



Did forest fires maintain mixed oak forests in southern Scandinavia? A dendrochronological speculation

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ABSTRACT

In northern Europe, a long history of human exploitation effectively eliminated legacies of natural disturbances in mixed oak forests and we currently lack understanding of the role of natural disturbance factors in affecting oak regeneration into the forest canopies. We compiled dendrochronological, observational and paleochronological data from Southern Sweden to discuss the role of forest fires in oak (*Quercus* spp.) dynamics. We analyzed oak age structure and its growth dynamics in six southern Swedish forests, which experienced fires between 42 and 158 years prior to our sampling. Extending our analysis over longer time frames, we studied the relationship between sediment charcoal and oak pollen in an area of south-eastern Sweden, where oak has been a common canopy species. In three of the study sites, forest fires resulted in increased oak regeneration. Although fires were generally not associated with a wave of growth releases in surviving trees, the mean basal area growth rate of oaks increased by a range of 108% to 176%, following the fires. The overall pattern indicated that historical fires in oak-dominated forests were of low severity, did not kill canopy oaks, and yet provided a window of regeneration opportunities for that species. Post-fire sprouting of oak and an increase in oak seedling densities following modern prescribed fires are consistent with this explanation. Consistent with this conclusion were significant positive correlations between charcoal concentration and the oak pollen percentage in a site in southeastern Sweden. We discuss the co-occurrence of oak and pine in the historical southern Swedish landscape, as a possible analogy to eastern North American oak-pine forests. Modern conservation policies aimed at the preservation of oak in the southern Swedish landscape should consider the use of low severity fires to maintain natural oak regeneration.

1. Introduction

Forests which experienced little human impact are rare in Europe and it specifically applies to mixed oak ecosystems. There is a strong conservational interest to preserve remnants of these species-rich communities in their close-to-natural states (Nilsson 1997; Hilszczanski & Jaworski 2018). However, a decline in oak (*Quercus robur* / *Q. petraea*) regeneration during the last decades puts this vision at risk. Darker forest environments, commonly resulting from the development of dense and shade-tolerant understories, have been viewed as a factor

contributing to the oak regeneration declines in southern Scandinavia (Pettersson et al. 2019), Ukraine (Rumiantsev et al. 2018) and European Russia (Shishov 1983; Selochnik 2014). The abundance of browsers and competition with woody and herbaceous vegetation have been further demonstrated to lower oak seedling and sapling densities (Jensen & Löf 2017; Pettersson et al. 2019). In Southern Sweden the decline of the genus the last millennia has been generally attributed to cuttings and increasingly common browsing by cattle (Lindbladh & Foster 2010, Eliasson, 2004). Similarly, low levels of oak regeneration has attracted much attention in the Baltic Sea region and in Poland (Bobiec, 2002;

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Kokareviča et al., 2015; Spínu et al., 2020).

As the oak (*Q. robur* and *Q. petraea*) has been traditionally considered as a climax, i.e. late-successional, species (Neshataev et al., 1974; Falinski, 1988), a general decline in its recruitment into the canopies of mature and old-growth forests in Europe over the 20th century questioned that view. The consideration of oak-dominated forests as “transient” (sensu Bobiec et al., 2011) communities depending on the various disturbance events aimed to reconcile the observations with the phytosociological theory. In Europe, the hypothesis of Frans Vera (Vera 2000) has pictured regeneration of high-canopy forest (not necessarily oak-dominated) as a sequence of stages involving a close canopy stage with largely unsuccessful regeneration due to ungulate browsing. The hypothesis proposed that canopy tree mortality ultimately leads to open landscapes where tree seedlings regenerate under the protection of the thorny bushes, eventually reaching the height of the mature trees and forming closed canopies. Indeed, experimental and observational studies have shown positive effects of canopy openness on the establishment, survival, and growth of oak seedlings (Frost & Rydin 2000; Kelly 2002; Götmark 2007; Dillaway et al. 2007). Although oaks have been generally associated with the late and intermediate serial stages of forest development, both in Europe and North America (McCune & Cottam 1985; Abrams et al. 1997; Götmark and Kiffer, 2014; Selochnik 2014), they generally exhibit only a moderate tolerance to shade (Larsen & Johnson 1998; Niinemets & Valladares 2006; Kharchenko 2012). It is, therefore, not surprising that oaks reveal a generally positive response to natural and human-mediated disturbances that result in the complete or partial removal of the shade-tolerant forest understory, opening up forest canopies, thus reducing competition on the ground floor and improving access to mineral seedbeds (Löf et al. 2006; Harmer & Morgan 2007; Götmark and Kiffer, 2014). In this context, windstorms (Götmark and Kiffer, 2014), logging (Orwig & Abrams 1994) and forest fires (Niklasson et al. 2002) have all been regarded as important disturbance agents promoting oak regeneration. In particular, it has been proposed that low intensity ground fires support oak recruitment into the canopies in both North American (Batek et al. 1999; Shumway et al. 2001; Rieske 2002) and European deciduous forests (Björkman 1998; Niklasson et al. 2002). In southern Sweden, tree-ring reconstructions in combination with pollen and charcoal analysis at the scale of single stands have revealed the presence of oak under frequent fires (Niklasson et al. 2002; Hannon et al. 2010).

In northern Europe, a long history of human exploitation effectively eliminated legacies of natural disturbances in mixed oak forests. Oak dominated forests have been commonly used for grazing, the gathering of acorns, and as a source of timber and firewood (Ståål 1986). Archaeological evidence points towards a widespread use in oak forests in the Mesolithic ages (Steensberg 1979; Lindman 1991) but few written historical sources exist on the use of oaks during more modern times. In Sweden, oaks lost their protection from the King around the year 1830 (Eliasson, 2002; Eliasson, 2004). This was followed by a dramatic decrease in the amount of semi-natural oak-dominated stands in the southern part of the country. Beside higher cutting rates, oak disappearance from the landscape was likely facilitated by the cessation of fires, increased woodland grazing by livestock, conversion of oak-dominated sites into agricultural fields and later - into spruce monocultures grown for timber production (Niklasson & Nilsson 2005; Lindbladh et al. 2014).

As all low-land European forests have been subject to human impact, the partitioning between the natural vs. human causes of disturbance is a challenging task. The definition of the “naturalness” in respect to oak regeneration dynamics remains, therefore, a topic of much debate. The complexity of the question is well illustrated by dendrochronological studies of oak regeneration in Białowieża forest, the largest remaining area of natural yet human-impacted European low-land forests (Bobiec 2012; Spínu et al., 2020). Land use promoting fires and forest clearing prior to mid-1800s and the prohibition of these activities afterwards had immediate effects on oak recruitment.

Exploring the forest history of the remaining semi-natural oak forests is of immediate help to identify natural and human-related processes maintaining oak in the canopy. There is, however, a considerable risk that the site-specific history of the remaining semi-natural oak forests may limit our possibilities in designing sufficiently general conservation strategies. These forests currently exist only in a number of locations in Scandinavia (such as Hallands Väderö and Dalby Söderskog, Brunet & Berlin 2004), within the Białowieża Primeval Forest (Hilszczanski & Jaworski 2018), and within a number of small reserves in the European part of Russia (Kharchenko 2012). The general lack of knowledge on fire regimes is of particular concern, since it prevents us from conceptualizing the role of fire in oak dynamics in these ecosystems. Studies analyzing fire effects in a network of such semi-natural sites are, therefore, highly warranted.

In this paper, we report the results of dendrochronological analyses of six southern Swedish forests where dated fire scars on oak trees and stumps provided evidence of historical fire occurrence. All of the forests were located in the boreo-nemoral zone (Fig. 1) and featured dominant or co-dominant oak in the upper canopy. Based on the knowledge of fire effects on oak regeneration in eastern North America (Abrams 2016 and references therein) and paleochronological studies from Scandinavia (Björkman 1998), we hypothesized (H1) that fire resulted in the increased oak regeneration (H1.1) and improved growth (H1.2), as compared to pre-fire conditions. Our reference to eastern North America in the analysis of Southern Swedish oaks is justified by the observation that both regions share broadly similar climatic conditions (Supplementary Information Fig. 1) and feature temperate mixed forests where oaks have been historically an important component of dominant canopies. As research on fire ecology of oak-dominated ecosystems has been conducted almost exclusively in Eastern North America, we believe it is instrumental to relate discussion on fire-oak relationships in Southern Sweden to the relevant Eastern North American studies. To support the discussion of H1, we used pollen and charcoal data to analyze the role of fire in supporting oak recruitment in a landscape located in south-eastern Sweden. This region is characterized by generally fire-prone conditions during the summer months, high levels of both historic fire activity and oak abundance in historical forests (Lindbladh et al. 2003; Niklasson et al., 2010a, 2010b; Petersson et al. 2019). We further hypothesized (H2) that the variability in post-fire regeneration was correlated with the severity of drought conditions in respective fire years, with fire under more severe drought resulting in higher post-fire regeneration, due to higher accessibility of mineral seedbeds (Schimmel & Granström 1996) and increased light levels. To the best of our knowledge, this study is the first to provide multi-site analyses of the long-term fire effects on oak regeneration in northern Europe.

2. Material and methods

2.1. Study area

The study region predominately exhibits a sub-oceanic climate with mean annual temperatures ranging between 5 and 8 °C. The mean temperature in January varies between −4 and 0 °C; and in July, between 15 and 16 °C. There is a large precipitation gradient between the western (up to 1200 mm/year) and the eastern (650 mm/year) parts of the Southern Sweden (Fig. 1). During the growing season the western part is characterized by high precipitations (>150 mm), while the eastern part commonly experiences droughts (<50 mm), (Lundin 2009).

Westerly or south-westerly winds typically prevail in southern Sweden (Raab & Vedin 1995). The growing season, the period with the average daily mean air temperature above 5 °C, lasts for 180–240 days (Nilsson 1996). Snow cover often occurs from November-December to late February-March. The dominant soil types are podzols and cambizols (Fredén 2002). The forests studied here were located on moderately rocky and well-drained substrates.

The region stretches over both the nemoral and boreo-nemoral

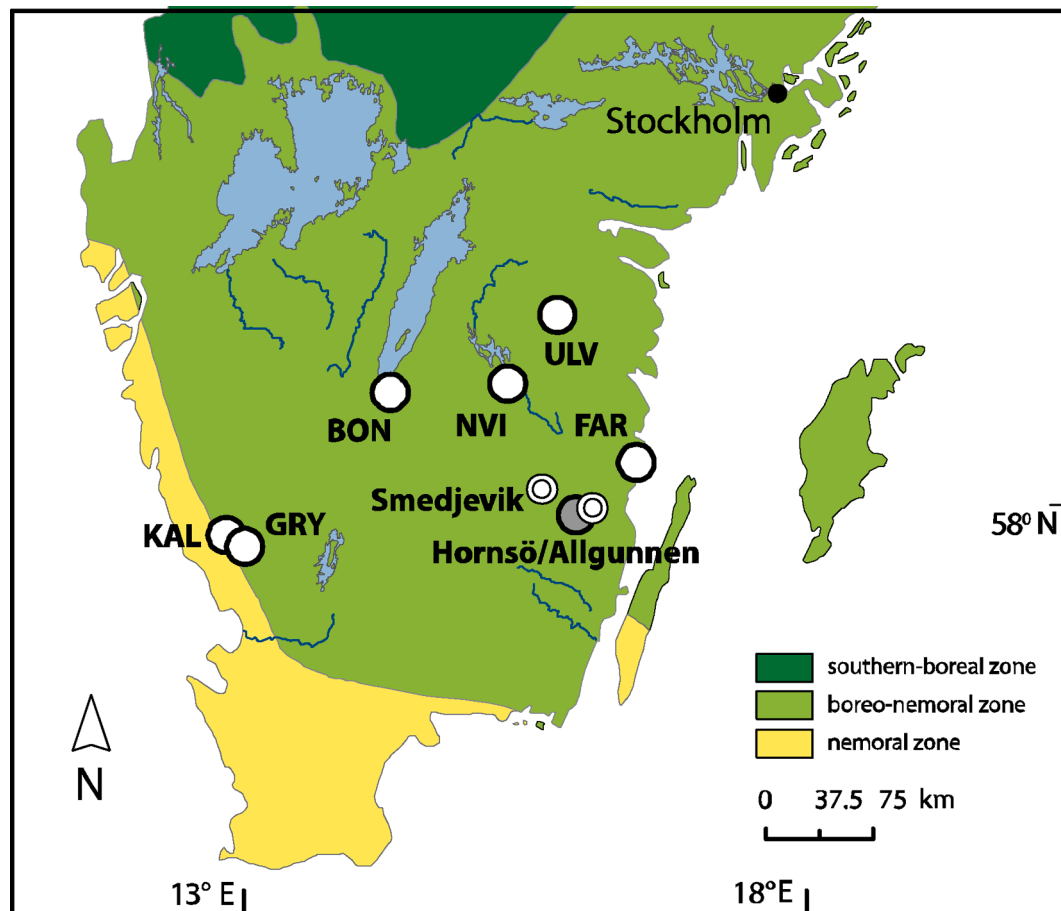


Fig. 1. Location of the study sites in southern Sweden and biogeography of the region. Filled circle indicates location of the Hornsö-Allgunnen paleo site. Full names of the other sites are given in Table 1. Double circle sign indicate sites where the post-fire oak seedling densities were studied (Smedjevik and Hornsö-Allgunnen).

phytogeographical zones (Fig. 1, Ahti et al., 1968). A major part of the study region is a transition zone between the boreal and nemoral biomes, where both coniferous and deciduous trees are/were naturally common. Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) are currently the main coniferous species ($\geq 80\%$ of the volume of standing trees in the area, Nilsson et al. 2019). Oak (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.) and beech (*Fagus sylvatica* L.), together with small-leaved species (birches, *Betula* spp., aspen, *Populus tremula* L., mountain ash, *Sorbus* spp. and alder, *Alnus glutinosa* (L.) Gaertn.) are common deciduous trees. Although the two oak species have generally similar ecology, *Q. robur* exhibits a more northern distribution limit in Scandinavia (up to 61° N). Oak appeared in southern Sweden around 10 000–9 000 years ago and has been abundant there during most of the Holocene (Berglund et al. 1996; Giesecke 2016). The current proportion of oak cover in southern Sweden is around 3%, which corresponds to 4.1% of the total volume of standing trees. Oaks in Southern Sweden typically grow in mixed forests and in production spruce forests often hosting sparsely spaced, intermediate-sized and occasionally older oak trees (Drobyshev et al. 2019).

2.2. Rationale for analyses in relation to the hypotheses tested

To test H1.1 we studied dendrochronologically reconstructed patterns of oak regeneration over the stands' lifespan. To extend the discussion of H1.1 over millennia timescales we reanalyzed oak pollen and charcoal chronologies in a site in South-Eastern Sweden. To test H1.2 we analyzed growth patterns of oak and other canopy trees following fire events on six dendrochronologically studied sites. Finally, to test H2 we related fire dates obtained through dendrochronological dating of fire

scars to the historic fire-prone conditions. As such we used reconstructions of sea level pressure (SLP) and precipitation, both being considered as proxies of drought conditions. In the case of SLP, high-pressure atmospheric cells are associated with sunny and precipitation-free periods, making both pressure SLP records correlate with regional levels of annual fire activity (Drobyshev et al 2015). Here we relied on superposed epoch analysis to check for associations of fire dates and effects of particular fires with the severity of fire-prone conditions, as revealed by two climate proxies.

2.3. Data sampling in the field and laboratory methods

Locations of fire-affected forests have been initially identified during the course of several research projects, including the Swedish Oak Project (Götmark 2019). Due to this fact, the field protocol exhibited variability with respect to the areas sampled and the total amount of data available from each site (Table 1). Sample plots were established in areas centered on oak trees with basal damages indicative of temperature-related cambium mortality following a fire (Smith & Sutherland 1999). In each forest, we established a study plot (0.06–0.125 ha in size, Table 1), where all trees with the diameter above breast height (DBH) above 9 cm were cored with the increment corer approximately 10 cm above the ground. We also used a chainsaw to cut wedges and/or cross-sections of the trees to obtain samples with the fire scars and pith dates on living trees and stumps. On site Fårbo (code FAR), only the largest canopy oaks were sampled. This limited our ability to quantify the cohort structure. Data from this site, therefore, were used only for the analyses of oak growth response to fire and climate-fire interactions (see below).

Table 1

Site properties and sampling details. Canopy composition is assessed as a proportion of the total basal area associated with a species, in fractions of ten. QR - *Quercus robur*, FS - *Fagus sylvatica*, PS - *Pinus sylvestris*, PA - *Picea abies*, BP - *Betula* spp., TC - *Tilia cordata*, FE - *Fraxinus excelsior*, AP - *Acer platanoides*. The total amount of trees sampled in each site is given in SiteID field.

SiteID	Full name	Coordinates	Canopy composition	Dated fires	Sampled area, ha	The year sampled
ULV (n = 37)	Ulvsdal	58.062°N 16.221°E	3QR:2PS:1PT: 1PA:2TC:1AP	1888	0.120	2002 & 2016
BON (n = 42)	Bondberget NR	57.771°N 14.247°E	3QR:3PS:1PT: 1FE:1PA:1TC	1957, 1960	0.06	2002 & 2016
NVI (n = 41)	Norra Vi NR	57.876°N 15.331°E	5QR:1PT: 2PA:1PS:1BP	1871, 1912	0.100	2002 & 2016
GRY (n = 47)	Grytåsen, Biskopstorp NR	56.781°N 12.892°E	3QR:4FS:3PS	1843	0.120	2001 & 2016
KAL (n = 65)	Kalvaberg, Biskopstorp NR	56.792°N 12.865°E	4QR:2FS:2PS:1PA:1BP	1843	0.125	2001
FAR (n = 17)	Fårbo	57.403°N 16.505°E	5QR:4PA:1AP	1935	0.100	2002

We cross-dated samples using the visual pointer year method (Stokes & Smiley 1968), measured them with the help of Coorecorder and CDendro software (Larsson 2018) and verified dating, by using the pointer years and the COFECHA program (Grissino-Mayer 2001).

2.4. Analysis of oak regeneration rates

We estimated the effect of fires on oak regeneration by evaluating the significance of the departure in the regeneration rate from the respective long-term mean. We calculated the regeneration rate as the number of trees with the projected pith date falling within a 10-year period. In other words, we operated with a proxy of oak regeneration, which reflects *effective establishment rate*, i.e. seedlings and saplings that succeeded in reaching forest canopy decades after the fire event, and integrates over multiple factors affecting the probability of a seedling to reach forest canopy (e.g. seedling and sapling mortality due to browsing and competition).

First, to obtain an estimate of the long-term regeneration rate for a site, we randomly bootstrapped the period covered by the tree regeneration dates within a site. Specifically, we resampled with replacement continuous ten year periods and for each period estimated regeneration rate, i.e. number of trees regenerated during that period. We performed 1000 such resampling experiments, obtaining the distribution of decadal regeneration rates. Second, to obtain an estimate of the regeneration rate associated with a fire event, we used an empirical cumulative distribution function, fitted by the function *ecdf* in R package *stats*. The function allowed us to calculate the probability of the regeneration rate reaching the values observed within a 10-year frame centered on the fire date in that site.

We studied oak seedling (<1 cm in diameter) in two sites that included sections subject to recent prescribed burns: Allgunnen-Hornsö and nature reserve Smedjevik (Fig. 1). A site in Allgunnen-Hornsö was subject to a prescribed burn in 2018 and a site in Smedjevik – in 2010. Both fires were done with biological conservation purposes in mind, primarily – to promote lighter conditions at the forest floor and regeneration of shade-intolerant species. The severity of both fires were similar, consumption of organic layer varying between 4 and 6 cm. We randomly established six 100 m² plots on the burned sections in each of the sites, eight control (non-burned) plots in Allgunnen-Hornsö and four – in Smedjevik. Using the maximum likelihood method, we fitted mixed effect model with a seedling number as the dependent variable, plot type (burned vs. unburned) as the fixed variable and the site as the random variable.

2.5. Analysis of growth patterns

Post-fire growth patterns of trees were studied in three ways: (a) through the identification of growth releases in chronologies of all trees that survived fires, (b) by calculating the ratio of oak growth rate prior and following the fire events, and (c) analyzing sprouting of oak trees in sites subject to prescribed fires. Growth release analysis has been initially developed to reflect responses of understory trees to the increases in light levels due to canopy disturbances (Abrams & Nowacki 1994; Abrams et al., 1997). Here this method aimed to characterize oak

growth reaction to fires, integrating various (not exclusively light levels) environmental conditions of surviving trees. By acknowledging the established terminology we present the method as “growth release analysis”. However, in the Discussion section we will refer to the results broadly in terms of growth patterns, and not necessarily as responses to light-induced changes in growth.

We identified growth releases with the help of radial-growth averaging criteria (Nowacki & Abrams 1997). The method is based on the running comparisons of sequential 10 year ring-width averages and the estimation of the percentage growth change in single tree chronologies. In this study, we used the common threshold of a 25% growth increase over ten years (Nowacki & Abrams 1997), as an indicator of canopy disturbance. We employed the R package *Trader* (Altman et al. 2014) to obtain growth release data on raw (non-detrended) chronologies. To this end, we relied on Nowacki and Abrams (1997) method realized in the function *growthAveragingALL*. The method is based on the calculation of the percentage growth change (%GC) between average radial growth during the preceding 10-year period, M1 (this includes the target year), and average radial growth over the following 10-year period, M2: %GC = [(M2-M1)/M1] * 100. We combined both moderate (25% increase in growth over 10 years) and major (50% increase) growth releases in our analyses. To assess the probability of the observed differences between post-fire regeneration rates and the long-term average, we employed an approach similar to the one used in the analysis of regeneration rates. In particular, we bootstrapped the distribution of growth release rates and used an empirical cumulative distribution function to estimate the probability of release rates reaching the values observed following the dated fire events.

We calculated the ratio of oak growth rates prior (denominator) and following the fire events (nominator), using a 10-year time frame and the R package *pointRes* (van der Maaten-Theunissen et al. 2015).

We assessed the sprouting capacity of oak at sites subject to prescribed fires (see the previous sub-section). Using the same plots as for the analysis of seedling densities, we recorded the presence of sprouts at the base of the oak trees (stems larger than 2 cm in diameter) in both control (unburned) and burned plots. Sprouting capacity was evaluated by Chi-squared test operating on the 2 × 2 table of frequencies of stems with/without sprouts in burned/unburned environments.

2.6. Climate-fire analysis

To test for the association of fire occurrence in the studied sites with climate variability, we conducted a superposed epoch analysis (SEA). SEA tests for consistency in departures of a climate variable during the event years from the long-term mean, which are regarded as a proxy for a climatological fire hazard. The analysis was based on the assumption that the tendency for a forest fire to occur during climatologically fire-prone periods is an indication of natural causes promoting fire occurrence and spread. SEA used two climate records: gridded reconstruction of summer precipitation (Pauling et al. 2006) and sea level air pressure (Allan & Ansell 2006; Kuttel et al. 2010). Precipitation reconstruction was based on a variety of long instrumental precipitation series, various historical evidence and natural proxies (e.g. tree-ring chronologies). The pressure reconstruction was based on a compilation of a large number of

terrestrial and marine observational datasets. The reconstructions have been developed independently, overlapped with the period with the dated fires, and were considered as proxies of the summer drought signal, both of them reflected the severity of fire-prone conditions. For each site, we extracted the values for the closest grid cell of the respective reconstruction. To enhance high-frequency variation in the time series, we detrended the resulting chronologies by the spline function with the 50% frequency cut-off at 32 years, using the R package *dplr* (Bunn 2008). SEA was carried out with the help of the R package *burnr* (Malevich 2019). We used the time window of 10 years around the fire year and 1000 bootstrap resamples to estimate the statistical significance of departures during fire and lagging years.

2.7. Analysis of oak pollen and charcoal chronologies

We re-analyzed the association between fire and oak abundance in chronologies of oak pollen proportions and charcoal influx previously developed from the Hornsö-Allgunnen, an area located in south-eastern Sweden (Niklasson et al. 2002; Lindbladh et al. 2003) (Fig. 1). The area is currently dominated by Scots pine and Norway spruce forests, with scattered occurrences of oak in the modern forest overstories. Paleo- and dendrochronological records have documented frequent forest fires in

these landscapes (Lindbladh et al. 2003). The percentage of oak pollen in all terrestrial pollen provided a proxy for the abundance of tree species, while the charcoal concentrations were used as a proxy of fire activity over millennia-long timescales. The pollen and charcoal site was a wetland, ca 50 * 30 m², forested with mainly birch trees. The core was taken ca 8 m from the upland area and not more than ca 20 m from the closest burned pine stump at a site, suggesting that the sampling point had a good chance to be subjected to fires in the past. The many boulders are conspicuous in the surrounding upland that is dominated by pine and birch trees of different sizes. The sediment in the wetland was sampled with a Wardenaar corer. The 1 m long monolith consisted of uniformly colored detritus peat up to about 10 cm from the surface, from 10 cm to the top it consisted of coarse detritus peat with some wood. Samples (0.4–1.14 cm³) were taken from the center of the core for the pollen analysis. In total 44 levels were analyzed, and a minimum of 400 pollen grains was counted at all levels except one, where 300 grains were counted. Samples (0.4–1.3 cm³) for the charcoal analysis were sieved through meshes with a net size of 2, 1, 0.5 and 0.25 mm. The charcoal fragments from the different residuals were counted with the help of a magnifier, in total from 103 levels. The pollen and charcoal analysis were carried out contiguously, however from 28 cm (ca AD 200) and below the density of the charcoal levels was much higher.

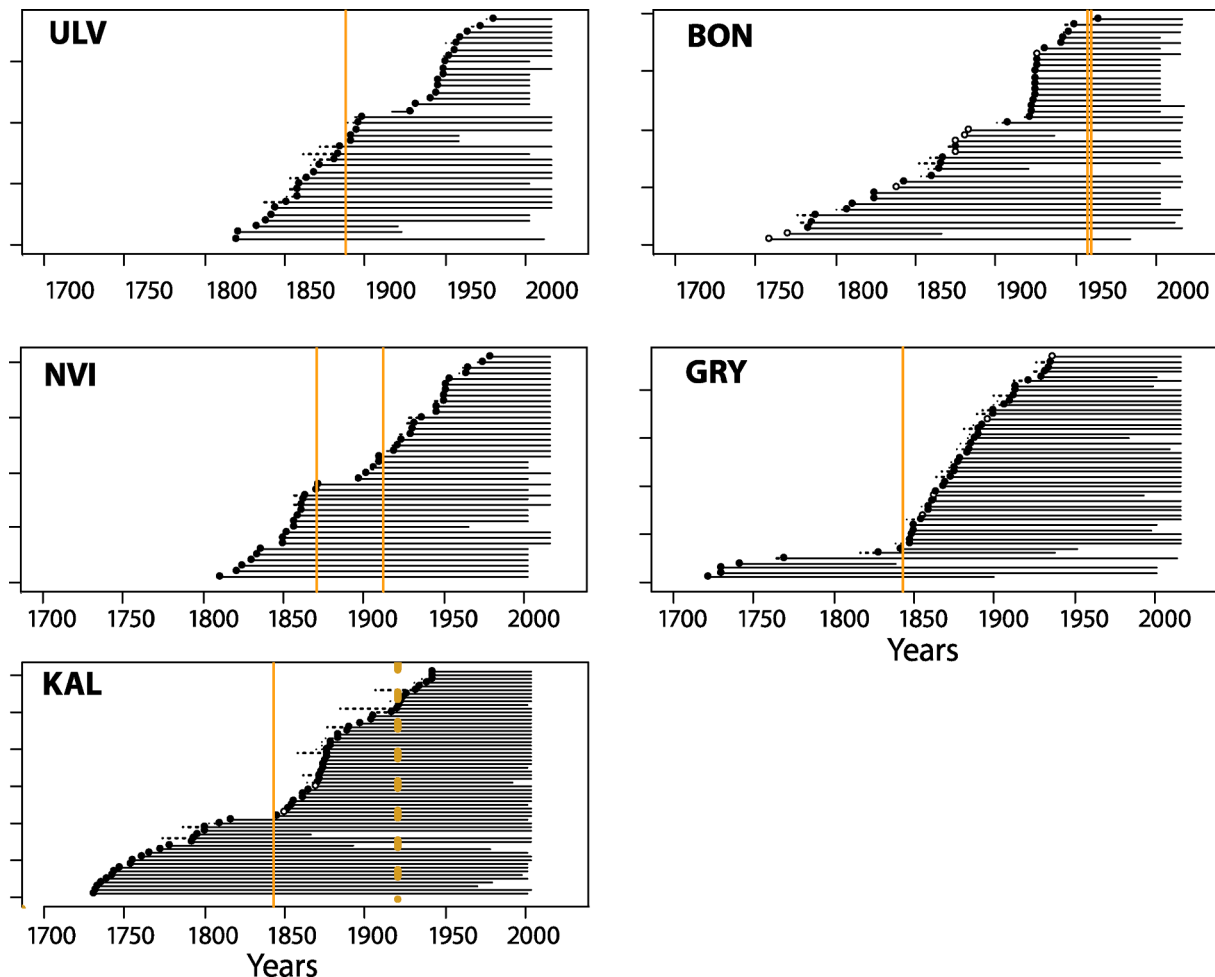


Fig. 2. Age structure of canopies in the studied forests. Each line represents a tree (an oak or a tree of other species). Dashed lines indicate the portions of lifespans estimated from the pattern of the ring border bending on the samples taken from the trees affected by wood rot. Empty circles at the end of the lines indicate trees where estimation of the pith dates was not possible. Orange solid lines mark fire event, and orange dotted line – a thinning event on site KAL. Note that a considerable number of trees with the youngest ring dated to 2002 (sites ULV, BON and NVI) was due to a portion of the field sampling being carried out during that year and, therefore, does not represent tree mortality. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

From there on one level for every cm was analyzed for charcoal, compared to, on average, one level per four cm for pollen. For more information consult Lindbladh et al (2003).

We studied the temporal association between pollen and charcoal records, by computing cross-correlation between two chronologies with the time lags stretching from -5 to 5 time units. The mean length of time unit (i.e. mean across all intervals between neighboring dated points) was 136 ± 130 years (mean \pm SD). The sedimentation rate on that site was well approximated by the linear function for the analyzed period (Fig. 3 in Lindbladh et al. (2003)).

3. Results

In total there were 256 trees included in the study, of which 176 were oaks. Overstory trees in the studied forests were established between the early 1700s and the early 1900s, with most of the sites exhibiting periods of uneven recruitment (Fig. 2). For oaks, the long-term mean “effective establishment rate” (a product of total recruitment minus mortality) varied between 8 and 40 trees/(ha*decade) (Table 2). Oak effective establishment rates associated with the disturbance events (all fires, except a thinning on site KAL, Table 1) showed moderate variability (8–40 trees/(ha*decade)). After fires at GRY, NVI, and ULV the rate reached beyond the 0.8 percentile of its long-term distribution, indicating an association between effective establishment and disturbance events. Similarly, a thinning event at KAL resulted in increased tree establishment. On recently burned sites, oak recruitment was significantly favored by fire, as indicated by the mixed effect ANOVA (Fig. 4B and SI Table 1).

Long-term growth release frequencies, aggregated over all tree species, were similar across sites, at around 30–50 releases per decade and hectare (Table 2, Fig. 3). Release frequencies did not reveal the disturbance-related dynamic, as the post-disturbance rates were often smaller than the respective long-term estimates (Table 2). However, the thinning which occurred at KAL in 1920, resulted in almost a doubling of the release rates there.

Fires and the thinning event on site KAL had a generally positive effect on oak growth rates (Fig. 4), with the growth increases being in

Table 2

Recruitment and release rates following disturbances in the studied forests. Effective establishment rates refer to oak trees only, whereas release rates refer to all species. In all cases, except for the 1920 thinning event in KAL, the events refer to the dated forest fires.

Site ID	Event date	Event rate, trees / (10 years*ha)	Event percentile	Mean rate, trees/(10 years*ha)
<i>Effective establishment rates</i>				
BON	1957	16.7	0.52	16.7
BON	1960	16.7	0.52	
GRY	1843	33.3	0.82	8.3
KAL	1843	8	0.28	16
KAL	1920	32	0.85	
NVI	1871	20	0.53	20
NVI	1912	40	0.86	
ULV	1888	41.7	0.96	16.7
<i>Release rates</i>				
BON	1957	14.8	0.16	50.5
BON	1960	7.25	0.05	
GRY	1843	0	0.01	26.3
KAL	1843	0	0.05	22.1
KAL	1920	45.5	0.88	
NVI	1871	33.3	0.51	35.5
NVI	1912	45.8	0.71	
ULV	1888	38.0	0.79	25.5

the range of 108–176%. Oak growth response did not significantly correlate with the establishment rates ($r = 0.16$, $p = 0.7$, $n = 8$). Dated fires occurred during wetter-than-average summers, which tended to exhibit negative pressure departures. These observations argue against climatic drivers of these fires (Fig. 5).

Oak pollen and charcoal data from the Hornsö-Allgunnen revealed a significant and positive association between these records, observed at zero and one time unit lags (Fig. 6). The lag corresponded approximately to 140 years. Oak pollen percentage and charcoal have exhibited a declining trend since approximately 500 AD.

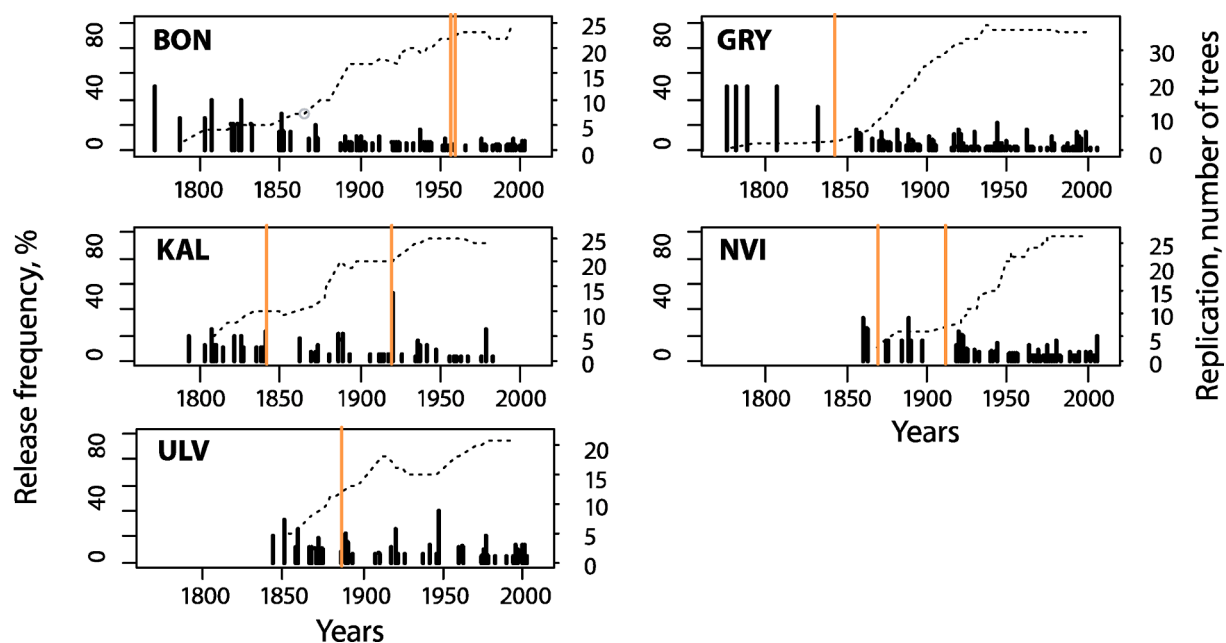


Fig. 3. The pattern of growth releases following disturbances in the studied forests. Vertical bars represent release frequency (left axis, black bars), as identified through the application of Nowacki and Abrams (1997) criterion, and replication (right axis, black dashed line). Orange lines mark the timing of the disturbance events. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

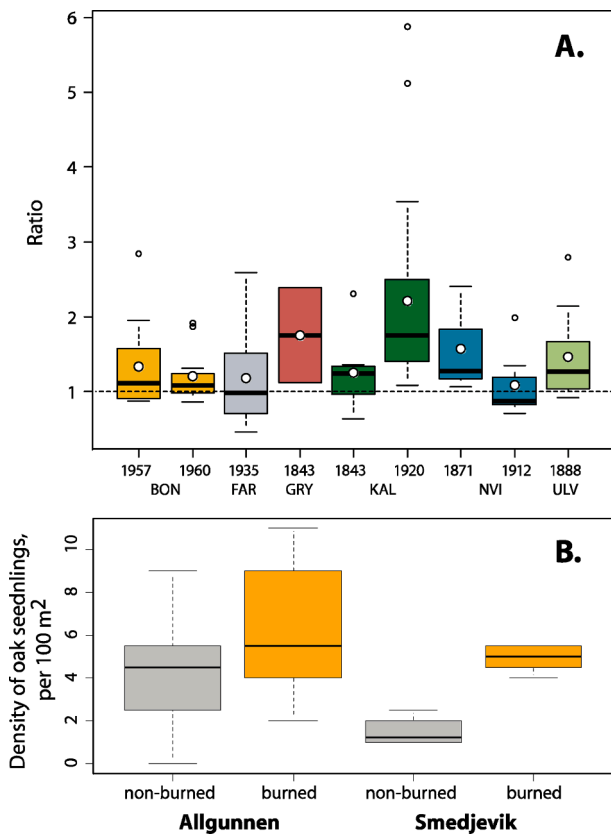


Fig. 4. Reaction of oak growth to fire and thinning (A) and post-fire change in seedling densities (B). A - The bars represent the ratio between oaks' basal area increment (BAI) ten years following the disturbance year and ten years prior to that year, with the line at $Y = 1$ indicating no impact of disturbance. The thick solid line inside the bar and the white dot inside the bars are the median and the mean of the distribution respectively. The dashed line represents the situation with no growth reaction. B - Differences in the number of oak seedlings (<1 cm in DBH, but above 10 cm in height) on 100 m² plots among burned and unburned sites. Effect of burn is significant with $p = 0.026$. Statistical details of the mixed-effect ANOVA are in the SI Table 1.

4. Discussion

4.1. Fires and oak recruitment

The overall pattern suggested that historical fires in oak-dominated forests were of low severity as they tended to not kill a considerable proportion of canopy oaks (Fig. 2), occasionally resulted in a wave of growth releases in surviving trees (Figs. 3 and 4), and provided a window of regeneration opportunities for that species (Fig. 2). The occurrence of these fires during generally wetter fire seasons (Fig. 5) points to the human-related nature of fire ignitions, consistent with a history of fire used for agricultural purposes in this part of Scandinavia (Niklasson et al. 2002). Although dendrochronological reconstruction of age structures does not provide a mechanistic explanation of the increase in the post-fire oak recruitment, it is likely that a combination of reduced competition and higher light levels in post-fire environments were the factors that favored the oak. Even at a small stem size, the oak cambium is surprisingly resistant to high temperatures, which apparently gives oak a competitive advantage in fire-prone environments (Pettersson et al., 2020). A combination of cambium resistance to sub-lethal temperatures and active re-sprouting (Larsen & Johnson 1998), along with the commonly well-developed root system (Sander 1971; Göransson et al. 2006), likely makes oak advanced regeneration a successful re-colonizer of burned sites under moderate and low browsing pressure (Pettersson et al. 2020). Our results suggest that sprouting could be a mechanism for

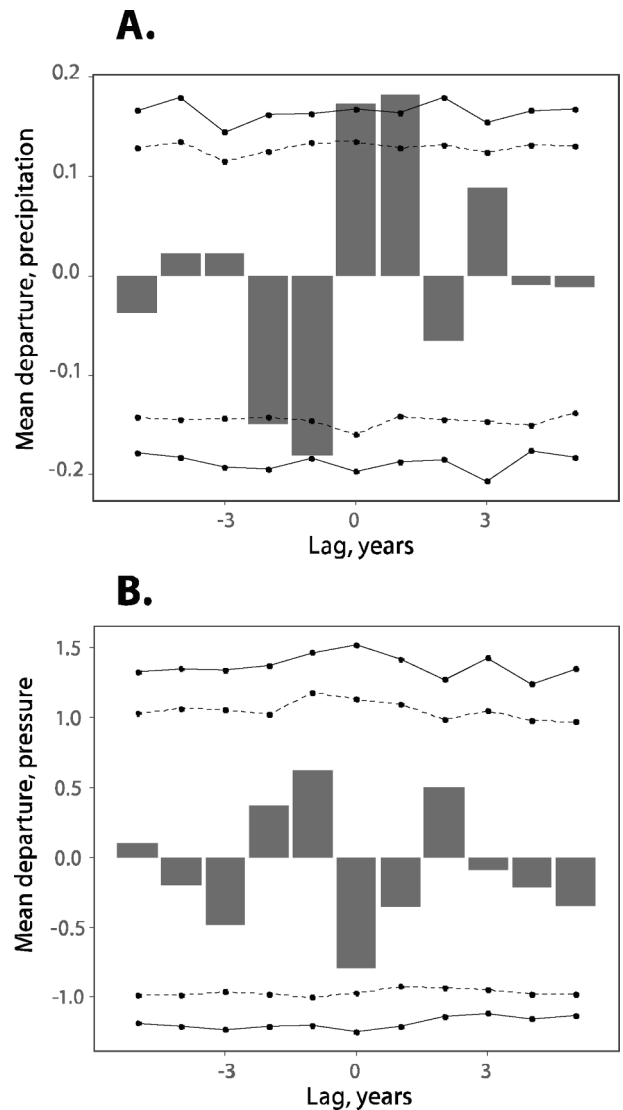


Fig. 5. Superimposed epoch analyses of precipitation (A) and sea level pressure (B) during fire and lagging years on the studied sites. The solid and dashed lines refer to 0.01 and 0.05 confidence envelopes, respectively.

oak to re-establish on burned sites. This is consistent with the observations that recently burned sites in southern Sweden often reveal vigorous sprouting of small and medium sized oaks, where above-ground parts were killed by the fire (MN, personal observations, Backman 2004). In addition, a strong and positive response of oak growth (in both height and diameter) to increased light levels (Larsen & Johnson 1998) shortens the period when the low height of oak saplings makes them susceptible to browsing, which is a matter of particular concern in southern Sweden, where oak saplings are preferentially browsed by ungulates (Götmark et al. 2005; Leonardsson et al., 2015). It is also possible that higher mineralization rates (Boerner et al. 1988; Gray & Dighton 2006) and higher soil temperatures observed in the soil following the fire further favor oak growth and survivorship.

Oak recruitment was favored by prescribed fires on sites Hornsö-Allgunnen and Smedjevik (Fig. 4B, SI Table 1), supporting the view on fire as a promoter of oak regeneration. However, we observed large differences among sites with respect to oak recruitment after the reconstructed fires, which varied from 8 to 41 trees/ (10 years*ha) (Table 2). Our data do not provide a conclusive explanation for this variability. We speculate that differences in the removal of understory vegetation, organic layer and/or density of browsers (including

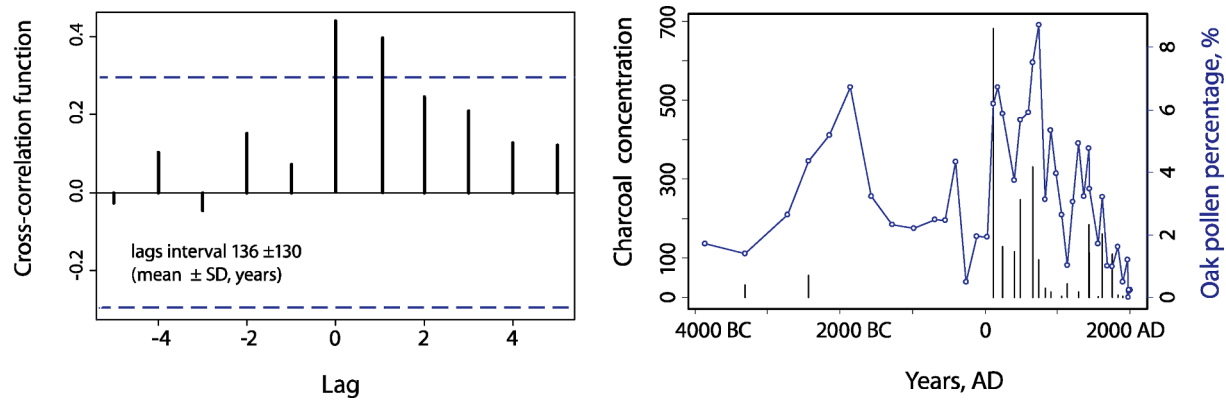


Fig. 6. Association between the proportion of oak pollen and charcoal amount in two locations in south-eastern Sweden: Hornsö-Allgunnen area (Lindbladh et al 2003), as revealed by analysis of sediments from small forest wetlands. Left graph - bars represent a cross-correlation of oak percentage and charcoal abundance at different time lags. The bars reaching the dashed line indicate significant correlation at $p < 0.05$. Charcoal abundance is the lead variable, i.e. the lagging correlations represent the relationship between oak pollen percentage at time t and charcoal abundance at time $t + \text{lag}$. Right graph - chronologies of both variables plotted against the time axis. The charcoal chronologies represent particles above 0.5 mm in size. The raw data were initially published in the respective paper.

livestock, historically), and a time since fire (10 years for Smedjevik site and only two years for Hornsö-Allgunnen) could play a role. It is, however, unlikely that the degree of main canopy disturbance was responsible for the observed variability, since none of the sites revealed a spike in growth release frequencies, following the fires (Fig. 3). Selective removal of oaks by harvesting at some sites, indicated by some old stumps at KAL, BON, ULV and NVI (authors pers. obs.), could be another explanation of the observed pattern, although the reconstructed forest age structure did not indicate any strong thinning events, except for the thinning event at KAL site in 1920.

Overall, in a large number of southern Swedish forests inventoried by our group over the last decades, oak stands with traces of fire are rare. For example, out of 25 sites studied in the Swedish Oak Project (Götmark 2019), we found fire scars in only five locations. It is unclear whether such a low percentage reflects the actual proportion of oak-dominated forests, which experienced past fire disturbance, or this estimate is heavily affected by the long history of intensive land use in these ecosystems, destroying the wood which once recorded fire events. Still, fires are rather rare events in Sweden generally, compared to countries with less fire suppression like Canada (Pinto et al 2020).

4.2. Response of canopy oaks to fires

Our dendrochronological reconstruction did not identify a single large oak tree that died at or immediately after the fire event, suggesting that a considerable proportion of oaks survived fires. Oak heartwood is relatively resistant to rot and few or no oak stumps in our study areas supports this conclusion. Although some mortality in small diameter classes likely took place, a large number of canopy oaks surviving fire and ultimately reaching forest canopies indicated its adaptation to this type of disturbance. The ability of canopy oak to withstand fires suggests that the tree can effectively withstand heat-induced necrosis of cambium and phloem, as well as xylem damage (Pettersson et al. 2020). Oaks are well-known for quick over-healing of partial cambial necrosis from fire (Smith & Sutherland 1999), confirmed by our observations of completely over-healed scars in many samples. Thick bark and a generally low amount of ladder fuels (i.e. fuels, which allow fire to move from fuels on the forest floor to tree crowns) are believed to be the primary factors supporting adaptation to fire in this species.

Oak growth rates improved following the fires (Fig. 4). It is a pattern that is likely caused by a post-disturbance decline in stand density, an improvement of soil nutrient conditions, and moderate tree mortality increasing light levels and access to soil resources to surviving oaks. Similar to our study, fires scarring white oak (*Q. alba*) in the central U.S. have been shown to result in positive post-fire growth trends

(Stambaugh et al. 2017). In another North American study, the severity of prescribed fires has been a strong predictor of oak basal area growth (Anning & McCarthy 2013). It is possible that the observed changes in diameter growth may underestimate the oak response to fire, also integrating changes in carbohydrate allocation patterns within the tree. A study of post-fire dynamics of boreal conifer stands in northern Quebec revealed an increased allocation to tree roots during the first 200 years following fire (Baret et al. 2015).

4.3. Speculation on the presence of fire-driven pine-oak forests in southern Scandinavia

Mixed oak forests of eastern North America provide a mechanistic analogy for the interpretation of fire-related dynamics of oak in southern Sweden at a variety of temporal and spatial scales. A broad similarity in both winter and summer climatologies of two regions (Suppl. Info. Fig. 1), their biogeographies (Ahti et al. 1968; Abrams, 1996), and an important role of fire in historical disturbance regimes, all indirectly support this comparison. An association of oaks with pines in fire-driven ecosystems, as observed in eastern North America, likely reflects a series of adaptations in both species (see the previous sub-section). It is worth noting that in most of the forests studied here, we observed Scots pine (*Pinus sylvestris* L.), which is well-adapted to low and moderate severity surface fires (Sannikov & Goldammer 1996).

We speculate that mixed pine-oak forests represent an ancient and largely lost type of southern Scandinavian forests adapted to periodic low-intensity fires. Earlier, a composite paleo- and dendrochronological reconstruction has suggested an association of these species in a semi-natural forest of the Swedish boreo-nemoral zone (Niklasson et al. 2002). Oak-pine forests (mostly of the mesic type) currently occupy only around 45 000 ha in southern Sweden (Drössler et al. 2012) and fire activity is almost non-existent in these ecosystems. However, observational data and dendrochronological reconstructions indicate a close association of both oak and pine with fire-disturbed habitats in southern Sweden (Niklasson et al. 2002; Lindbladh et al. 2003; Niklasson 2011). A combination of nutrient-poor habitats and such a disturbance regime might have prevented shade-tolerant species from outcompeting pine and oak in the past, a pattern which has been recently documented in many protected areas lacking natural disturbances.

The eastern section of southern Sweden (particularly the Swedish southeastern counties of Kalmar and Östergötland), residing primarily on nutrient poor granite bedrock, could represent the regions, where such ecosystems were present in the past. This region is one of the driest in Sweden (summer precipitation ~ 180 mm), has the highest number of lightning ignitions, $\sim 0.23/10\,000$ ha/yr (Granström 1993), and features

one of the earliest onsets of the fire season (April– May). These environmental settings would promote frequent fires (particularly early season fires), whose size and severity would be likely limited by the moisture in the deeper soil layers, due to winter precipitation/snow accumulation, along with the abundance of “low quality” deciduous fuels in the respective landscapes. Swedish oak-pine forests would be functionally similar to a variety of pine-oak forests in the eastern U.S., where fire has been a historically important factor maintaining these ecosystems (Abrams et al. 1995; Shumway et al. 2001). Similar to its North-American counterparts (Cogbill et al. 2002), fire-controlled oak-pine forests in southern Scandinavia would be an extra-zonal vegetation, i.e. the vegetation controlled, to a considerable degree, by topography and local soil conditions. These speculations are partly supported by palynological data. A study of 37 regional pollen sites (i.e. sediment records from lakes and larger bogs) in southern Sweden has identified a rich mixed pine forest with a significant oak component. It is a forest type which is rare in modern Southern Sweden (Björse & Bradshaw 1998). According to that study, this forest type was particularly common in southeast Sweden 1500–2000 years ago. In the modern pine-dominated forests oak saplings are common due to favorable light conditions (Götmark et al. 2005), supporting the notion of oak-pine association.

We found a significant and positive association between percentage of oak pollen and charcoal abundance in an area of southeastern Sweden (Fig. 6). The pattern indicated that fire favored oak recruitment at that location. However, a study across a network of sites in southern Sweden found a weak negative correlation between oak pollen and charcoal particles in the sediments, suggesting that oak might be disfavored by fires (Bradshaw et al. 2010). Those data came from small forest hollows (*sensu* Jacobson & Bradshaw 1981), which tend to reflect the more mesic parts of the landscape, as small hollows with peat are mostly found in wet areas, which are much less fire-prone. In such habitats, both pine and oak are outcompeted by more shade-tolerant and fire sensitive species, like beech and spruce. It is also likely that past fires were infrequent but of high severity, which could disfavor oak. Another factor, which might obscure the evidence pointing to the presence of pine forests with oak in the overstory, might be the limited geographical extent of such ecosystems, making their pollen “signal” blended to the signal of a more regional vegetation cover.

Our suggestion of historically more open mixed oak forests in the hemi-boreal zone of southern Scandinavia conceptually connects to the hypothesis postulating the driving role of large herbivores in supporting transient open landscapes of European primeval forests (Vera 2000) (see a critique of this view in Mitchell 2005). Similar to Vera’s hypothesis, we propose the presence of an external factor (in our case - low severity fires) controlling the understory composition and recruitment opportunities for canopy dominants. Modern studies of browsing patterns in southern Sweden and our dendrochronological data are consistent with the vision that both disturbance factors might co-interact in shaping the forest recruitment patterns in some landscapes of this region.

Does the generally positive relationship between fire and oak (*Q. robur* and *Q. petraea*), documented in this study, exist also in other parts of Europe? The answer probably depends on particular combinations of fire regimes and site environments. We speculate that fire was likely an important driver of oak recruitment in more xeric forests. Such communities are less productive than more mesic forest types and, at the same time, are more prone to recurring fires. Lower productivity and frequent fires likely acted in concert to keep both fuel loads and fire severity low. Such conditions would favor oak regeneration through resprouting and acorns. With an increase in forest productivity and a resulting increase in the fuel loads, particularly – ladder fuels (i.e. fuels, which allow fires to jump from the forest floor to the canopies), the fire would decrease in frequency but likely increase in severity. This would make it increasingly difficult for the oak to maintain itself through the above-mentioned mechanisms. However, very little data exists from truly fertile soils. The Spinu et al study (2020), was done on relatively

rich soils- and shows a strong relationship between fire and oak but eventually shade tolerant species took over (*Picea*, *Acer*, *Carpinus*), with more shady conditions that precluded fires.

4.4. Management implications

The knowledge of fire impacts on oak regeneration in European forests is limited, which hinders the development of management programs mimicking natural disturbance regimes. Recurring surface fires have been documented to promote oak regeneration in a wide range of North American ecosystems (Crow et al. 1994; Rieske 2002; Abrams 2016), and the role of non-fire disturbance for oak recruitment has been documented for southern European forests (Rozas 2003).

Our data exemplify and explain compositional trends in many southern Swedish deciduous and mixed forests, where the dominance of shade-tolerant species has been increasing due to the decline in the frequency and severity of canopy disturbances (Niklasson et al. 2002; Lindbladh et al. 2003). Similar successional patterns are observed in the Białowieża Forest (Niklasson et al., 2010a, 2010b, Hilszczanski & Jaworski 2018; Spinu et al. 2020). We propose that the use of fire should be considered as a management tool to promote oak regeneration and to preserve forests with co-dominating oak and pine in southern Scandinavia. Our analyses of climate vs. fire association pointed to the potentially important role of past forest management in controlling reconstructed fire events.

Understanding the effects of different fire severities, i.e. the degree of fire-caused transformation of initial habitat, appears to be of critical importance. Studies in eastern North America demonstrated non-linear effects of fire severity on the success of oak recruitment (Black et al. 2018). Similarly, complex patterns might also be in operation in Scandinavia, where our field observations of experimentally burned stands indicate that the survival of oak stem meristems in the organic layer defines the chances for the oak to re-sprout after fires. It is logical to expect that this survival rate will be directly controlled by the fire severity, i.e. by consumption of the organic layer, which is, in turn, jointly affected by fuel loads and the severity of the drought conditions.

In the context of future climate variability, the prescribed burning of oak forests may be a valuable tool to reduce the risks of uncontrolled and stand-replacing fires under a climate with more frequent strong drought episodes. Specifically, lowering fuel loads would lower the risk of severe fires damaging underground meristems and, as a result, their resprouting potential. Along with supporting oak regeneration, prescribed fires may, therefore, also function as an element of climate change mitigation policies (Clark et al. 2014).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118853>.

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