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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(*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
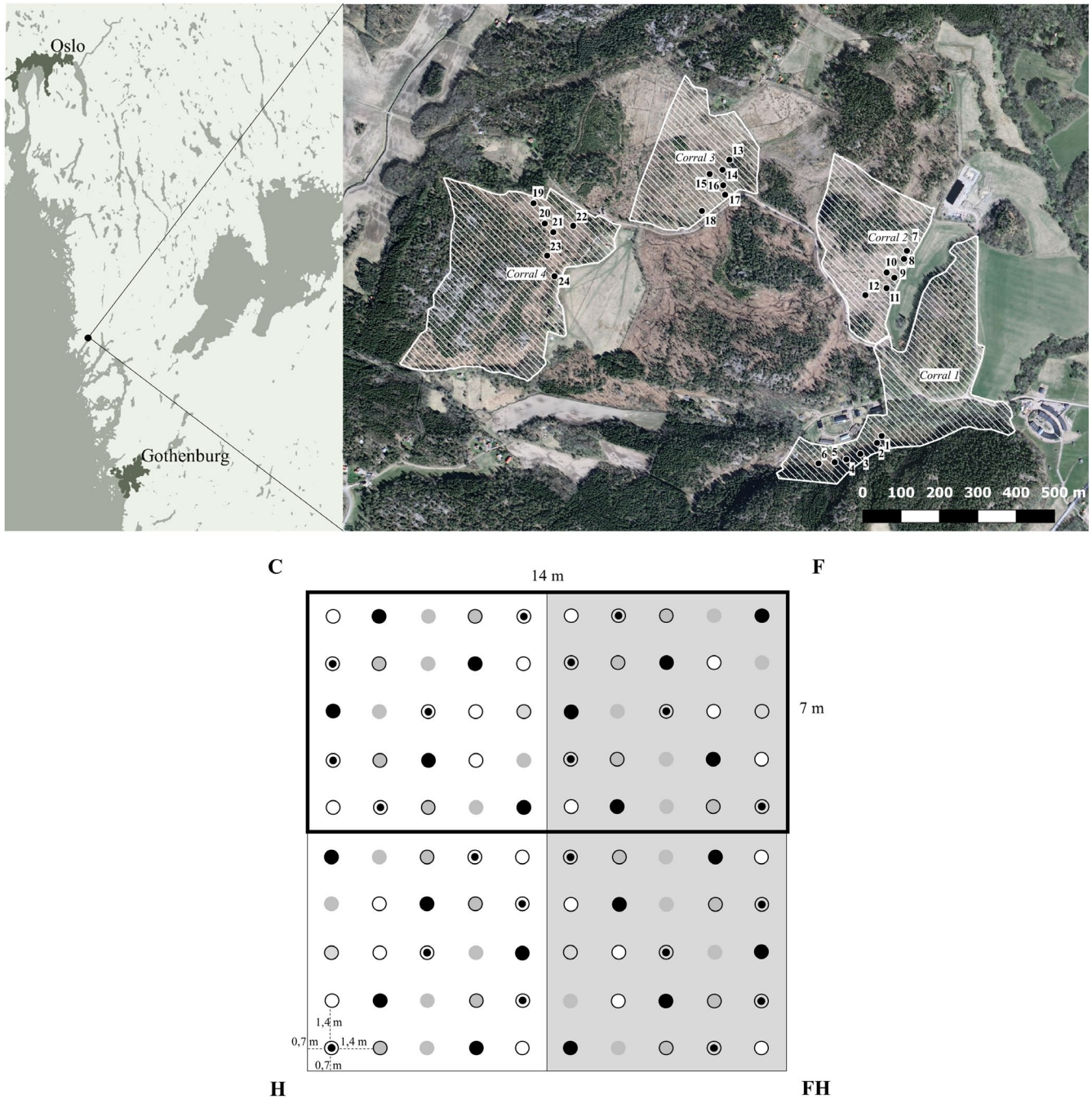
FIGURE 1 Location of study area on the Swedish West Coast (upper left), position of study plots in the area (upper right) and study plot design (lower middle). All 24 study plots were divided into four subplots; no-fire:no-herbivory (C), fire:no-herbivory (F), no-fire:herbivory (H) and fire:herbivory (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 ʟᴍᴇʀᵀᴇꜱᴛ 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

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.

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).

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
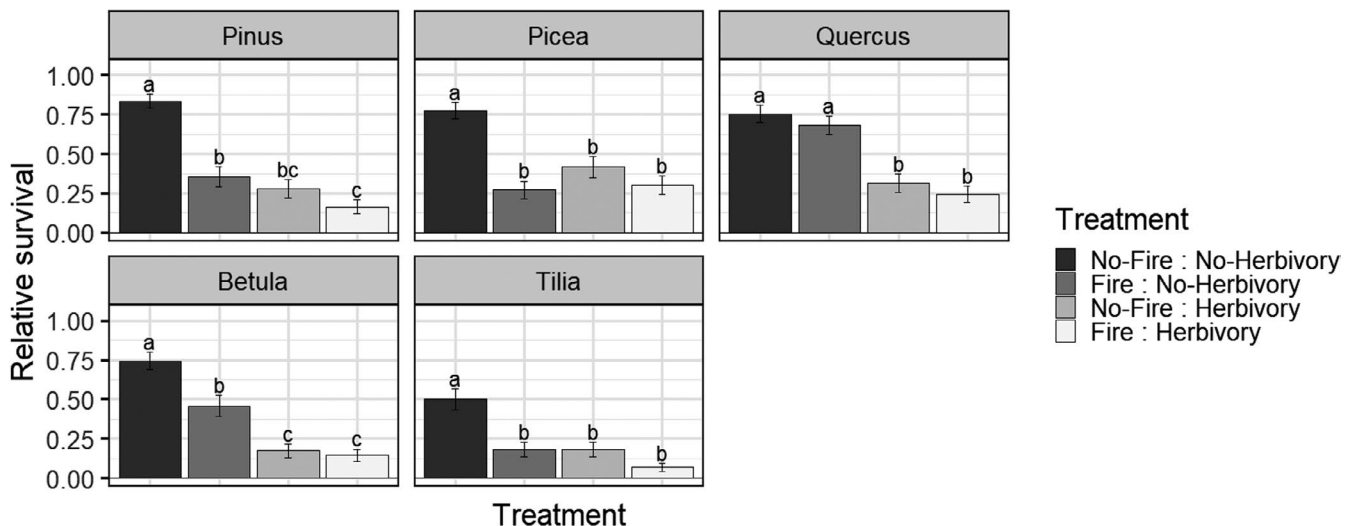
FIGURE 2 Relative survival of tree saplings in four experimental treatments (no-fire:no-herbivory, fire:no-herbivory, no-fire:herbivory and fire:herbivory), 3 years after planting (error bars represents ±1 *SE*). Significance within each species is indicated with letters (test statistics can be found 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
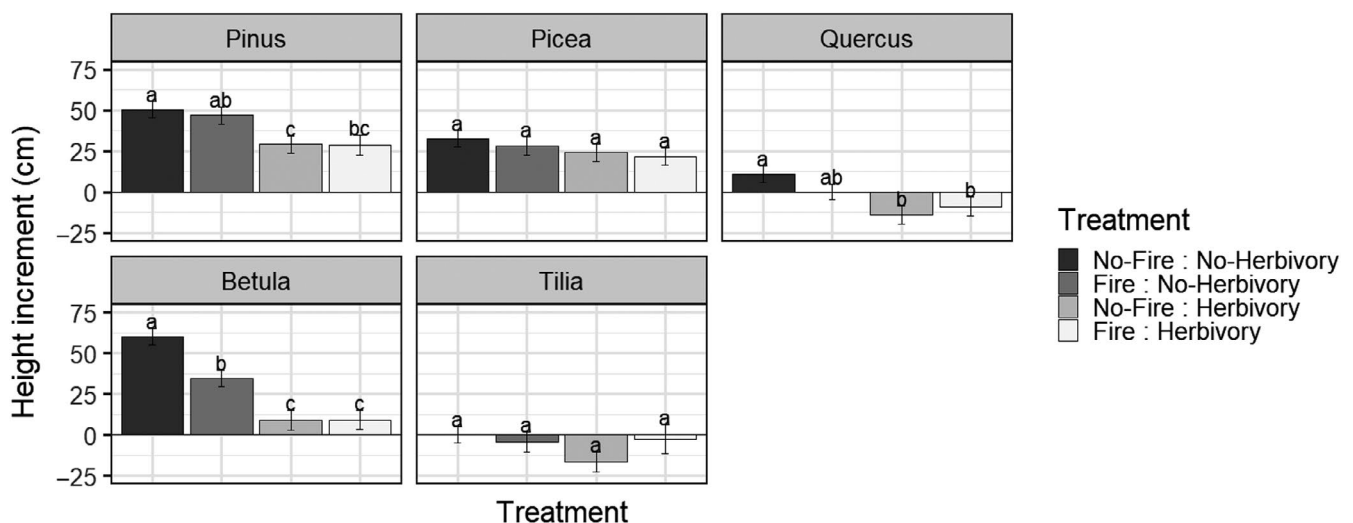
present at relatively low numbers. Herbivory had an overall strong negative effect on sapling survival but with large variation among species (Figure 2), demonstrating clear consumer control in our study with potential filtering effects on tree community composition. Height increment was either reduced 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.

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.

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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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