment year is indicated with letters ($P<0.05$). Treatments as appearing in figure: FH=*fire+herbivory*, H=*herbivory*, F=*fire*, and C=*control*.

In the study by Staver et al. (2009), the combination of fire and herbivory was most effective in inhibiting woody encroachment. In our study, we did not find a difference between the treatment with only herbivory and the treatment with both fire and herbivory in the amount of tree biomass (Figure 12A). The most probable reason for this is the low fuel load in the treatments, due to herbivory, leading to a low fire intensity, which is described in Paper **III**. Similar results were also found in a study by Ngugi et al. (2022) in Kenya, where the amount of fuel was reduced by the cattle to the level where fire had no longer an effect on tree establishment and recruitment.

In contrast to tree biomass, the highest biomass of grass was found in the treatment with only fire and we also found a difference between the two grazed treatments, with higher grass biomass in the treatment with only herbivory than when fire was also added (Figure 12B). This could be an effect of pyric herbivory, described in more detail in Paper **II** and by Fuhlendorf et al. (2009).

The high tree biomass in the *control* treatment had a significant reducing effect on the herbaceous vegetation (Figure 13). With a two-year advantage in the 2015-plots, grass biomass was even reduced to the level of the grazed treatments, which is a clear effect of shading from the woody vegetation (Scholes & Archer, 1997). The high tree biomass, relative to grass biomass, in the *control* treatment is an indicator of the importance of woody species in the structure of vegetation (Bond, 2008). The grass biomass reached the carrying capacity in the treatment with only fire, with no further increase even after a two-year fire release in the 2015-plots. However, not unexpectedly, tree biomass had not reached the carrying capacity and continued to increase with a higher biomass in the 2015-plots than 2017-plots. A continuation of the study would probably lead to a further out-shading of herbaceous vegetation in the *control* treatment, i.e., a transition to a closed canopy forest (Hoffmann et al., 2012).

The fire regime in this study included burning every year in early spring and was used to mimic the most recent anthropogenic use of fire, which was annually burning of meadows for improved pasture for livestock (Weimarck, 1979). The high reduction of woody vegetation in our spring fires somewhat contradicts results from other studies that found a higher mortality in late summer fires, due to higher fire intensity (Ansley et al., 2021; Laris et al., 2021; N'Dri et al., 2022; Novak et al., 2021). However, since all present trees were removed at the start of our experiment, there were only newly re-sprouted seedlings and saplings that were exposed to fire, and as discussed in Paper **I**, it takes time for trees to develop traits to survive fire, such as thick bark (Bär & Mayr, 2020; Fernandes et al., 2008; Pausas, 2015; Zin et al., 2015).

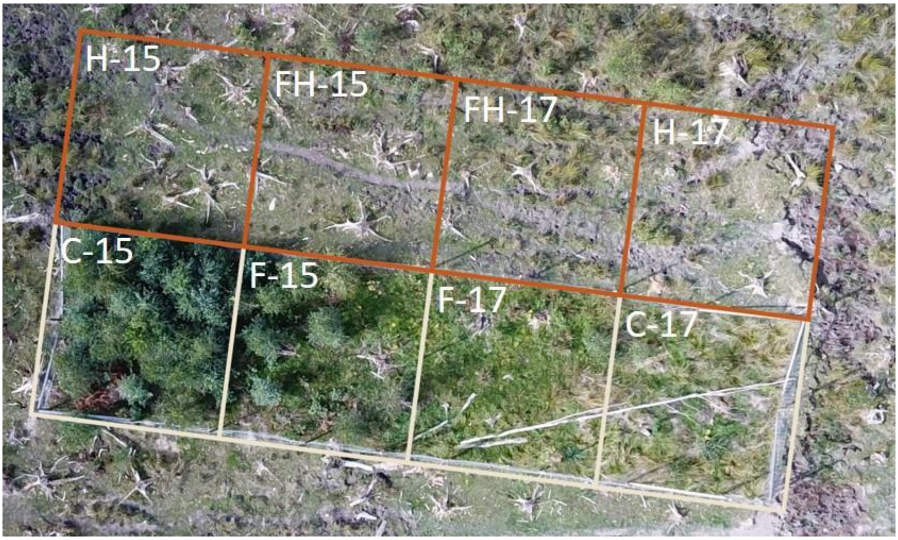

Figure 13. Vegetation structure in 2020 in one of the plots. Red lines determine the grazed subplots, and white lines determine the ungrazed (fenced) subplots. Letters and numbers indicate the treatment in and establishment year (2015 and 2017) of each subplot. Treatments as appearing in figure: FH=*fire+herbivory*, H=*herbivory*, F=*fire,* and C=*control*.

In this study, we used cattle as a substitute for large wild herbivores, as suggested by Capozzelli et al. (2020). Studies have shown that cattle can have a foraging pattern similar to that of American bison *Bison bison* (Fuhlendorf & Engle, 2004; West et al., 2016). However, there are also studies that have compared different types of herbivores, such as grazers and browsers, and also animal size and density, which show that they can have a largely different impact on the vegetation (Donaldson et al., 2022; Grellier et al., 2012; Laris et al., 2021; Riginos, 2009; Sankaran et al., 2013; Staver & Bond, 2014). This highlights that the aggregated effect of herbivory is complex and needs to be considered in management planning.

5. Main conclusions from each paper

(**I**) Fire and herbivory significantly affected the survival and development of tree saplings. We showed that different tree species have contrasting strategies (avoidance vs. tolerance) to persist in the presence of these biomass consumers, and our findings illustrate the strong consumer control that fire and herbivory can exercise in a temperate Northern European open ecosystem, comparable to other continents. The adaptation of different Northern European tree species to fire and herbivory suggests that both fire and herbivory played an important role in the structuring of temperate European landscapes in the past.

(**II**) The shade-intolerant forbs in our study strongly depended on herbivory or fire for their establishment, since almost none were established under consumer-free conditions. However, fire promoted the reproduction potential of established plants. We also showed that a release in herbivory improves reproductive success. This shows the importance of combining herbivory and fire during the life cycle of grassland forbs. It is also clear that we need a better understanding of the role of fire and herbivory in temperate European grasslands, to mitigate the biodiversity crisis related to decreasing grasslands in Europe.

(**III**) Our study showed that pyric herbivory can be used as a management tool also in temperate Northern European wood-pastures, by fire affecting cattle foraging behaviour. We showed that the effect was connected to fire intensity and that increased herbivory in burned areas reduced the fuel for future fires. Furthermore, fire and herbivory altered the plant species composition and also the composition of the vegetation in respect to life-forms. By implementing pyric herbivory in management, we could likely create landscapes with high heterogeneity, which promotes biodiversity.

(**IV**) Fire and herbivory had a great impact on the trees-grass ratio also in our temperate Northern European landscape, with fire promoting grasses and forbs. The absence of both fire and herbivory quickly results in an increase in tree biomass, which gradually out-shads the herbaceous vegetation. We show that these biomass consumers play a key role in preventing open ecosystems from growing into forests, and our results also illustrate the complexity of tree-grass coexistence in temperate open ecosystems.

6. Implications for biodiversity management of open ecosystems

The overall goal of this thesis was to examine whether the concept of consumer control acts in similar ways in a temperate Northern European open ecosystem as has been shown for other continents. Our results show that both fire and herbivory can have significant effects on both woody and herbaceous vegetation. What is obvious in our studies is that, without fire and herbivory, many open habitat species, which are important for other taxa, such as insects, will sooner or later be out-shaded under a closed tree canopy (**II** and **IV**).

Evidence from paleoecological and dendrochronological studies of prehistoric fires and the presence of mega- and meso-herbivores until the previous century gives the basis for theories of a mixed open-, semi-open, and closed landscape as the ‘natural state’ of temperate Europe (Svenning, 2002; Vera, 2000). The anthropogenic use of fire for centuries and long-term farming of livestock were not the origin of open ecosystems of temperate Europe but rather a substitute for ceased natural processes (Bocherens, 2018; Feurdean et al., 2018; Pokorný et al., 2015). Our results add further evidence to these theories by showing that both woody and herbaceous temperate vegetation are adapted to and can even be dependent on fire and/or herbivory (**I** and **II**), indicating adaptation to the presence of plant biomass consumers. This is important knowledge when planning the management of these highly diverse natural habitats (Veldman et al., 2015).

The traditional practice of nature management, with an ‘intermediate state’ as the target vision, needs to be reconsidered (Bonari et al., 2017; Briske et al., 2003; Fuhlendorf & Engle, 2001). Instead, we need to think in the terms of a shifting mosaic landscape, with varying levels of management both over time and space. Our studies show that fire and herbivory create different habitats with different species (**I**, **II**, and **III**) and promote different life-forms (**III** and **IV**). This, in turn, has the potential to create heterogeneity in the landscape, improving the conditions for open habitat species and higher biodiversity. Using fire and herbivory simultaneously creates different conditions compared to the effect of these consumers separately due to complex interactions, which increases spatial and temporal heterogeneity.

In this experiment, we used an annual fire regime without spatial and temporal rotation, which is a characteristic of pyric herbivory. Further, we only used cattle, and even if cattle are supposed to have similar effect on the vegetation as bison (Towne et al., 2005), other herbivore species and types also need to be tested. Previous studies have demonstrated the complexity of fire-herbivory interactions, and some of these studies have even shown negative effects of fire and herbivory on biodiversity (McGlinn & Palmer, 2019; McGranahan, Engle, et al., 2013; Scasta et al., 2016). Further research is therefore needed to understand how different fire regimes, such as variation in fire frequency, seasonality, and intensity, and also grazing regimes, such as herbivory type, and animal density, affect the ecosystem and also how they interact in a temperate European ecosystem.

Today, when biodiversity is being lost at an alarming rate and there is a demand for higher food production, we need sustainable management methods that both improve conditions for biodiversity and that can maintain a sustainable livestock production. Using fire and herbivory has been shown to help solve both these problems, by increasing livestock productivity and at the same time, promote heterogeneity and diversity in the landscape (Allred et al., 2014; Fynn, 2012; Limb et al., 2011; McGranahan et al., 2014; McGranahan & Kirkman, 2013). Furthermore, there is also a new threat to open ecosystems, in afforestation, which is conducted to mitigate climate change (Bond, 2019). There are indeed areas that have been deforested, which are suitable for *re*-forestation, however, many targeted areas for planting of new forests for carbon storage are often ancient open ecosystems, such as the Brazilian cerrado (Bond, 2019). Afforestation of these ecosystems would lead to a great loss of open ecosystem biodiversity, not accounted for (Bond, 2019). Nevertheless, open ecosystems can still be used in other ways to reduce the consequences of a changing climate, where fire and herbivory can decrease the risk of future wildfires, which are predicted to increase in magnitude (Johnson et al., 2018). Therefore, both fire and herbivory should be included in nature management to a greater extent.

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Popular science summary

Today, the loss of biological diversity is occurring at an alarming rate worldwide. One significant reason for this drastic reduction is the decline of open ecosystems, which are some of the most species-rich ecosystems in the world.

Open ecosystems are defined by their lack of a shading tree canopy, with the ground instead covered by light-demanding plants, such as grasses and herbs. In many cases, climate determines the type of vegetation found in a particular area. If it is warm enough with sufficient rainfall, the conditions allow forests to grow. However, in cooler and drier areas, forests cannot be established, and these areas are dominated by other types of vegetation. Yet, there are areas that are warm enough and receive enough rainfall for forests to grow, but the landscape still consists mostly of semi-open grasslands with isolated or groups of trees. It was long believed that these landscapes were the result of significant disturbances, such as fires or storms, and that they were merely a successional stage on the way back to dense forests. However, research has shown that open ecosystems are stable states that have existed for a long time and have even developed their own species communities. So, what determines whether a landscape remains open in areas where conditions favour forest growth?

This is a well-studied question, particularly in African savannas where large open areas still exist. Researchers now agree that it is fire and large herbivores that keep these landscapes open and prevent it from growing into forest. Fire and herbivory prevent trees from growing large and form dense tree canopies, thus keeping the landscape open for a variety of species of animals and plants that are dependent on light.

Fire and herbivory also interact with each other, as herbivores tend to forage in areas that have recently been burned, attracted by the highly nutritional vegetation that re-sprouts after a fire. Herbivory reduces the amount of fuel in the new-burned area, reducing the risk of further fires, while in ungrazed areas, fuel is accumulated which increases the risk of fire. Once a new area burns, herbivores are attracted to it, and the process is repeated. This creates a mosaic landscape with different stages of vegetation, ranging from well-grazed grasslands immediately after a fire to areas with more vegetation where even trees can occasionally grow into adult trees. Such a landscape contains many different habitats suitable for a variety of species.

Despite this knowledge, the origin of the few remaining open areas in Europe is still debated. Many believe that open areas in Europe are solely the result of human influences on nature, such as livestock grazing and the use of fire in various contexts. However, there are now an increasing number of studies showing that Europe was partly an open landscape, even before humans arrived. This can be demonstrated through fossil findings of large herbivores such as giant deer and woolly rhinoceros, as well as aurochs and wild horses that survived until the last centuries. Paleoecological evidence also indicates that regularly occurring fires had a significant impact on the landscape. Additional evidence includes the presence of species adapted to both fire and herbivory, with features, such as like thick bark, to protect against fire and thorns and spines to protect against herbivores.

In this thesis, I have studied whether fire and herbivory can have a similar impact on a Northern European open landscape, specifically a wood-pasture on former forest land, as has been shown in other parts of the world. By establishing study plots in wood-pastures grazed by cattle, where we both prevented herbivory by fencing and conducted prescribed burnings each spring, we could study how different types of vegetation were affected by these two processes, and how fire and herbivory influenced each other.

Both planted and naturally regenerating trees in the study plots were strongly affected by herbivory and fire. After eight years, the number of trees in the grazed parts of the study plots was very low compared to the parts without fire or herbivory. The patches that were only burned also had fewer trees than those without any treatment, but not as few as with herbivores present. For herbs, the situation was different, as we barely saw any germination of sown herbs in the patches without fire or herbivory. However, both fire and herbivory improved the conditions for both the establishment and reproduction of these species. In general, fire and herbivory influenced which species that naturally occurred in the different treatments and the type of vegetation, e.g., whether it was woody plants or low-growing herbs.

In addition to affecting vegetation, we also observed that these two processes influenced each other. Similar to how wild herbivores are drawn to newly burned areas in, e.g., savannas in Africa, we observed that the cattle in our study chose to graze on the recently burned patches instead of the adjacent unburned patches. This, in turn, affected the amount of fuel available and thus the intensity of the following fires.

Our results provide clear indications that both fire and herbivory can have a significant impact on vegetation even in a Northern European landscape. Both processes can reduce the number of trees that reach maturity, thereby preventing open habitats from closing-up, but can also improve the conditions for herbaceous vegetation. We also show that fire and herbivory can be used to create a mosaic landscape with diverse habitats where different species thrive. Today, there is a significant need to protect the few remaining open habitats in Europe and to restore new ones. This requires management methods that consider the processes that once created these ecosystems. Using fire and herbivory can be a good and sustainable way to restore nature's own ecological processes, and thus improve the conditions for a rich biological diversity.

Populärvetenskaplig sammanfattning

Idag pågår förlusten av biologisk mångfald i en alarmerande takt över hela världen. En viktig orsak är den drastiska tillbakagången av öppna ekosystem, som är några av de mest artrika ekosystemen i världen.

Öppna ekosystem, definieras av att de inte har en skuggande trädkrona, utan att fältskiktet istället är täckt av ljusälskande växter, så som gräs och örter. I många fall är det klimatet som avgör vilken typ av växtlighet som finns på en speciell plats. Är det tillräckligt varmt och mycket nederbörd, finns förutsättningarna för skog men i svalare och torrare områden kan inte skog växa och dessa områden domineras istället av annan växtlighet. Men det finns områden som är tillräckligt varma och som har tillräckligt mycket nederbörd för att skog ska kunna växa men där landskapet ändå består till större delen av öppna gräsmarker med enstaka eller grupper av träd. Länge trodde man att dessa landskap var resultaten av stora störningar, så som bränder eller stormar, och att de endast var en successionsfas på väg tillbaka till tät skog. Men forskning har visat att öppna ekosystem i själva verket är stabila stadier, som har funnits under lång tid och till och med har utvecklat egna artsamhällen. Vad är det då som avgör om ett landskap är öppet, i områden där förutsättningarna egentligen är goda nog för att skog ska växa?

Detta är en välstuderad fråga i bland annat Afrikas savanner, där stora öppna områden fortfarande finns kvar. Där är forskare nu överens om att det är eld och stora betesdjur som håller landskapet öppet och hindrar det från att växa igen. Brand och bete hindrar träd från att växa upp till stora träd som kan bilda en tät trädkrona, vilket gör att landskapet hålls öppet så att en mängd arter som är beroende av solljus, både växter och djur, kan samexistera.

Brand och bete påverkar också varandra, då betande djur gärna betar där det just har brunnit, eftersom att vegetationen som kommer upp efter brand är betydligt mer näringsrik än innan branden. Betet i sig minskar mängden bränsle i området som betas vilket gör att risken för brand minskar, medan det i andra områden som inte betas, istället blir en ansamling av bränsle och risken för brand ökar. När det väl brinner i ett nytt område lockas betesdjuren dit istället och processen börjar om. Detta skapar ett mosaiklandskap med olika stadier av vegetation med allt från välbetad gräsmark just efter brand till områden utan bete med mer vegetation där enstaka träd till och med kan växa upp. Ett sådant landskap innehåller många olika habitat, passande för en rad olika arter.

Trots denna kunskap, är ursprunget till de få kvarvarande öppna markerna i Europa, fortfarande debatterat. Många anser att öppna områden i Europa endast är resultaten av människans inverkan i naturen, som boskapsbete och brukandet av eld i olika sammanhang. Men det finns nu en mängd studier som visar på att Europa delvis var ett öppet landskap, även innan människan kom hit. Detta kan man dels bevisa genom fossila fynd av stora växtätare, så som jättehjortar och ullhåriga noshörningar, men också uroxar och vildhästar som dog ut så sent som under de senaste århundradena. Paleoekologiska fynd visar också att regelbundet återkommande bränder också hade en stor inverkan på landskapet. Ytterligare bevis är närvaron av arter som har anpassningar till både brand och bete, så som tjock bark som isolerar från brand och taggar och tornar som skyddar från betande djur.

I den här avhandlingen har jag studerat om brand och bete kan ha samma inverkan på ett nordeuropeiskt öppet landskap, närmare bestämt en betesmark på före detta skogsmark, som har visats i andra delar av världen. Genom att upprätta provytor i beteshagar som betades av nötkreatur, där vi dels förhindrade bete men också eldade varje vår, kunde vi studera hur olika typer av växtlighet påverkades av dessa två processer men också hur bete och brand påverkade varandra.

Träden i provytorna, både planterade och naturligt uppkomna träd, påverkades starkt av både brand och bete. Efter åtta år vara antalet träd i de betade delarna av provytorna väldigt få till skillnad från de delar som varken betades eller brändes. Delarna som bara brändes hade också färre träd men inte lika få som med bete. För örter såg det annorlunda ut, där vi knappt såg någon groning av ett antal sådda örter i behandlingen utan varken brand eller bete. Däremot förbättrade båda processerna förutsättningarna för både etablering och reproduktion för dessa arter. Generellt så påverkade brand och bete vilka arter som förekom naturligt och även typen av vegetation, det vill säga om det var vedartade växter eller lågväxande örter.

Förutom att brand och bete påverkade vegetationen, kunde vi även se att de båda processerna påverkade varandra. På liknande sätt som vilda växtätare dras till nybrända områden i t.ex. Afrika, såg vi att korna i vår studie valde att beta på de nybrända ytorna istället för de obrända intilliggande ytorna. Detta påverkade i sin tur mängden bränsle till nästkommande brand, med en minskning i mängden bränsle och därmed brandens intensitet.

Våra resultat ger tydliga indikationer att både brand och bete kan ha stor inverkan på vegetationen även i ett nordeuropeiskt landskap. Båda processerna kan minska antalet träd som når vuxen ålder och därmed hindra öppna områden att växa igen men också förbättra förutsättningarna för gräs och örter. Vi visar också att brand och bete kan användas för att skapa ett mosaiklandskap med varierande habitat där olika arter trivs. Idag är behovet att skydda de få kvarvarande öppna livsmiljöerna i Europa stort, men också att återskapa fler. För detta krävs skötselmetoder som tar hänsyn till de processer som en gång skapade dessa ekosystem. Att använda brand och bete kan vara ett bra och hållbart sätt att återskapa naturens egna ekologiska processer och därmed förbättra förutsättningarna för en rik biologisk mångfald.

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RESEARCH ARTICLE

Fire- and herbivory-driven consumer control in a savanna-like temperate wood-pasture: An experimental approach

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Abstract

1. Fire and herbivory are fundamental top-down processes, structuring grass–tree ratios in ecosystems across a diversity of climates. Both are plant consumers that can strongly control the recruitment of woody seedlings and saplings to taller height classes. Without consumer control, many grass-dominated ecosystems would convert into woodlands or forests. While extensively studied in savannas, few have explored the effects of these disturbance regimes on woody recruitment under temperate conditions.
2. We exposed saplings of five common European tree species to fire and herbivory in a full factorial experiment in a savanna-like wood-pasture. After 3 years, we evaluated the effects of fire and herbivory on tree sapling survival and height increment. The tree species used, varying in traits and in expected response to fire and herbivory, were Scots pine *Pinus sylvestris*, Norway spruce *Picea abies*, European oak *Quercus robur*, Silver birch *Betula pendula* and Small-leaved lime *Tilia cordata*.
3. Fire and herbivory had a negative effect on sapling survival for all species except for *Q. robur*, which was not affected by fire. Both processes reduced height increment of *B. pendula*, while only herbivory reduced the height increment of *P. sylvestris* and *Q. robur*. At the same time, *B. pendula* and *P. sylvestris* had some of the highest increments, together with *P. abies*, which had unaffected height increment in all treatments. *T. cordata*, on the other hand, had a negative height increment across all treatments. Overall, the combined effect of fire and herbivory was similar to the effect of herbivory alone on both survival and height increment, indicating no additional effect of fire when herbivores were present.
4. *Synthesis*. Our experiment showed how fire and herbivory can strongly affect the recruitment of European temperate tree saplings on a wood-pasture, potentially leading to comparable consumer control described for ecosystems elsewhere (e.g. savannas). Two strategies to deal with fire and herbivory were identified: tolerance

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Marcin Churski and Mats Niklasson contributed equally as senior authors.

(*Q. robur*) and avoidance (*P. sylvestris* and *B. pendula*). We conclude that both fire and herbivory may have been important drivers of structure and species composition in open ecosystems in temperate Europe in the past.

KEYWORDS
consumer control, disturbance regime, fire, herbivory, landscape ecology, temperate ecosystem, tree sapling recruitment

1 | INTRODUCTION

The drivers of open, grass-dominated, wood-pastures and heathlands in the temperate zone of Europe have been debated since long (Birks, 2005; Bobek et al., 2017; Bond, 2005; Feurdean et al., 2018; Hejcman et al., 2013; Mitchell, 2005; Svenning, 2002; Vera, 2000). These types of habitats have generally been referred to as 'man-made ecosystems' resulting from anthropogenic fire and livestock grazing regimes, dating back as early as to Neolithic culture (e.g. Leuschner & Ellenberg, 2017). This view is challenged by ecologists and palaeoecologists, claiming that savanna-like open and semi-open ecosystems were present in central and northwestern Europe already in the early Holocene and that they survived the 'mid-Holocene bottleneck' in certain portions of this landscape such as in river valleys or on thin and sandy soils (e.g. Pokorný et al., 2015; Svenning, 2002). Based on palaeoecological evidence of molluscan fauna, microcharcoal and subfossil remains from extinct megaherbivore fauna, several studies have argued that, now partly extinct, large mammalian herbivores (Bakker et al., 2016; Hejcman et al., 2013; Malhi et al., 2016; Svenning, 2002; Vera, 2000), fire (Feurdean et al., 2018; Svenning, 2002) or a combination of both (Svenning, 2002) controlled woody recruitment and kept European landscapes open. Neolithic livestock grazing and anthropogenic fires then replaced the role of wild herbivores and fire in controlling woody vegetation (Feurdean et al., 2018; Pokorný et al., 2015; Vera, 2000).

On a global scale, fire and mammalian herbivory are two fundamental top-down processes that are strong drivers of vegetation structure in many terrestrial ecosystems (Archibald & Hempson, 2016; Bond et al., 2005; Keeley et al., 2011; Kuijper, Jędrzejewska, et al., 2010; Kuijper et al., 2015; Veldman et al., 2015). They are both consumers of plant biomass (Archibald & Hempson, 2016; Bond & Keeley, 2005), although they may differ in their occurrence, selectivity and the way they consume plants. For example, while herbivory is a more continuous process in comparison with fire and may be spatially heterogeneous, fires occur less frequently in time but are often more uniform in space (Archibald & Hempson, 2016). Moreover, fires 'select' (sensu Archibald & Hempson, 2016) dry and nutrient-poor vegetation (Schwilk, 2015) while herbivores 'select' fresh and nutrient-rich vegetation (Owen-Smith & Novellie, 1982). Regardless of these differences, both fire and herbivory can strongly control the recruitment of trees to the next demographic stage by affecting seedling and sapling survival and growth (consumer control: Archibald et al., 2005; Bond, 2005; Churski et al., 2017; Smit et al., 2015; Staver et al., 2009). Studies in savannas have shown how fire and herbivory can keep trees in the so-called 'fire-' and 'browse traps' and preventing them to grow into adult trees (LaMalfa et al., 2019; Sankaran et al., 2013; Skowno et al., 1999; Staver & Bond, 2014) with profound effects on ecosystem structure (Higgins et al., 2000; Sankaran et al., 2013; Staver & Bond, 2014).

Due to differences in the way fire and herbivory affect survival and growth in tree saplings, woody plants have evolved different traits to avoid or tolerate each process. Spinescence, for example, enables trees to prevent mammalian herbivory, while thick bark insulates the cambium from lethal temperatures caused by fire (Charles-Dominique, Beckett, et al., 2015; Charles-Dominique et al., 2017; Keeley et al., 2011; Kruger et al., 2017). Some traits may be adaptations to both fire and herbivory, for example, re-sprouting (Coughenour, 1985; Keeley et al., 2011). As a result, the presence of fire and herbivory may ultimately lead to the development of evolutionary divergent, consumer-controlled communities, characterized by species with different traits (Archibald & Hempson, 2016; Bond, 2005; Hoffmann et al., 2012; Keeley et al., 2011; Ratnam et al., 2019; Stevens et al., 2018).

Bond (2005) divided consumer-controlled ecosystems into fire- and herbivory-adapted plant communities, based on whether fire or herbivory is the main disturbance. In fire-controlled systems ('black world' sensu Bond, 2005), communities with fire-adapted woody species with traits such as thick bark, bud protection and accessory buds dominate (Charles-Dominique, Staver, et al., 2015; Kruger et al., 2017). In herbivore-controlled systems ('brown world'), species with structural defences, such as thorns, spines and cagy architectures, dominate (Charles-Dominique, Staver, et al., 2015; Kruger et al., 2017). In the absence of herbivores and fires, resource availability (e.g. light, water, nutrients), as set by climate and soil conditions, limits plant growth ('green world': Bond, 2005). In such 'resource-controlled' systems, plant communities are dominated by species with resource-acquisition traits, such as high vertical growth rate and shade tolerance, when plant productivity is high (Charles-Dominique, Staver, et al., 2015; Kruger et al., 2017; Niinemets & Valladares, 2006). In addition, communities may have elements of all three possible ecosystem states (green, brown and black) depending on the relative importance of top-down (consumers) versus bottom-up (resources) mechanisms (Bond, 2005; Churski et al., 2017).

The role of fire and herbivory as key drivers of woody plant community structure has been extensively studied in tropical savannas (e.g.

Archibald & Hempson, 2016; Charles-Dominique, Staver, et al., 2015) and in temperate North American prairies and savannas (e.g. Briggs et al., 2002; Veach et al., 2014). However, few studies have looked at the effects of fire and herbivory on woody species in temperate European systems, where trees and grass coexist, such as wood-pastures. In fact, the consumer control model (Bond, 2005) stands in contrast to the classical successional models emphasizing competition and facilitation for resources as the main driver in the temperate zone (Bond, 2005; Connell & Slatyer, 1977; Van Andel, 1993). Recent studies imply that the impact of large herbivores in European temperate ecosystems can be strong and that temperate tree species differ largely in their response to herbivory (Churski et al., 2017; Kuijper, Cromsigt, et al., 2010; Kuijper, Jędrzejewska, et al., 2010; Smit et al., 2015; Van Uytvancket al., 2008). Moreover, palaeoecological and dendrochronological studies suggest that fires were also an integral part of the disturbance regimes in (pre-)historic European temperate ecosystems (Bond & Keeley, 2005; Carcaillet et al., 2009; Niklasson et al., 2010).

Today, in temperate Europe, only small remnants of semi-open landscapes (e.g. wood-pastures and silvopastoral grasslands) controlled by fire and grazing remain (e.g. Ziobro et al., 2016). Moreover, abandonment of rural areas has led to a reduced use of wood-pastures for livestock and a general decline of large herbivorous mammals in the landscape (Bradshaw et al., 2003; Bradshaw & Mitchell, 1999; Ceballos, 2017; Dirzo et al., 2014; Estes et al., 2011; Ripple et al., 2015). Similarly, over most of Europe, but also elsewhere globally, active prevention of fires has led to its near absence (Archibald et al., 2013; Bowman et al., 2011; Niklasson et al., 2010). In southern Europe, abandonment of traditional grazing practices is now leading to increased frequency and intensity of fires due to accumulated fuel loads (Johnson et al., 2018). More recently, however, large herbivores are again returning to European landscapes as a consequence of passive and active rewilding (Pereira & Navarro, 2015). As an example of passive rewilding, across Europe, different deer species are increasing in numbers and expanding their ranges (Linnell et al., 2020). As an example of active rewilding, free-ranging cattle and horses are introduced across Europe as substitutes of extinct Aurochs *Bos primigenius* and Tarpan *Equus ferus ferus* as a restoration tool (Cromsigt et al., 2018). To understand how fire and mammalian herbivory may affect the structure and functioning of Europe´s temperate ecosystems, we need to explore how these consumers influence the recruitment process of dominant tree species.

In this paper, we experimentally tested if and how fire and herbivory, as two different plant consumers, control the growth and survival of saplings of five common European temperate tree species (*Pinus sylvestris*, *Picea abies*, *Quercus robur*, *Betula pendula* and *Tilia cordata*). We hypothesized that (a) fire and herbivory would induce strong consumer control (in terms of reduced sapling survival and growth) in these temperate species but that (b) responses to fire and herbivory would vary among the tree species. Based on an extensive review of the literature (Table S1), we predicted *P. sylvestris*, *Q. robur* and *B. pendula* to be 'black world' species with higher survival and growth in response to fire than in response to herbivory, indicating adaptations to more fire-controlled systems. In contrast, we predicted fire to reduce survival and growth of *P. abies* and *T. cordata* relative to the herbivory treatment and to the other species, therefore being more 'brown world'-species adapted to more herbivore-controlled systems. To test these hypotheses, we carried out a full-factorial experiment manipulating fire and herbivory, in a savanna-like wood-pasture. The study plots were exposed to annual low-intensity surface fire and herbivory by cattle and wild herbivores for 3 years and evaluated with respect to survival rates and net height increment.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in the Ecopark of Nordens Ark (ENA, Figure 1) in the county of Västra Götaland in the western part of Sweden (58°27′N 11°25′E). ENA has a total area of 400 ha and is located next to the Åby fjord on the coast. The climate is strongly influenced by the Atlantic with mild winters and cool summers (Wastenson et al., 2004). The average annual mean temperature is 6–7°C (January −2 to −1°C and July +16 to +17°C) and average annual precipitation is 800–900 mm, with a higher mean in the summer (standard period 1961–1990, https://www.smhi.se/klimatdata, 2019-04-25). Evaporation is 400–500 mm per year and snow covers the ground for an average of 50–75 days per year (standard period 1961–1990, https://www.smhi.se/klimatdata, 2019-04-25). Acid granites, mainly Bohus granite, dominate the bedrock in the area (Berglund, 1988). Soils are highly variable with very deep clay layers in valleys, glacial tilt in slopes and xeric rocky outcrops on the higher lying areas (Blomgren & Falk, 2011). In the region and in the study area, ice age accumulations of clamshells from previous shorelines have locally enriched the soils with more base-rich material (Hallberg, 1971).

The area and the region have had a long history of human use of fire. Until the previous century, *Calluna vulgaris*-dominated heathlands were maintained by frequent burning every 3–10 years (Atlestam, 1942; Lindholm, 2019). Burning grass in early spring has an equally long history and was used to improve grass quality for livestock (Weimarck, 1979). Today, lightning may ignite forest fires, sometimes even very early in spring, however, at a lower frequency than anthropogenic fires (Granström, 1993). There is no doubt that natural fires were an integral part of the landscape also throughout the Holocene (Högbom, 1934).

ENA and the experimental site were mostly used for wood-pastures grazed by cows and sheep until the early 1900s brought a period of commercial forestry (Ernby, 2010). In 2011 and 2012, as a part of a restoration program, 100 ha of conifer plantation was converted into wood-pastures by harvesting of planted spruce. The area was fenced into several corrals, with a 1.0 m electric fence with five wires, and since then the area has been grazed mainly by cattle and to a minor extent by sheep, goats and horses (i.e. herbivory

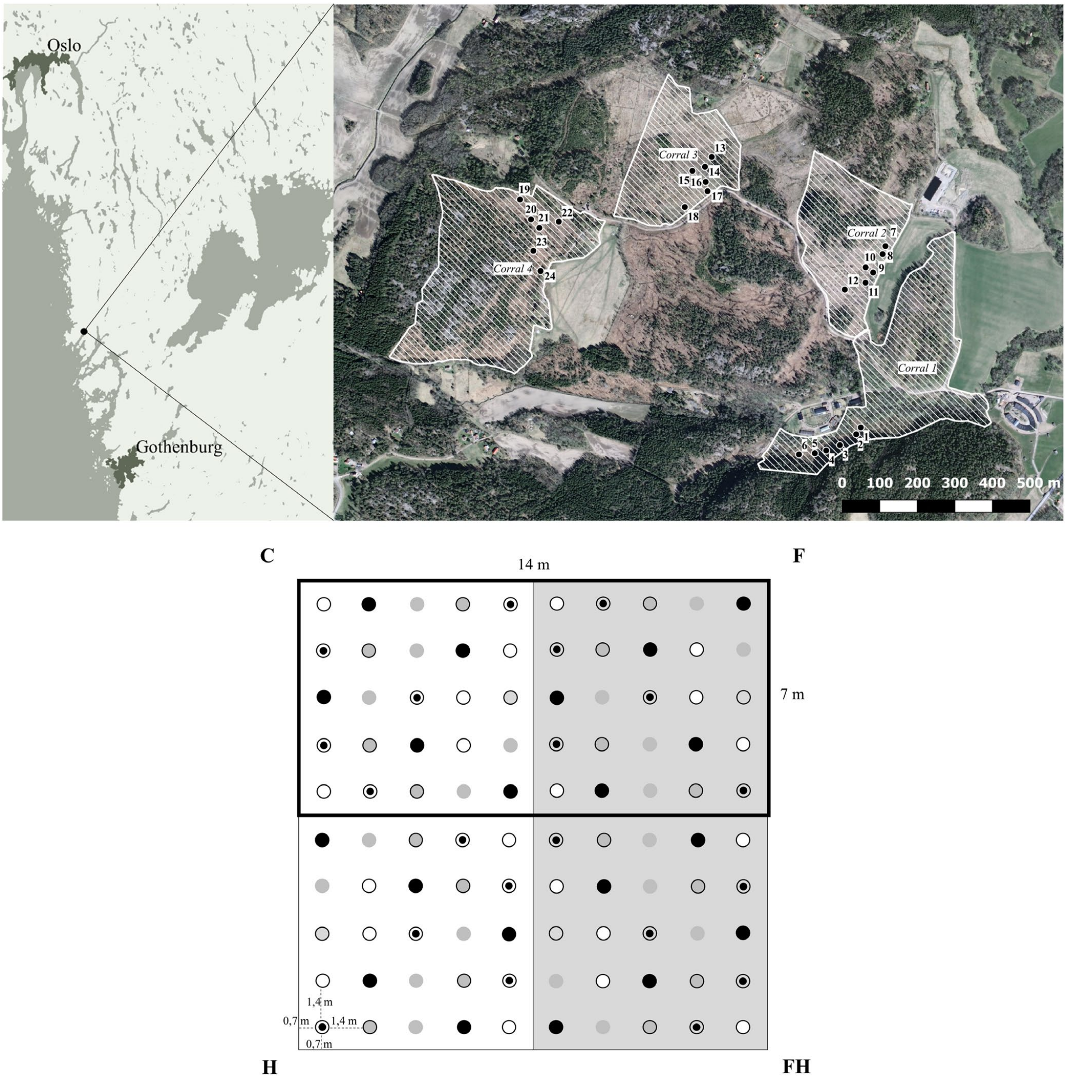

FIGURE 1 Location of study area on the Swedish West Coast (upper left), position of study plots in the area (upper right) and study plot design (lower middle). All 24 study plots were divided into four subplots; no-fire:no-herbivory (C), fire:no-herbivory (F), no-fire:herbivory (H) and fire:herbivory (FH). The thicker line indicates the fenced subplots and the grey colour indicates the subplots exposed to fire. In each subplot, 25 tree saplings of five different species (Scots pine *Pinus sylvestris* L., Norway spruce *Picea abies* (L.) H. Karst., European oak *Quercus robur* L., Silver birch *Betula pendula* Roth., Small-leaved lime *Tilia cordata* Mill., here represented by different colour dots) were planted, with each row (here horizontal) containing one sapling of each species planted in a random order

consisted mainly of grazers). During the study period, the main grazers were adults, juveniles (1–2 years) and calves of cattle *Bos taurus* of the Swedish breeds Rödkulla and Fjällnära and the English breed Hereford. Each year, the grazing period started in May–June and ended in August–October. We aimed at creating similar livestock densities across all corrals, but livestock management issues caused some variations in grazing pressure among the corrals, which we documented during the study period (Table S2). Wild large herbivores in the overall area, surrounding our study site, included moose *Alces alces*, fallow deer *Dama dama*, roe deer *Capreolus capreolus* (*browsers*), mouflon *Ovis orientalis orientalis* (*grazer*) and wild boar *Sus scrofa* (*omnivore*) (17, 20, 195, 21 and 134 animals, respectively, were shot in the whole local hunting unit, *Sotenäs*, covering 11.360 ha, according to hunting statistics from 2019). The fence type of the corrals allowed all wild herbivores to freely enter the corrals by jumping over or going under it. However, our camera trap surveys of all experimental plots showed that wild large herbivores were rarely present and comprises far <1% of all visiting herbivores (K. Amsten, unpubl.).

Since the logging of spruce, the area has undergone a drastic transformation. From shady forest conditions with little herbaceous vegetation under the spruce monoculture, grassland now dominates the area (mainly *Poa*, *Festuca* and *Deschampsia* spp.) after a short phase of early successional species, dominated by mainly raspberry *Rubus idaeus*. Several woody species have managed to regenerate naturally, also in the corrals despite the grazing, mainly birches *Betula* sp., oaks *Quercus* sp., Scots pine *Pinus sylvestris* and Norway spruce *Picea abies* (Hedlund, 2019).

2.2 | Experimental design

In spring 2015, we established 24 study plots, in four of the corrals in ENA, with six plots in each (Figure 1). The plots were randomly placed in the corrals, while avoiding large trees and rocks inside the plots. Each plot measured 14 × 14 m and contained four equally sized experimental subplots of 7 × 7 m each. Before the start of the experiment, we surveyed the plots carefully for naturally regenerated tree seedlings and saplings, which we removed by pulling them up by the roots or, in a few cases, cutting them at root level. During the following years, we did not remove natural regeneration. Two of the subplots were fenced with a 2.0 m high mesh wire, excluding all ungulates from entering, and one of the fenced and one of the unfenced subplots in each plot was randomly chosen for treatment with a low-intensity spring surface fire. This full-factorial design gave us four different treatment combinations: no-fire:no-herbivory (*control*), fire:no-herbivory (*fire*), no-fire:herbivory (*herbivory*) and fire:herbivory (*fire:herbivory*) with 24 replicates of each (Figure 1).

An initial burning of *fire* and *fire:herbivory* subplots took place during spring in April 2015 before planting. Thereafter, we burned every year in spring at a time when the grass was dry enough but before green-up (usually in mid-April). Using a drip torch, we applied uniform ignition technique in all subplots. We walked one drip-line at surface level to mimic a low-intensity surface fire across the 7-m subplot, starting at the wind exit side of the subplot. If this first line did not spread by its own due to a low fuel load, we walked five more drip-lines across the subplot, 1.0 m apart, against the wind.

After the first burning, in 2015, we planted 2,400 saplings of five temperate tree species (Scots pine *Pinus sylvestris* L. (hereafter *Pinus*), Norway spruce *Picea abies* (L.) H. Karst. (hereafter *Picea*), European oak *Quercus robur* L. (hereafter *Quercus*), Silver birch *Betula pendula* Roth. (hereafter *Betula*), Small-leaved lime *Tilia cordata* Mill. (hereafter *Tilia*)) in the study plots. We selected the five species in a stepwise selection procedure as follows. We started our list of potential species with all native tree species found in the temperate part of Sweden followed by additional selection criteria (in brackets are given the number of species available after each selection step): extant in Sweden (27), extant in our study area (25), competitive outside wet soils (23), dominant or co-dominant position on national level or at stand level (6), seedlings available on market in Sweden during start of the study (spring 2015) (5). In each subplot, we planted 25 saplings from a forest plant nursery, five of each species, in a 5 × 5 grid with 1.4 m spacing, with each row containing one sapling of each species, in a random order within each row (Figure 1). Seedlings were 1–2 years old but differed in initial size; average height for *Betula* 68.8 (±0.7 *SE*) cm, *Tilia* 48.6 (±0.8) cm, *Quercus* 41.6 (±0.5) cm, *Picea* 28.1 (±0.5) cm and *Pinus* 20.9 (±0.4) cm.

2.3 | Tree sapling survival and growth

Three years after planting, before the annual spring burning, we recorded sapling survival and height increment to the nearest cm. At this time, the saplings had been exposed to three growing seasons with herbivory by mainly cattle and wild herbivores, and low-intensity spring surface fires in 2016 and 2017. We noted the status of each sapling in three classes (live/dead/gone), with dead defined as a sapling with a dry and brittle stem, a brownish colour under the bark and no leaves or needles. If a sapling was broken near the roots with less than 5 cm left of the above-ground stem and no signs of living buds or sprouts above ground, it was also noted as dead in this study. When there were no signs of the sapling, it was noted as gone and treated as dead in the analysis. Sapling height was measured from the soil surface to the highest point of the main top while stretching it. Only saplings noted as live were measured for height.

2.4 | Data analysis

Some of the saplings were destroyed accidentally during corral maintenance in 2015, so we had to exclude four of the plots from the analysis (Plot 12, 16, 17 and 18; Figure 1). Therefore, only 20 replicates were included in the analysis. For all statistical analysis, we used the program R 3.4.3 (R Foundation for Statistical Computing).

To compare the initial heights of the species, we used a general linear mixed-effects model with a normal distribution using the LMERTEST package ('lmer' function) (Kuznetsova et al., 2018). This analysis confirmed that, although the species differed in initial height ($F = 1{,}045.02$; $df = 4$; $p < 0.001$), these initial heights did not differ among the four treatment combinations ($F = 1.55$; $df = 3$; $p = 0.20$; Figure S1).

2.4.1 | Sapling survival

The effect of treatment (fire or no-fire; herbivory or no-herbivory) and the interaction between the treatments on sapling survival (sapling survival rate for each species in each subplot after 3 years) was analysed with a generalized linear mixed-effects model with a binomial distribution and logit link. We entered fire (binary), herbivory (binary) and tree species (five levels) as the fixed effects. As random effects, Plot ID was nested in Corral. In R, we used the lme4 package and 'glmer' function to run the model (Bates et al., 2018). For multiple pairwise comparisons among the levels of treatments and species separately, we conducted Tukey's post hoc tests using the 'emmeans' function in the emmeans package (Lenth et al., 2018).

2.4.2 | Height increment of saplings

We analysed the effect of treatments (fire or no-fire; herbivory or no-herbivory) and the interaction between treatments on height increment of saplings (mean net height increment for each species in each subplot after 3 years) with a general linear mixed-effects model with a normal distribution. We used the same model structure as for survival (i.e. fixed and random effects). In R, we used the lmerTest package and 'lmer' function to run the model (Kuznetsova et al., 2018). For multiple comparisons among the levels of treatments and species separately, we conducted Tukey's post hoc tests using the 'emmeans' function in the emmeans package (Lenth et al., 2018).

3 | RESULTS

3.1 | Sapling survival in relation to fire and herbivory

There was no significant difference in survival in the *control* subplots (no-fire:no-herbivory) between the species, except for *Tilia*, which had lower survival than all the other species (Table S3).

Fire and herbivory, and their combination, had significant effects on the survival of the saplings (Table 1). As individual effects, they reduced survival of *Pinus*, *Picea* and *Tilia*, and their survival did not differ between the two treatments (Figure 2; Table S4). Survival of *Betula* was higher in the *fire* (fire:no-herbivory) than in the *herbivory* (no-fire:herbivory) subplots (Figure 2; Table S4). Herbivory reduced survival of *Quercus*, whereas fire did not (Figure 2; Table S4). Adding fire to the herbivory treatment (*herbivory* vs. *fire:herbivory*) did not further reduce survival for any of the species (Figure 2; Table S4).

3.2 | Height increment in relation to fire and herbivory

Pinus, *Picea* and *Betula* had the highest positive increment and *Quercus* and *Tilia* the lowest (Figure 3). *Quercus* and *Tilia* had negative average height increments in some of the treatments, which means that they decreased in height compared with initial planting height (Figure 3). *Quercus* had a negative increment in both the *herbivory* and *fire:herbivory* subplots (Figure 3). *Tilia* showed positive increment only in the *control* subplots without fire and herbivory. Due to the low annual increment of 0.3 cm (±5.0), *Tilia* was one of the shortest after 3 years while being the second tallest at the beginning of the study (Figures S1 and S2).

TABLE 1 Analysis of deviance based on the generalized linear mixed-effect model explaining the variation in relative survival of five species of tree saplings (Scots pine *Pinus sylvestris* L., Norway spruce *Picea abies* (L.) H. Karst., European oak *Quercus robur* L., Silver birch *Betula pendula* Roth., Small-leaved lime *Tilia cordata* Mill.) exposed to two treatments (fire and herbivory) and their interactions, 3 years after planting

Factor	χ^2	*df*	*p*-value
Fire	91.564	1	**<0.001**
Herbivory	201.377	1	**<0.001**
Species	71.770	4	**<0.001**
Fire:Herbivory	19.586	1	**<0.001**
Fire:Species	15.249	4	**0.004**
Herbivory:Species	24.328	4	**<0.001**
Fire:Herbivory:Species	9.649	4	**0.047**

Note: Plot ID was nested in corral as random factors.
Abbreviations: *df*, degrees of freedom; χ^2, type II Wald χ^2 tests.
Statistically significant values are indicated in bold text.

Again, both treatments and the combination had significant effects on height increment, although not as clear as for survival (Table 2). Fire had no significant effect on the height increment of *Pinus*, *Picea*, *Quercus* or *Tilia* (Figure 3; Table S5). Fire did reduce the height increment of *Betula*, but not as much as herbivory (Figure 3; Table S5). Herbivory also reduced height increment of *Pinus* and *Quercus* (Figure 3; Table S5). Again, adding fire to herbivory did not lead to a further reduction in height increment for any of the species compared to herbivory only (Figure 3; Table S5).

4 | DISCUSSION

In grass-dominated ecosystems, such as African savannas, fires and herbivores are important plant biomass consumers that control the survival and growth of woody species (Bond et al., 2005; Staver et al., 2009). Our experiment with contrasting disturbance regimes in a savanna-like temperate wood-pasture revealed strong and varying effects from both fire and herbivory across tree species (Tables 1 and 2). Our results suggest that fire and herbivory may exert strong consumer control in these temperate systems in ways that are functionally comparable to herbivore- and fire-controlled savanna ecosystems (e.g. Bond et al., 2005; Staver et al., 2009).

4.1 | Consumer control in a savanna-like temperate ecosystem

In our experiment, mammalian herbivory mainly consisted of large grazers (cattle), whereas the wild ungulates (mainly browsers) were

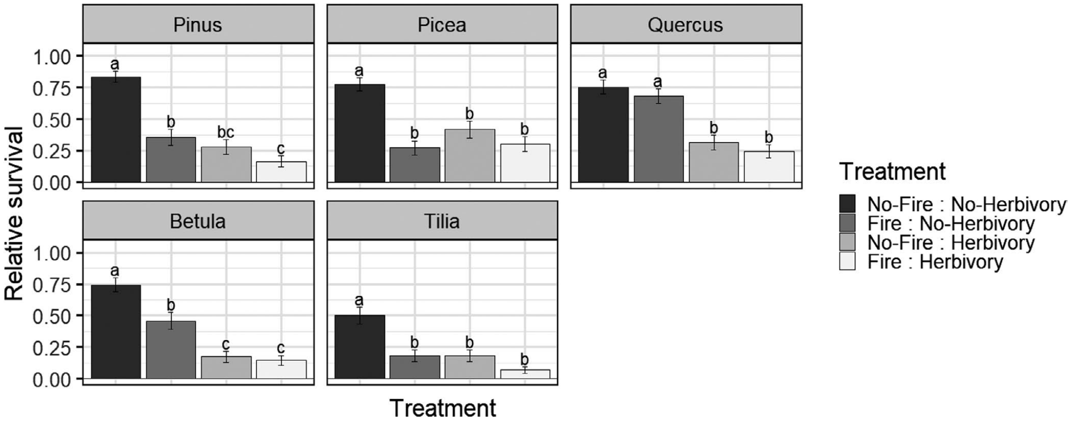

FIGURE 2 Relative survival of tree saplings in four experimental treatments (no-fire:no-herbivory, fire:no-herbivory, no-fire:herbivory and fire:herbivory), 3 years after planting (error bars represents ±1 *SE*). Significance within each species is indicated with letters (test statistics can be found in Table S4, $p < 0.05$). Species as appearing in figure: Pinus *Pinus sylvestris* L., Picea *Picea abies* (L.) H. Karst., Quercus *Quercus robur* L., Betula *Betula pendula* Roth., Tilia *Tilia cordata* Mill

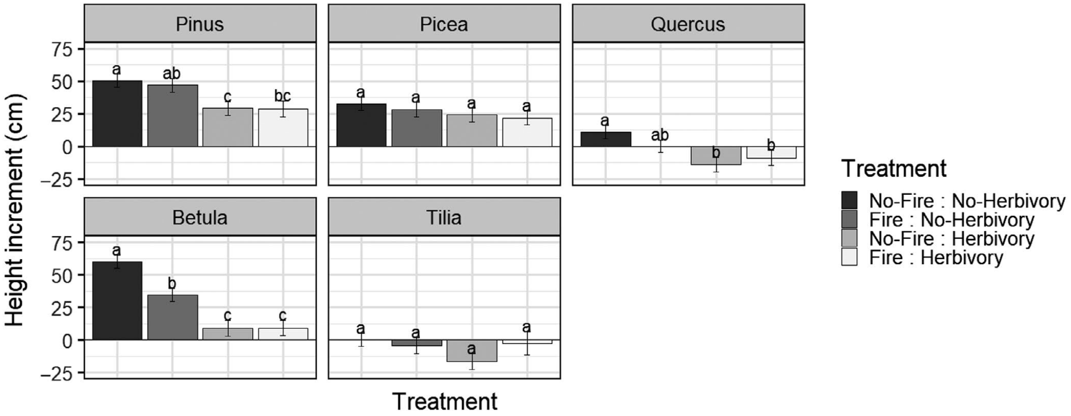

FIGURE 3 Average height increment of tree saplings in four experimental treatments (no-fire:no-herbivory, fire:no-herbivory, no-fire:herbivory and fire:herbivory), 3 years after planting (error bars represents ±1 *SE*). Significance within each species is indicated with letters (test statistics can be found in Table S5, $p < 0.05$). Species as appearing in figure: Pinus *Pinus sylvestris* L., Picea *Picea abies* (L.) H. Karst., Quercus *Quercus robur* L., Betula *Betula pendula* Roth., Tilia *Tilia cordata* Mill

present at relatively low numbers. Herbivory had an overall strong negative effect on sapling survival but with large variation among species (Figure 2), demonstrating clear consumer control in our study with potential filtering effects on tree community composition. Height increment was either reduced or not affected at all depending on tree species (Figure 3). The variable effect of herbivory on height increment between different tree species can be explained by grazers being the dominant herbivore, which may affect different tree species in a more variable way than browsers (Staver et al., 2009). Archibald et al. (2005) and others suggested that grazing in African ecosystems, in contrast to browsing, may increase growth rate in some tree species by reducing grass competition (Belayneh & Tessema, 2017; Holdo et al., 2009; O'Connor et al., 2014), a pattern which has also been shown in Europe (Smit et al., 2015). Our results do not provide clear support for such a positive effect of grazers on growth rate because herbivory reduced the height increment of all species in our experiment, except *Picea* that was not affected. Importantly, a reduction in tree sapling height (i.e. negative height increment) may not only result from direct foraging impact but also other effects of the cattle, particularly trampling (Van Uytvanck & Hoffmann, 2009).

Fire reduced survival of all species except for *Quercus* (Figure 2), but in terms of height increment of surviving saplings, fire only

TABLE 2 Analysis of deviance based on the general linear mixed-effect model explaining the variation in height increment of five species of tree saplings (Scots pine *Pinus sylvestris* L., Norway spruce *Picea abies* (L.) H. Karst., European oak *Quercus robur* L., Silver birch *Betula pendula* Roth., Small-leaved lime *Tilia cordata* Mill.) exposed to two treatments (fire and herbivory) and their interactions, 3 years after planting

Factor	*F*	*df*	*p*-value
Fire	5.990	1	**0.015**
Herbivory	75.934	1	**<0.001**
Species	78.089	4	**<0.001**
Fire:Herbivory	7.929	1	**0.005**
Fire:Species	1.784	4	0.13
Herbivory:Species	6.471	4	**<0.001**
Fire:Herbivory:Species	1.168	4	0.33

Note: Plot ID was nested in corral as random factors.

Abbreviations: *df*, degrees of freedom; *F*, type II Wald *F* tests with Kenward–Roger *df*.

Statistically significant values are indicated in bold text.

significantly reduced the increment of *Betula* (Figure 3). In general, these results imply that fire had a lethal effect on saplings but did not significantly suppress growth of surviving individuals. This is in line with models by Higgins et al. (2000), who stated that fire can limit tree succession by preventing the establishment of saplings. Staver et al. (2009), on the other hand, found that fire only affected height increment in survivors and not mortality of tree saplings. A possible explanation for the lack of effect on height increment in our study is the relatively low flame height, never reaching the top of the saplings (Figure S3), and also the relatively short study period of 3 years.

Interestingly, we found an interaction between fire and herbivory (Tables 1 and 2). While fire decreased the survival of all species except *Quercus* in subplots without herbivory (*control* vs. *fire*), it had no significant additional negative effects in subplots with herbivory (*herbivory* vs. *fire:herbivory*) for any of the species (Figure 2). Studies from savannas have highlighted how grazing can decrease the occurrence and severity of fires by reducing the amount of fuel and creating firebreaks (Archibald & Hempson, 2016; Hierro et al., 2011; Kimuyu et al., 2014; Leonard et al., 2010). In this way, grazing may control the effects of fire and lead to a lower fire intensity or even complete fire exclusion compared to conditions without herbivores (Archibald & Hempson, 2016; Staver & Bond, 2014). In our experiment, despite high ignition efforts, grazed subplots rarely contained sufficient fuel loads to support a self-propagating fire (Figure S4). Summarizing, herbivores and fires create interactive as well as competing effects (Archibald & Hempson, 2016). The combination and interaction of different biomass consumers creates habitat diversity which, in turn, affects species composition and increases species diversity (Archibald & Hempson, 2016; Royo et al., 2010). As seen in this study, already after 3 years, grazing limited fire intensity, similar to what has been observed in African savannas (Archibald & Hempson, 2016; Gambiza et al., 2000).

4.2 | Species effects and strategies towards consumers

The three top surviving species (*Quercus*, *Betula* and *Pinus*) under our experimental fire regime have been previously shown to be strongly associated with fires in temperate and boreal zones (Table S1; Bond & Midgley, 2012; Carcaillet et al., 2009; Fréjaville et al., 2018; Niklasson et al., 2010; Richardson, 2000; Spînu et al., 2020). However, the differences in observed height increment among these species suggest that they likely differ in strategies to cope with fire. After 3 years, both *Pinus* and *Betula* were the tallest in the *fire* subplots, indicating that they invested in height growth to escape the flame zone (LaMalfa et al., 2019; Skowno et al., 1999). *Quercus*, on the other hand, although ranking among the best surviving species in response to the fire regime, did not show this height increment following fire, indicating investment in other mechanisms. The *Quercus* genus is widely acknowledged as fire-resistant through a high re-sprouting capacity (Abrams, 1992; McEwan et al., 2011; Ziobro et al., 2016). This re-sprouting capacity likely enabled the high survival of *Quercus* in our study as well, as has been shown for oak saplings exposed to fire in similar experiments elsewhere (Petersson et al., 2020). Re-sprouting has also been described as an important fire-adapted trait for several African savanna species (Keeley et al., 2011; Kruger et al., 2017). It is important to note that strategies to respond to disturbances vary with the life stage of a tree (e.g. Barton & Koricheva, 2010; Linder et al., 1998). For example, bark thickness is an important trait that increases fire resistance of many tree species, but this trait is strongly governed by the time individuals require to develop this trait (Bär & Mayr, 2020; Fernandes et al., 2008; Pausas, 2015; Zin et al., 2015). During the timeframe of our experiment, the saplings were still small and had not yet developed a thick bark to protect against fires. The saplings thus depended on other traits to resist fire, such as rapid height growth for *Pinus* and *Betula* and re-sprouting for *Quercus*.

Both, *Tilia* and *Picea*, the two species that had the lowest survival with fire in our experiment conform with previous studies suggesting that these species are not generally associated with fires in the temperate zone (Table S1; Bär & Mayr, 2020; Molinari et al., 2020; Niklasson et al., 2010).

The presence of herbivory induced two major changes in species survival ranking in comparison to exposure to fires: *Picea* became the best survivor and *Betula* had lowest survival. Moreover, *Quercus* remained one of the best survivors, accompanied by *Pinus*. High survival rates of the two conifers in subplots with herbivores present conforms with previous studies in the temperate and boreal zones, showing that conifer species dominate tree communities in the presence, but not in the absence, of herbivores (Table S1; Lorentzen Kolstad et al., 2018; Pastor et al., 1988; Speed et al., 2013). Similarly, we attribute the relatively high survival of *Picea* and *Pinus* in our experiment to their lower preference by cattle and wild herbivores in our experiment compared to the deciduous species *Betula*, *Quercus* and *Tilia* (Figure S5).

Out of the three deciduous species, *Quercus* showed the highest survival rates under herbivory, despite being intensively browsed

(Figure S5), indicating the strongest tolerance to herbivory among the tested deciduous trees. Interestingly, *Tilia*, a species regarded as tolerant to herbivory (Table S1), showed lowest survival rates and was the most intensively browsed species (Figure S5). The low overall performance of this species in our experiment could additionally be explained by it being a shade-adapted species potentially poorly adapted to the open conditions in our experimental sites (Brzeziecki & Kienast, 1994; Niinemets & Valladares, 2006). Indeed, *Tilia* had relatively low survival rates and height increments even in the *control* subplots, without fire and herbivory. The relatively low survival rates of *Betula* in subplots with only herbivory stands in contrast to its high survival in subplots with only fire. This result suggests a rather low tolerance of *Betula* to herbivory by large mammals in open temperate ecosystem. Nevertheless, when some individuals escape browsing, their height growth capacity may allow them to outgrow the browse trap, again suggesting that rapid height growth can be an important adaptation in *Betula* to both herbivory and fire.

As discussed above, high survival in response to fire or herbivory did not automatically imply a large height increment, suggesting species-specific strategies to cope with biomass consumers (i.e. fires and herbivores). This is in line with the two highly contrasting plant strategies to cope with different disturbances suggested by Belsky et al. (1993) and Rosenthal and Kotanen (1994): the 'tolerance strategy' and the 'avoidance strategy'. The first strategy entails tolerating the disturbance and maximizing survival at the cost of increasing in height (Belsky et al., 1993; Rosenthal & Kotanen, 1994), such as the response of *Quercus* in our experiment. The second strategy entails avoiding the disturbance by defence or investing in the growth of surviving individuals to increase the ability to escape the bottleneck created by the disturbance (Belsky et al., 1993; Rosenthal & Kotanen, 1994), such as *Pinus and Betula* in our experiment.

5 | CONCLUSIONS

Our study shows that both fire and herbivory may interactively affect the survival and development of the sapling of widespread temperate European tree species. Currently, both these major consumers, and particularly fire, are absent from large parts of Europe as natural processes. We show that the response to these consumers may vary widely among tree species with different life histories and that highly contrasting strategies (tolerance vs. avoidance) towards consumers are present among temperate tree species. This suggests that these common European tree species are adapted to fire and herbivory to varying degrees and in different ways. Moreover, our study illustrates that fire and herbivory may impose a strong consumer control in open temperate savanna-like ecosystems, with the potential to lead to comparable consumer control as described for African savannas, which may have important consequences for plant community structure. These findings imply that both fire and herbivory have played significant important roles in structuring tree communities and drivers of ecosystem structure also under temperate conditions in the past European landscapes.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHORS' CONTRIBUTIONS

K.A., J.P.G.M.C., D.P.J.K., M.C. and M.N. planned and designed the research; K.A. and M.N. performed the experiment and conducted the field work; K.A., M.C. and J.M.L. analysed the data; K.A. and M.N. drafted and revised the manuscript; M.C., J.P.G.M.C., D.P.J.K. and J.M.L. contributed to the revising of the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data used to obtain the results of this study are available at SND (Svensk nationell datatjänst) https://doi.org/10.5878/wd8j-2c36.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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Journal of Ecology **Supporting Information**

Article title: **Fire- and herbivory-driven consumer control in a savanna-like temperate wood-pasture: An experimental approach**

Authors: Karin Amsten, Joris P. G. M. Cromsigt, Dries P. J. Kuijper, Jenny M. Loberg, Marcin Churski & Mats Niklasson

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The following Supporting Information is available for this article:

Figure S1 Initial height of tree saplings

Figure S2 End height of tree saplings

Figure S3 Mean flame height in subplots with prescribed fire

Figure S4 Mean portion of area scorched in subplots with prescribed fire

Figure S5 Portion of browsed tops in subplots with herbivores

Table S1 Review on species traits and responses related to fire and herbivory by large herbivores

Table S2 Grazing period and pressure in the four corrals included in the study

Table S3 Multiple pairwise comparisons test of relative survival between all tree species

Table S4 Multiple pairwise comparisons test of relative survival between experimental treatments

Table S5 Multiple comparisons test of net height increment between experimental treatments

Table S6 Search queries on Web of Science

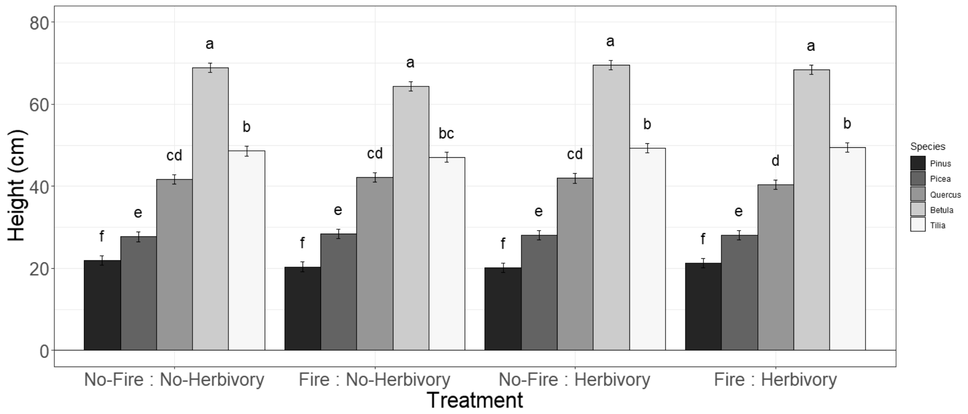

Figure S1 Initial height of tree saplings (error bars represent ±1 SE), prior to implementation of experimental treatments. Significance is indicated with letters (*P*< 0.05). Species as appearing in figure: Pinus *Pinus sylvestris* L., Picea *Picea abies* (L.) H.Karst., Quercus *Quercus robur* L., Betula *Betula pendula* Roth., Tilia *Tilia cordata* Mill.

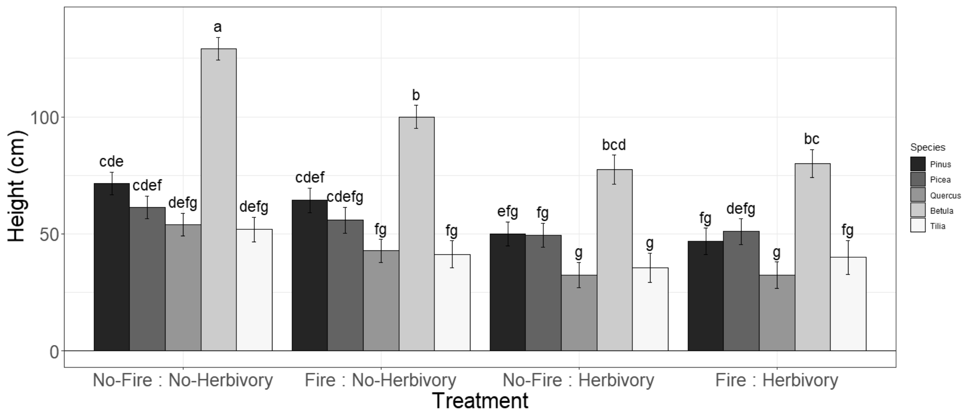

Figure S2 Height of tree saplings (error bars represent ±1 SE) after three years. Significance is indicated with letters (*P*< 0.05). Species as appearing in figure: Pinus *Pinus sylvestris* L., Picea *Picea abies* (L.) H.Karst., Quercus *Quercus robur* L., Betula *Betula pendula* Roth., Tilia *Tilia cordata* Mill.

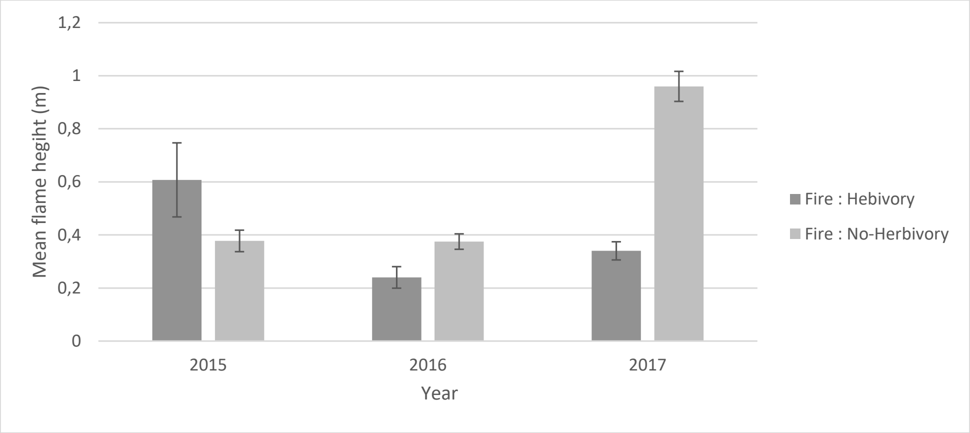

Figure S3 Mean flame height in subplots with prescribed fire during three years (error bars represent ±1 SE). In 2015 the fire was conducted right after the fences in the plots were established and before the saplings were planted.

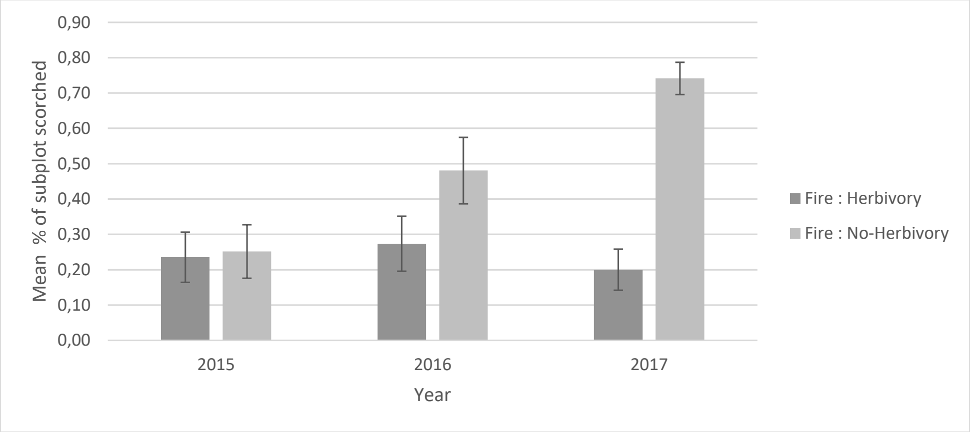

Figure S4 Mean portion of area scorched in subplots with prescribed fire during three years (error bars represent ±1 SE). In 2015 the fire was conducted right after the fences in the plots were established and before the saplings were planted.

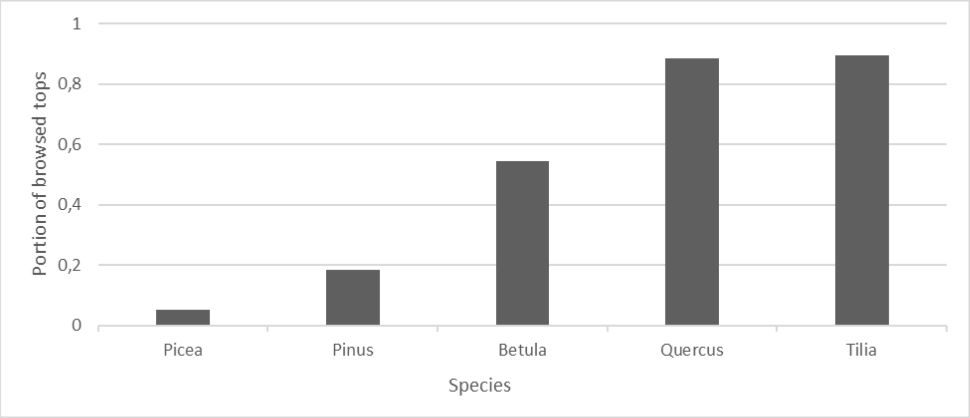

Figure S5 Portion of browsed tops in surviving saplings in 2018 in subplots with herbivores (Fire : Herbivory; No-Fire : Herbivory).

Table S1 Species traits and responses related to fire and herbivory by large herbivores, based on a literature review (see Table S6). The results of the maximum five most relevant papers are presented, including ranking of at least two of the species included in our experiment. For traits and responses to fire, an additional paper including ranking of all five species was also included in the table, even if not emerged in the systematic search results (Molinari et al., 2020).

Species	**Traits and responses to fire**	**Traits and responses to large mammalian herbivores**	**Summary of traits and responses and suggested affiliation to ecosystem states (sensu Bond, 2005)[1]**
Pinus sylvestris	High bark insulation (Bär & Mayr, 2020)	Low mortality in cattle grazing experiment (Ameztegui & Coll, 2015)	*Fire tolerant* *Moderately herbivory tolerant* *(Black world)*
	Thick bark (Ilek & Kucza, 2014)	No impact on abundance from herbivory (Bernes et al., 2018)	
	High survival in fires (Kolström & Kellomäki, 1993)	Very low survival probability under browsing (index=5, Didion et al., 2011[2])	
	Fire-prone (Molinari et al., 2020)	Strong negative impact on abundance (Kuijper et al., 2010)	
	Fire-promoted (Spînu et al., 2020)	Minor susceptibility to browsing (Lyly et al., 2014)	
Picea abies	Low bark insulation (Bär & Mayr, 2020)	Unpalatable but reduced survival with herbivory (Churski et al., 2017)	*Fire intolerant* *Herbivory tolerant* *(Brown world)*
	Thin bark (Ilek & Kucza, 2014)	Very low survival probability under browsing (index=5, Didion et al., 2011)	
	Killed in fires (Kolström & Kellomäki, 1993)	Very low susceptibility and high survival (Lyly et al., 2014)	
	Fire-intolerant (Molinari et al., 2020)		
Quercus robur	High bark insulation (Bär & Mayr, 2020)	Low height increment under herbivory (Bergquist et al., 2009)	*Moderately fire tolerant* *Herbivory intolerant* *(Black world)*
	Thin bark (Ilek & Kucza, 2014)	Negative impact on abundance and height from herbivory (Bernes et al., 2018)	
	Fire-tolerant (Molinari et al., 2020)	Palatable and reduced survival with herbivory (Churski et al., 2017)	
	Sprouting after fire (Petersson et al, 2020)	Very low survival probability under browsing (index=5, Didion et al., 2011)	
	Fire-promoted (Spînu et al., 2020)		
Betula pendula	Low bark insulation (Bär & Mayr, 2020)	High mortality (Ameztegui & Coll, 2015)	*Moderately fire tolerant* *Herbivory intolerant* *(Black world)*
	Thick bark (Ilek & Kucza, 2014)	No impact on abundance from herbivory but negative impact on height (Bernes et al., 2018)	
	Moderately low survival in fires (Kolström & Kellomäki, 1993)	High survival probability under browsing (index=2, Didion et al., 2011)	
	Fire-prone (Molinari et al., 2020)	Tree survival considered unlikely (Gill, 1992)	
		Low survival (Lyly et al., 2014)	
Tilia cordata	Fire-intolerant (Molinari et al., 2020)	No impact on abundance from herbivory (Bernes et al., 2018)	*Fire intolerant* *Herbivory tolerant* *(Brown world)*
	Colonisation after reduction in fire (Spînu et al., 2020)	High survival with herbivory (Churski et al., 2017)	

		Moderately high survival probability under browsing (index=3, Didion et al., 2011)	

[1] Tolerance was defined as ability to grow in the presence of herbivory or fire (Bond, 2005)

[2] Survival probability index sensu Didion et al. (2011): 1 (very) high, 2 high, 3 (moderately) high, 4 low, 5 (very) low. Survival probabilities for species were derived from ForClim v.2.9.6.

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Table S2 Grazing period and pressure in the four corrals included in the study.

	Corral	**Corral 1 (12.6 ha)**	**Corral 2 (8.5 ha)**	**Corral 3 (7.9 ha)**	**Corral 4 (16.8 ha)**
	Plot ID	1-6	7-12	13-18	19-24
2015	**Grazing period**	15/5-30/10	14/5-22/10	28/5-31/10	2/6-3/9
	CD*	875	1349	1648	1344
	Breed**	RK, HF	RK, HF	RK, FN, HF	HF
2016	**Grazing period**	13/5-7/11	13/5-10/11	19/5-3/10	19/5-22/9
	CD*	761	1032	753	682
	Breed**	FN, JU	RK, FN, HF, JU	RK	HF, JU
2017	**Grazing period**	11/5-25/10	1/6-1/10	16/5-18/8	17/5-19/8
	CD*	862	726	1420	659
	Breed**	FN	RK, JU	HF	RK

* CD=Cow-days (Number of cows*number of grazing days)

** RK=Rödkulla, FN=Fjällnära, HF=Hereford, JU=Juveniles of all breeds (1-2 years)

*** Animals only present for a few sporadic days

Table S3 Multiple pairwise comparisons test (Tukey´s) of relative survival between all tree species in each experimental treatment.

Treatment	**Species combination**	**Value**	P_{inf}
Fire : Herbivory	*Pinus – Picea*	-0.14	0.14
	Pinus – Quercus	-0.08	0.64
	Pinus – Betula	0.02	0.996
	Pinus – Tilia	0.09	0.23
	Picea – Quercus	0.06	0.87
	Picea – Betula	0.16	0.06
	Picea – Tilia	0.23	<0.001
	Quercus – Betula	0.10	0.40
	Quercus – Tilia	0.17	0.01
	Betula – Tilia	0.07	0.41
No-Fire : Herbivory	*Pinus – Picea*	-0.14	0.27
	Pinus – Quercus	-0.03	0.99
	Pinus – Betula	0.10	0.39
	Pinus – Tilia	0.10	0.48
	Picea – Quercus	0.10	0.57
	Picea – Betula	0.24	0.002
	Picea – Tilia	0.23	0.004
	Quercus – Betula	0.14	0.16
	Quercus – Tilia	0.13	0.21
	Betula – Tilia	-0.01	0.999
Fire : No-herbivory	*Pinus – Picea*	0.08	0.73
	Pinus – Quercus	-0.33	0.002
	Pinus – Betula	-0.10	0.58
	Pinus – Tilia	0.17	0.06
	Picea – Quercus	-0.41	<0.001
	Picea – Betula	-0.19	0.06
	Picea – Tilia	0.09	0.56
	Quercus – Betula	0.22	0.02
	Quercus – Tilia	0.50	<0.001
	Betula – Tilia	0.28	<0.001
No-Fire : No-herbivory	*Pinus – Picea*	0.06	0.82
	Pinus – Quercus	0.08	0.62
	Pinus – Betula	0.09	0.52
	Pinus – Tilia	0.33	<0.001
	Picea – Quercus	0.02	0.997
	Picea – Betula	0.03	0.99
	Picea – Tilia	0.27	0.001
	Quercus – Betula	0.01	0.999
	Quercus – Tilia	0.25	0.004
	Betula – Tilia	0.24	0.01

Species as appearing in table: Pinus *Pinus sylvestris* L., Picea *Picea abies* (L.) H.Karst., Quercus *Quercus robur* L., Betula *Betula pendula* Roth., Tilia *Tilia cordata* Mill.

Plot ID was nested in corral as random factors.

Table S4 Multiple pairwise comparisons test (Tukey´s) of relative survival between experimental treatments within each tree species.

Species	**Treatment combination**	**Value**	P_{inf}
Pinus	Fire : Herbivory – No-Fire : Herbivory	-0.12	0.20
	Fire : Herbivory – Fire : No-herbivory	-0.19	0.01
	Fire : Herbivory – No-Fire : No-herbivory	-0.67	<0.001
	No-Fire : Herbivory – Fire : No-herbivory	-0.07	0.68
	No-Fire : Herbivory – No-Fire : No-herbivory	-0.56	<0.001
	Fire : No-herbivory – No-Fire : No-herbivory	-0.48	<0.001
Picea	Fire : Herbivory – No-Fire : Herbivory	-0.11	0.35
	Fire : Herbivory – Fire : No-herbivory	0.03	0.97
	Fire : Herbivory – No-Fire : No-herbivory	-0.47	<0.001
	No-Fire : Herbivory – Fire : No-herbivory	0.14	0.15
	No-Fire : Herbivory – No-Fire : No-herbivory	-0.36	<0.001
	Fire : No-herbivory – No-Fire : No-herbivory	-0.50	<0.001
Quercus	Fire : Herbivory – No-Fire : Herbivory	-0.07	0.68
	Fire : Herbivory – Fire : No-herbivory	-0.44	<0.001
	Fire : Herbivory – No-Fire : No-herbivory	-0.51	<0.001
	No-Fire : Herbivory – Fire : No-herbivory	-0.37	<0.001
	No-Fire : Herbivory – No-Fire : No-herbivory	-0.44	<0.001
	Fire : No-herbivory – No-Fire : No-herbivory	-0.07	0.68
Betula	Fire : Herbivory – No-Fire : Herbivory	-0.03	0.93
	Fire : Herbivory – Fire : No-herbivory	-0.31	<0.001
	Fire : Herbivory – No-Fire : No-herbivory	-0.60	<0.001
	No-Fire : Herbivory – Fire : No-herbivory	-0.28	<0.001
	No-Fire : Herbivory – No-Fire : No-herbivory	-0.57	<0.001
	Fire : No-herbivory – No-Fire : No-herbivory	-0.28	<0.001
Tilia	Fire : Herbivory – No-Fire : Herbivory	-0.11	0.08
	Fire : Herbivory – Fire : No-herbivory	-0.11	0.08
	Fire : Herbivory – No-Fire : No-herbivory	-0.43	<0.001
	No-Fire : Herbivory – Fire : No-herbivory	0	1
	No-Fire : Herbivory – No-Fire : No-herbivory	-0.32	<0.001
	Fire : No-herbivory – No-Fire : No-herbivory	-0.32	<0.001

Species as appearing in table: Pinus *Pinus sylvestris* L., Picea *Picea abies* (L.) H.Karst., Quercus *Quercus robur* L., Betula *Betula pendula* Roth., Tilia *Tilia cordata* Mill.

Plot ID was nested in corral as random factors.

Table S5 Multiple comparisons test (Tukey´s) of net height increment between experimental treatments within each tree species.

Species	**Treatment combination**	**Value**	P_{inf}
Pinus	Fire : Herbivory – No-Fire : Herbivory	-0.54	0.999
	Fire : Herbivory – Fire : No-herbivory	-18.41	0.05
	Fire : Herbivory – No-Fire : No-herbivory	-21.80	0.01
	No-Fire : Herbivory – Fire : No-herbivory	-17.87	0.03
	No-Fire : Herbivory – No-Fire : No-herbivory	-21.26	0.003
	Fire : No-herbivory – No-Fire : No-herbivory	-3.39	0.95
Picea	Fire : Herbivory – No-Fire : Herbivory	-2.55	0.98
	Fire : Herbivory – Fire : No-herbivory	-6.74	0.76
	Fire : Herbivory – No-Fire : No-herbivory	-10.90	0.30
	No-Fire : Herbivory – Fire : No-herbivory	-4.20	0.92
	No-Fire : Herbivory – No-Fire : No-herbivory	-8.36	0.52
	Fire : No-herbivory – No-Fire : No-herbivory	-4.16	0.91
Quercus	Fire : Herbivory – No-Fire : Herbivory	5.39	0.86
	Fire : Herbivory – Fire : No-herbivory	-8.82	0.51
	Fire : Herbivory – No-Fire : No-herbivory	-19.60	0.01
	No-Fire : Herbivory – Fire : No-herbivory	-14.21	0.12
	No-Fire : Herbivory – No-Fire : No-herbivory	-24.99	<0.001
	Fire : No-herbivory – No-Fire : No-herbivory	-10.78	0.24
Betula	Fire : Herbivory – No-Fire : Herbivory	0.11	1
	Fire : Herbivory – Fire : No-herbivory	-25.38	0.001
	Fire : Herbivory – No-Fire : No-herbivory	-50.87	<0.001
	No-Fire : Herbivory – Fire : No-herbivory	-25.49	0.002
	No-Fire : Herbivory – No-Fire : No-herbivory	-50.98	<0.001
	Fire : No-herbivory – No-Fire : No-herbivory	-25.48	<0.001
Tilia	Fire : Herbivory – No-Fire : Herbivory	13.91	0.50
	Fire : Herbivory – Fire : No-herbivory	1.66	0.998
	Fire : Herbivory – No-Fire : No-herbivory	-2.84	0.99
	No-Fire : Herbivory – Fire : No-herbivory	-12.24	0.39
	No-Fire : Herbivory – No-Fire : No-herbivory	-16.75	0.07
	Fire : No-herbivory – No-Fire : No-herbivory	-4.50	0.92

Species as appearing in table: Pinus *Pinus sylvestris* L., Picea *Picea abies* (L.) H.Karst., Quercus *Quercus robur* L., Betula *Betula pendula* Roth., Tilia *Tilia cordata* Mill.

Plot ID was nested in corral as random factors.

Table S6 Search queries on Web of Science. Date for search 2021-06-24.

Search no	**Disturbance**	**Query**	**Number of papers**
1	Fire	TS=(fire*) AND TS=(Pinus sylvestris) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	440
2	Fire	TS=(fire*) AND TS=(Picea abies) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	488
3	Fire	TS=(fire*) AND TS=(Betula pendula) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	82
4	Fire	TS=(fire*) AND TS=(Quercus robur) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	58
5	Fire	TS=(fire*) AND TS=(Tilia cordata) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	10
6	Grazing	TS=(graz*) AND TS=(Pinus sylvestris) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	94
7	Grazing	TS=(graz*) AND TS=(Picea abies) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	93
8	Grazing	TS=(graz*) AND TS=(Betula pendula) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	33
9	Grazing	TS=(graz*) AND TS=(Quercus robur) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	73
10	Grazing	TS=(graz*) AND TS=(Tilia cordata) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	9
11	Browsing	TS=(brows*) AND TS=(Pinus sylvestris) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	108
12	Browsing	TS=(brows*) AND TS=(Picea abies) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	194
13	Browsing	TS=(brows*) AND TS=(Betula pendula) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	72
14	Browsing	TS=(brows*) AND TS=(Quercus robur) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	63
15	Browsing	TS=(brows*) AND TS=(Tilia cordata) AND TS=(tree*) AND TS=(sensitiv* OR toleran* OR survival* OR resistance* OR mortality* OR trait*)	17

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The aim of this PhD thesis was to study the effect of fire and herbivory on the vegetation in a Northern European temperate wood-pasture. While mortality and growth were species dependent, the overall effect was a reduction of woody vegetation, which was favourable for light-demanding herbaceous vegetation. The interaction between fire and herbivory altered conditions for future fires and herbivory, thereby generating heterogeneity in the landscape. Consequently, both processes should be taken into consideration in conservation management to promote biodiversity.

Karin Amsten completed her undergraduate degree at the Swedish University of Agricultural Sciences (SLU), and completed her courses at graduate level at several Swedish universities before being accepted as a PhD student at Southern Swedish Forest Research Centre at SLU.

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