Changing land use and increasing abundance of deer cause natural regeneration failure of oaks: Six decades of landscape-scale evidence

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ABSTRACT

Many tree species worldwide are suffering from slow or failed natural regeneration with dramatic consequences for biodiversity and ecosystem services. However, it is difficult to disentangle the complex effects of factors influencing regeneration processes on long-lived tree species at large scales. In this study, we use long-term data from the Swedish National Forest Inventory (1953–2015) combined with deer hunting data (1960–2015) to reveal experimentally-intractable processes impeding oak (*Quercus* spp.) regeneration in southern Sweden. Oak-dominated ecosystems are widespread in northern temperate regions, where oaks are foundation species with disproportionate importance for biodiversity and ecosystem functions. Our study reveals that during the last six decades, oak tree numbers and standing volume have continuously increased, while natural regeneration of oak declined steeply after the early 1980s. We connect this decline to denser and darker forests, combined with increased abundance of deer. Land use changes during the six decades, such as abandonment of traditional practices and large-scale introduction of forest management oriented towards high volume production, led to continuously denser forests and thereby reduced the oak regeneration niche. In addition, the impact of changed game management was evident. This was particularly clear from a natural experiment on Gotland, a large island free of deer until roe deer were introduced in the late 20th century, at which point oak regeneration began a steep decline. At the stand level, natural oak regeneration could be expected to mainly occur in pulses after disturbance events, followed by a period of low regeneration success as the cohort ages. However, at a landscape scale one would expect a mix of successional stages that would even out such demographic patterns. A prolonged period of low regeneration at a landscape scale will eventually lead to a large gap in the oak size distribution as was observed in this study. This could eventually hurt the many species dependent on old and large oak trees. Active management to restore the oak regeneration niche, i.e. forest habitats with more light and less browsing pressure, therefore seems essential. The latter includes developing strategies that manage both deer populations and their available food across landscapes. Our study is the first to link oak regeneration failure to long-term changes in land use and increased deer populations at a landscape scale in this region. Furthermore, our study show how historical data can clarify confounded processes impacting long-lived forest species.

1. Introduction

Many of the world's tree species are suffering from slow or failed natural regeneration, with seeds failing to germinate, and seedlings not surviving or growing in the understory (Abrams, 2003; Schulze et al., 2014; Bretfeld et al., 2016). Regeneration failure may have dramatic consequences for the biodiversity of trees and animals that rely on them, carbon sequestration, and other services that forests provide for

humanity (Rodewald and Abrams, 2002; Ellison et al., 2005). A range of reasons for such failure have been postulated, including changed land use, altered disturbance regimes, changed climate, pathogens, overabundance of herbivores and loss of seed dispersing animals (Terborgh et al., 2008; Lindbladh and Foster, 2010; Tomback and Achuff, 2010; Brunet et al., 2014; Schulze et al., 2014; Bradshaw and Waller, 2016). While all of these causes have been demonstrated to apply in narrow circumstances, their importance, impact and

interactions at the landscape scale are not well understood. The time and space constraints typical of ecological experiments and grant cycles make these long-term and large-scale processes difficult to study. In this paper, we use unique datasets to investigate these processes at a scale never before possible in an ecologically- and culturally-important tree genus, oak (*Quercus* spp.).

In much of the temperate northern hemisphere, traditional land-use practices like forest grazing, selective cutting, and low-intensity fires historically kept forest canopies relatively open (Vera, 2000; Abrams, 2003; Kirby and Watkins, 2015). With introduction of modern forest management, abandonment of these practices has led to increasingly dense forests (Nilsson, 1997; Abrams, 2003). This process may be further reinforced by climate change, which in temperate climates accelerate net production and indirectly increases standing wood volume (Boisvenue and Running, 2006; Gold et al., 2006). As a consequence, regeneration niches for light-demanding and disturbance-dependent plant species may be reduced.

Additionally, herbivore populations have grown rapidly in most north-temperate ecosystems during the last decades (Lavsund et al., 2003; Rooney and Waller, 2003; Milner et al., 2006; Takatsuki, 2009). These population increases can be due to changed game management, but are also often closely connected to changes in land use affecting food availability and milder winters (Lavsund et al., 2003; Apollonio et al., 2017). Overabundance of herbivores creates big management challenges, as preferential foraging can profoundly alter the structure and composition of forest communities (Beguin et al., 2016; Bradshaw and Waller, 2016; Apollonio et al., 2017). These processes may result in shifts in forest species composition and stand structure, changes that are widely reported from temperate ecosystems (Abrams, 2003; Takahashi et al., 2003; Rogers et al., 2008; Rohner et al., 2012).

Perhaps the most dramatic and widespread regeneration failure has been seen in oaks, whose status has been a cause for concern for over a century (e.g. Watt, 1919; Shaw, 1968; Crow, 1988; Annighöfer et al., 2015; Bobiec et al., 2018). Oaks are suffering from poor regeneration virtually everywhere they grow (Kelly, 2002; Li and Ma, 2003; Pulido and Díaz, 2005; Götmark, 2007; Fei et al., 2011), with cascading effects on associated biodiversity (Rodewald and Abrams, 2002; Ranius et al., 2008). Multiple factors have been shown to contribute to poor oak regeneration in different circumstances, including insufficient understorey light, increased competition during succession (Lorimer et al., 1994; Kelly, 2002; Li and Ma, 2003; Götmark, 2007), high browsing pressure (Rooney and Waller, 2003; Leonardsson et al., 2015), and pathogens (Rizzo and Garbelotto, 2003). However, the relative importance of these factors is difficult to study at a large scale.

Oaks are critical for biodiversity and ecosystem services in the temperate forests that ring the northern hemisphere (Johnson et al., 2009). They provide wood production, recreation, watershed protection, and possibilities for adaptation of forest management to climate change (Löf et al., 2016). Further, oaks are foundation species in temperate forests (Lindbladh and Foster, 2010) with disproportionate importance for biodiversity and ecosystem functions (Dayton, 1972; Ellison et al., 2005). Habitats created by oak endure for centuries due to the long lifespan of individual trees and the frequent presence of dead wood. Thus, oak is one of the most important temperate tree genera for endangered invertebrates (Tallamy and Shropshire, 2009; Milberg et al., 2016) and provides crucial habitat for lichens, fungi (Bernicchia et al., 2008; Ranius et al., 2008), and birds (Rodewald and Abrams, 2002; Felton et al., 2016).

To better understand which factors limit tree regeneration and abundance, one needs to consider interactions between land-use history, disturbance, and herbivory. Unfortunately, for large, long-lived species, landscape-scale changes are almost impossible to study experimentally. Repurposed historical data is increasingly recognized as a previously overlooked opportunity to answer experimentally-intractable questions (Primack and Miller-Rushing, 2012). However, such datasets are challenging to work with when they were originally collected for other purposes and are often complicated by changing or unclear protocols. Meeting these challenges requires creative analytical approaches. In this study, we investigate land use and deer population impacts on oak regeneration using Swedish National Forest Inventory (NFI) data from 1953 to 2015 and hunting data from 1960 to 2015. These exceptionally long and spatially broad datasets provide a unique opportunity to study changes in oak regeneration dynamics at landscape scales, and include a natural experiment, the introduction of deer to a large, previously deer-free, island. In this study, we seek to:

(1) Quantify changes in different demographic stages of the oak population during the last 60 years in southern Sweden.
(2) Evaluate the role of altered land use and deer browsing pressure in these changes.

Our results show that oaks have a robust and growing population of adult trees, in sharp contrast to their dramatic decline in forest understories in southern Sweden. Further, we provide evidence linking these outcomes to changing land-use practices and growing deer populations.

2. Material and methods

2.1. Study area

Our study area comprises all of southern Sweden, about 130,000 km^2 (Fig. 1). The region is lowland, 0–350 m.a.s.l., with a mosaic landscape of forests, farmland, and lakes. Mean annual precipitation decreases from about 1000 mm in the west to 600 mm in the east, and the mean temperature ranges from -3°C in January to 16 °C in July (reference time span 1961–1990). Forests cover about 85,000 km^2, of which 78,000 km^2 are considered productive, producing at least 1 m^3 wood ha^{-1} year^{-1} (SLU, 2017). Approximately 1% of the productive forestland consists of oak-dominated forest. From south to north, the study area gradually transitions from temperate to hemiboreal forest (Sjörs, 1965). Two ecologically and morphologically similar oak species, pedunculate oak (*Q. robur* L.) and sessile oak (*Q. petraea* (Matt.) Liebl.), are at the northern limit of their native distribution in this region (Fig. 1). The Swedish NFI does not distinguish between pedunculate and sessile oak, and for the purpose of this study they were combined. Due to active forest management favouring conifers, the two dominant tree species are Norway spruce (*Picea abies* (L.) Karst) and Scots pine (*Pinus sylvestris* L.), while birches (*Betula pendula* Roth and *B. pubescens* Ehrh.) are the most common broadleaved species, followed by Eurasian aspen (*Populus tremula* L.) and oaks (SLU, 2017).

2.2. The Swedish National Forest Inventory (NFI)

Since 1953, the Swedish NFI has conducted annual national forest inventories using a randomized cluster design (Fridman et al., 2014). Sample plots are aggregated in rectangular clusters, with plots located along the border of the rectangle. The edges of the clusters are 300–1500 m long, and cluster density increases towards the south. In 1983, the present system with a combination of permanent and temporary clusters was introduced (Ranneby et al., 1987). Permanent clusters are normally inventoried at five-year intervals, and new temporary clusters are installed with the same frequency. Reliable estimations of basal area and species' abundances generally require data from a five-year period. Plot data involve a multitude of variables, including detailed tree and sapling measurements, site conditions, and management history. Plot radius varies from 6.64 to 10 m depending on sample year, variable, and plot type (Fridman et al., 2014). In order to compensate for uneven sampling intensity over years and regions within the study area, plots were weighted by the forest area they represent when appropriate (Fridman and Walheim, 2000; Toet et al., 2007).
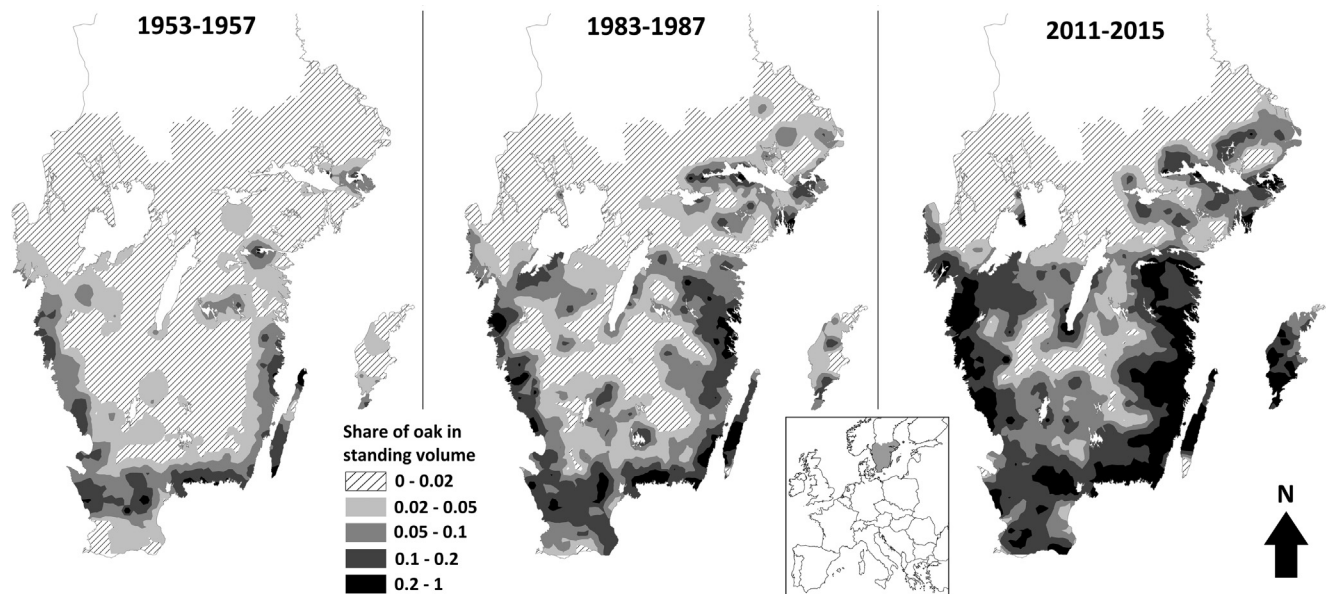
Fig. 1. The share of oak (%) in total forest standing volume for 1953–57, 1983–87, and 2011–15 in the study area of southern Sweden. The largest island east of the mainland is Gotland. Inset map shows location of study area in Europe.

Our analyses were based on NFI data from all plots located on productive forestland. The NFI defines productive forestland as land that can produce at least $1\,m^3$ wood $ha^{-1}\,year^{-1}$ and that is not significantly used for other purposes. This broad definition does not exclude any tree species, it includes open farmland and meadows that are no longer actively used, as well as grazed land where current tree growth is considered giving a higher net return. Thereby about 60% of the land area in southern Sweden is included. Low-productivity forests were excluded from our analysis, as were protected areas which cover less than 2% of productive forestland in the study area. Oak populations outside the forest landscape are also beyond the scope of this study. In total 308,700 plot visits were analysed, with the total annual number of plots varying from 2600 to 7100.

2.3. Deer populations

Four deer species are present in the study area: moose (*Alces alces* L.), roe deer (*Capreolus capreolus* L.), red deer (*Cervus elaphus* L.) and fallow deer (*Dama dama* L.). Moose and roe deer are considered browsers, while red deer is a mixed feeder and fallow deer tends even more towards grazing (Hofmann, 1989). Annual hunting data for 1960–2015 was used as a proxy for the population density of these deer species. This data was available at a county level (15 counties with area ranging between 3,000 and 24,000 km^2) and came from the Swedish Association for Hunting and Wildlife Management. As it is mainly based on voluntary reports of animals shot, it is not complete. Nonetheless, hunting data is a proven proxy for changes in deer population number over time (e.g. Ueno et al., 2014). To roughly quantify the expected combined browsing pressure of all deer species, we calculated a 'deer index' (Angelstam et al., 2017a). This was computed as the metabolically-corrected weight of animals shot:

$$deer\ \ index_c = \frac{\sum_i (n_{ic})(m_i^{.75})}{A_c}$$

where n_{ic} is the number of deer of species i shot in county c, m_i is the average body mass of species i, and A_c is the area of the county. We used live body mass values of adult individuals with equal proportions of males and females of 346 kg for moose, 21 kg for roe deer, 154 kg for red deer, and 52 kg for fallow deer (Silva and Downing, 1995).

2.4. Statistical analysis

All statistical analyses were performed in R version 3.5.0 (R Core Team, 2017). Area and mean basal area for broadleaf-dominated forest, conifer-dominated forest, mixed forest, and the total productive forestland were calculated as five-year averages for the study period. Forest types were based on dominant tree species defined by basal area proportion as follows: conifer-dominated forest is at least 65% conifer by basal area, broadleaf-dominated forest is at least 65% broadleaf trees by basal area, and mixed forest comprises all remaining forest. Furthermore, we calculated the productive forest area affected by pre-commercial thinning, i.e. if a predominant proportion of trees < 10 cm dbh had been removed in the previous three or five years, using five-year averages for 1953–1957 and 2011–2015.

For 1953–2015, total oak volume ($m^3\,ha^{-1}$) was calculated as annual values and 5-year moving averages. Oak stems were divided into three size classes: "saplings" defined as $\geq 1.3\,m$ tall and $\leq 9.9\,cm$ diameter breast height (dbh), i.e. diameter at 1.3 m; "small trees" defined as 10–34.9 cm dbh; and "large trees" defined as $\geq 35\,cm$ dbh. We used oak saplings as an indicator of natural oak regeneration. From 1953 to 2015, oak density (stems ha^{-1}) for each size class were calculated as annual values and 5-year moving averages. Further, oak sapling density in conifer- and broadleaf-dominated forest was calculated in the same manner. We compared changes in annual oak densities over time using simple linear regression and continuous piecewise regression with two segments (Toms and Lesperance, 2003). For each size class, Akaike's Information Criterion (AIC) was used to identify whether a piecewise model was justified and if so, the optimal breakpoint year.

To explain changes in oak sapling density, we used a zero-inflated Generalized Linear Mixed Model (GLMM), with site productivity, basal area, pre-commercial thinning (yes = 1), log(deer index + 1), and year as fixed factors, and plot cluster as a random grouping factor. Basal area was used as a proxy for light availability, as there is an overall negative relationship between basal area and understorey brightness (e.g. Jenkins and Chambers, 1989; Comeau and Heineman, 2003). While the NFI data has a high spatial resolution, the deer data is only available at the county level. We connected these levels by using the same deer index for all plots in each county and year. The logarithm of deer index was used as it is the simplest way to include an increasing but concave-down effect, as deer density generally does not have a strictly linear effect on browsing damage (e.g. Angelstam et al., 2017a). Year was

included in the model to account for other, unobserved variables that change over time, e.g. climate. Because the oak sapling density response variable has many zeroes and a long tail of high values, we used a zero-inflated GLMM with binomial error structure implemented with the glmmTMB() function in the "glmmTMB" package (Brooks et al., 2017). This model has two main components, a conditional model and a zero-inflation model that describes the probability of observing an extra zero that is not generated in the conditional model (Brooks et al., 2017). The GLMM included data from 1960 to 2015 (between 2600 and 7100 plots year^{-1}). Due to the large size of our dataset, it was not practical to do model selection using all possible combinations of independent variables and error structures. Instead, we began with the full model, and removed variables one at a time, and selected the best model according to AIC, which included all variables except for pre-commercial thinning. That model in turn was treated with the same procedure, removing variables one at a time. All of these had a higher AIC than their parent model (Appendix, Table S1), so we selected the model with all variables except pre-commercial thinning and examined the residuals using the function testUniformity() from the DHARMAa package (Brooks et al., 2019; Hartig, 2018).

Data from the island of Gotland (Fig. 1) was used to further investigate deer browsing effects on oak saplings. Gotland lacked large wild browsers until roe deer were deliberately introduced for hunting purposes at some point during the 1980s or 1990s (Kenczek, 2012). The exact date remains unclear as it was not sanctioned by the Swedish government. We calculated the number of roe deer shot km^{-2} using hunting data for 1960–2015. Oak sapling density (stems ha^{-1}) was calculated for 1953–2015 as annual values and 7-year moving averages, based on 11,834 plot visits, with the total annual number of plots varying from 38 to 401. The change in annual oak sapling density was investigated using a continuous piecewise regression, as described above. Also, multiple linear regression was calculated using data from 1960 to 2015 to predict annual oak sapling density based on year and log(deer index + 1). As mentioned previously, we used the logarithm of deer index as it is the simplest way to include an increasing but concave-down effect. We selected our final model using AIC, starting with the full model and comparing with all possible simpler models. No further variables from the NFI were included in the model, as it was based on annual averages instead of plot data.

3. Results

The total forest area in southern Sweden increased slightly during the study period, while the relative area of each forest type remained rather constant (Fig. 2a). In contrast, mean basal area increased substantially in conifer- and broadleaf-dominated forests (Fig. 2b). Pre-commercial thinning increased from about 1000 km^2 treated area in 1953–57 to 6700 km^2 in 2011–15, which corresponds to an increase from 2% to 9% of the total forested area treated.

Since 1960, deer populations in southern Sweden have increased dramatically. The number of animals shot by hunters has increased for all deer species (Fig. 3), although some species have declined since peaks in the 1980s or 90s. This increase was most obvious for roe deer, with 36,000 animals shot in 1960 and 92,000 in 2015, and a large peak of 350,000 animals in 1993. Moose follow a similar pattern with 14,000 to 29,000 animals shot, and with especially high numbers during the 1980s, peaking at 75,000 animals in 1982. Very few fallow deer and red deer were shot in 1960, but by 2015 the numbers had increased to 39,000 and 8,000, respectively. The annual total of deer shot increased from 52,000 in 1960 to 167,000 in 2015. In a similar way, the deer index increased from 11 to 31 kg$^{0.75}$ km^{-2} between 1960 and 2015, with peaks above 50 kg$^{0.75}$ km^{-2} in the 1980s (Fig. 3).

The oak proportion of total wood volume increased dramatically between 1953 and 2015 (Fig. 1). In the same period, total standing oak volume showed a steady significant increase, nearly tripling from 1.7 to 4.7 m^3 ha^{-1} (Fig. 4a; $F_{(1,61)} = 334$, $p < 0.001$, $R^2 = 0.85$). However,
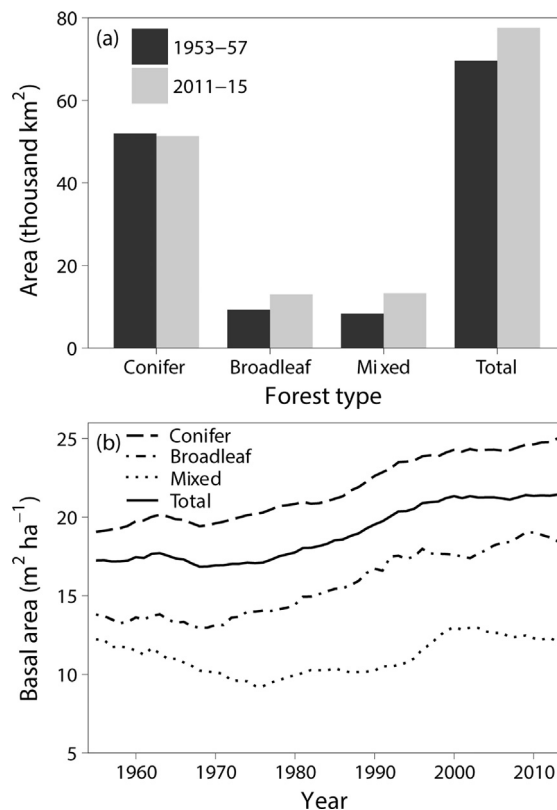

Fig. 2. Forest cover and density in southern Sweden where (a) is area in 1953–57 and 2011–15 and (b) is basal area as five-year moving average for conifer-dominated ($\geq$65% conifers of basal area), broadleaf-dominated ($\geq$65% broadleaf of basal area), mixed forest (remaining forests), and total forest land.
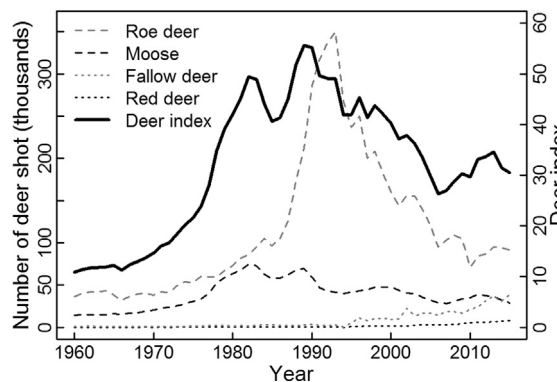

Fig. 3. Number of roe deer, moose, fallow deer, and red deer shot in southern Sweden (see Fig. 1) from 1960 to 2015. Deer index: the estimated total metabolic weight of deer shot per km^2 each year.

not all size classes followed this pattern. Large oak tree density increased continuously throughout the study period (Fig. 4b). The continuous piecewise regression analysis identified 1989 as the optimal breakpoint year, with the growth rate of large oak tree density doubling after this date ($F_{(2,60)} = 135.2$, $p < 0.001$, $R^2 = 0.81$). The density of small oak trees increased distinctly before 1979, at 0.07 stems ha^{-1} year^{-1} but levelled off to a gentle increase of only 0.01 stems ha^{-1} year^{-1} after that year (Fig. 4c; $F_{(2,60)} = 19.27$, $p < 0.001$, $R^2 = 0.37$). Oak saplings dramatically reversed from increasing to decreasing density (Fig. 4d), with 1982 as the optimal breakpoint year. Oak sapling density increased by 1.1 stems ha^{-1} year^{-1} before 1982 and decreased by 1.6 stems ha^{-1} year^{-1} after ($F_{(2,60)} = 67.68$, $p < 0.001$, $R^2 = 0.68$). In all cases reported here, piecewise regression had a lower
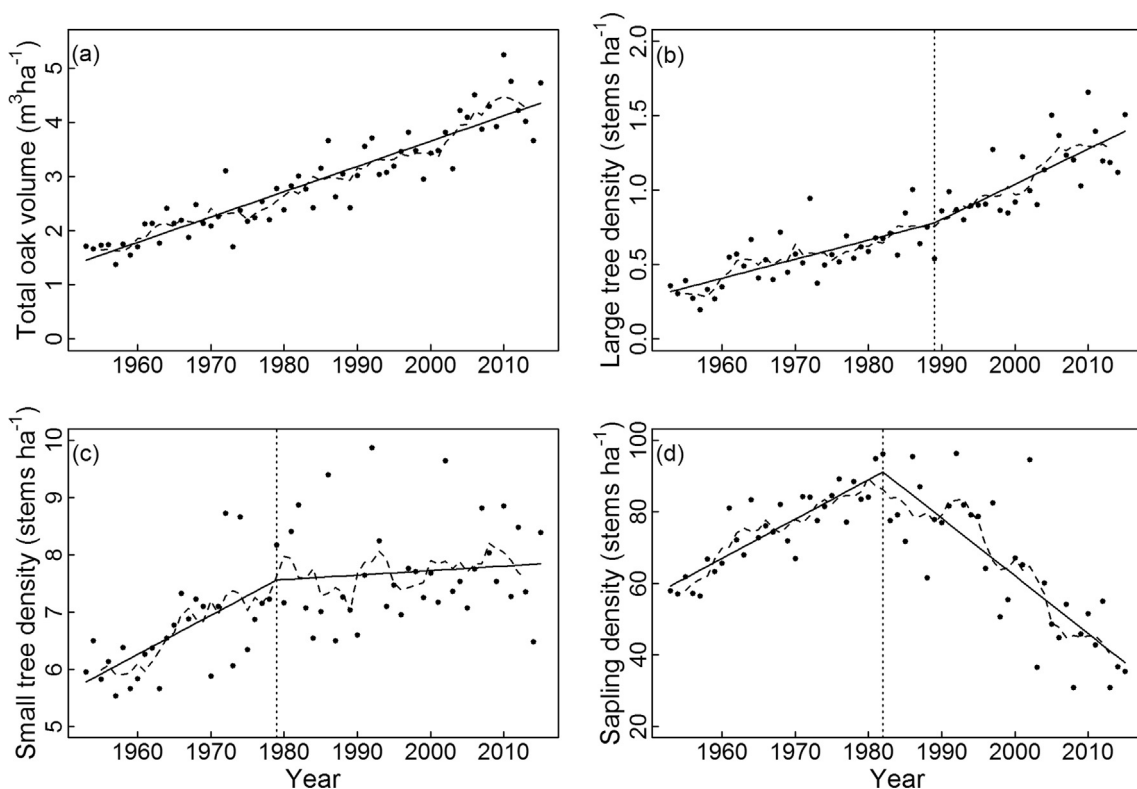
Fig. 4. Oak population demographics in southern Sweden from 1953 to 2015. (a) Total standing oak volume (m^3 ha^{-1}) and (b–d) density of oak stems for three size classes: (b) large oak trees, ≥ 35 cm dbh, (c) small oak trees, 10–34.9 cm dbh, and (d) oak saplings, ≥ 1.3 m tall and ≤ 9.9 cm dbh. Points = annual values, dashed line = five-year moving average, black line = linear regression which includes an AIC-supported breakpoint in (b), (c), and (d); in these cases, the vertical dotted lines mark the breakpoint years. Note the different scales on the y-axes.

AIC value than equivalent regressions with no breakpoint.

Throughout the study period, oak sapling density was consistently higher in broadleaf-dominated forests than in conifer-dominated forests, and distinct trends were evident in the two forest types (Fig. 5). In broadleaf forest, oak sapling density has been decreasing since 1953, although the pace accelerated after 1994 ($F_{(2,60)} = 59.66$, $p < 0.001$, $R^2 = 0.65$), with oak saplings decreasing by 2.0 stems ha^{-1} $year^{-1}$ before 1994 and by 4.4 stems ha^{-1} $year^{-1}$ afterwards. In contrast, in conifer-dominated forest, 1986 was the optimal breakpoint year ($F_{(2,60)} = 93.22$, $p < 0.001$, $R^2 = 0.75$), with oak saplings increasing by 1.2 stems ha^{-1} $year^{-1}$ before 1986 and decreasing by 1.4 stems ha^{-1}
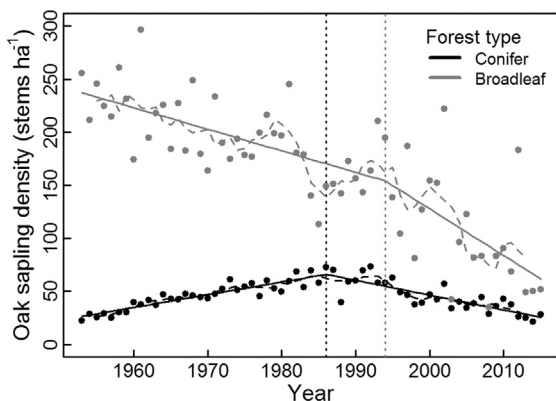

Fig. 5. Density of oak saplings (≥ 1.3 m tall and ≤ 9.9 cm dbh, stems ha^{-1}) in conifer- and broadleaf-dominated forest types in southern Sweden from 1953 to 2015. Points = annual values, dashed line = five-year moving average, solid line = continuous piecewise regression (for statistical fits see main text). The vertical dotted lines give the breakpoint for the continuous piecewise regressions.

$year^{-1}$ after.

The GLMM of oak sapling density in southern Sweden that included basal area, deer index, site productivity, and year proved the likeliest model. Our analysis showed that the conditional mean and zero-inflation both varied with basal area, deer index, site productivity, and year (Table 1). Oak sapling density (conditional model) decreased with greater basal area, while it increased with greater site productivity and over time. Further, the probability of not finding oak saplings (the zero-inflation model) increased with greater basal area, higher deer index, over time, and with lower site productivity (Table 1).

On the island of Gotland (Fig. 1), oak sapling density showed a sudden reversal, with 2001 identified as the optimal breakpoint year ($F_{(2,59)} = 23.29$, $p < 0.001$, $R^2 = 0.42$; Fig. 6). Oak sapling density increased by 2.9 stems ha^{-1} $year^{-1}$ before 2001 and decreased by 9.4 stems ha^{-1} $year^{-1}$ afterwards. The breakpoint coincides with a growing number of roe deer shot on the island (Fig. 6). The multiple

Table 1
Summary of zero-inflated Generalized Linear Mixed Model (GLMM) with negative binomial distribution showing the effect of the predictors on oak sapling density in southern Sweden.

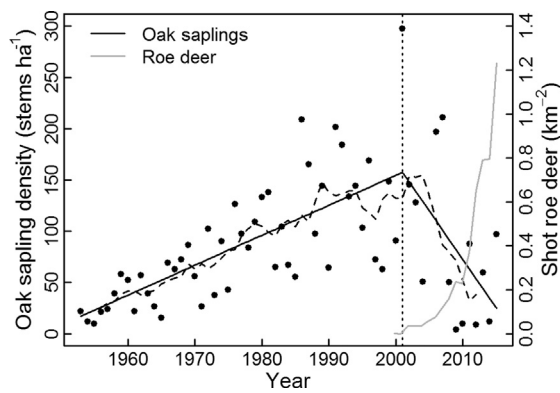| Predictor variable	Estimate	SE	z-value	P
Conditional model				
Basal area	−0.0027	0.0004	−6.30	< 0.001
Deer index	0.0396	0.0204	1.94	0.052
Site productivity	0.0087	0.0026	3.39	< 0.001
Year	0.0200	0.0008	26.20	< 0.001
Zero-inflation model				
Basal area	0.0027	0.0005	5.26	< 0.001
Deer index	0.3884	0.0337	11.53	< 0.001
Site productivity	−0.0824	0.0033	−25.18	< 0.001
Year	0.0454	0.0011	40.87	< 0.001

Fig. 6. Density of oak saplings (> 1.3 m height and < 9.9 cm dbh) and the number of roe deer shot per km[2] on the island of Gotland. Points = annual oak sapling density, dashed line = 7-year moving average for oak sapling density, black line = continuous piecewise linear regression (for statistical fit see main text), grey line = shot roe deer. The vertical dotted line gives the breakpoint for the continuous piecewise regression at the year 2001.

Table 2
Summary of multiple linear regression results used to examine the effects of roe deer on annual averages of oak sapling density on the island of Gotland.

Predictor variable	Estimate	SE	t-value	P
Deer index	-22620	8802	-2.570	0.013
Year	3.17	0.56	5.654	< 0.001
Interaction	11.20	4.37	2.562	0.014

linear regression including year, deer index and their interaction proved the likeliest model, and confirmed a significant negative relationship between roe deer density and oak saplings (Table 2). Mean basal area on the island increased from 14.0 in 1953–57 to 18.4 m^2 ha^{-1} in 2011–15.

4. Discussion

This study has used spatially-extensive long-term data sources to reveal complex impacts of changing land and game management practices on a culturally- and ecologically-important tree genus. While the volume and number of oak trees in southern Sweden has continued to increase, an initially-growing oak sapling population went into a steep and continuous decline after the early 1980s. Our analysis supports the view that these demographic changes are due in part to darker forest understories and deer overabundance. As we discuss below, these changes have not occurred in a vacuum, but are the result of ongoing changes in land and game management.

The significance of forest density and deer abundance in our model for southern Sweden suggests that these factors are important drivers of the observed decline in oak saplings even while adult oaks become ever more abundant. Further evidence on the role of deer is provided by the deer population peak in the 1980s coinciding with the breakpoints in the piecewise regression models. While this phenomenon cannot be fully quantitatively analysed due to multiple time lags in the response of saplings to different pressures, the coincidence of the roe deer population explosion and oak sapling decline on the island of Gotland is particularly striking.

Rapid land use change had far-reaching effects on Swedish forests during the 20th century (Nilsson, 1997). Traditional land-use practices like forest grazing by livestock, slash-and-burn cultivation, and selective wood cuttings that previously kept forest canopies relatively open were abandoned during the first half of the century (Nilsson, 1997; Dahlström, 2006). In the mid-20th century, modern forestry practices oriented towards high volume production were introduced (Ekelund

and Hamilton, 2001). Dense conifer plantations and improved material planted on clear-cuts became common, while the remaining scattered broadleaf forests were largely left unmanaged (Hamilton, 1998; Ekelund and Hamilton, 2001). In the early 1990s, legislation regulating forest management changed to include nature conservation, through e.g. introduction of green tree retention on clear-cuts (Kruys et al., 2013; Simonsson et al., 2015). The lack of management in broadleaf forest, in combination with increasing numbers of oak retention trees, likely explains the observed increase in oak standing volume and oak tree density. It is worth noting, however, that oak abundance had reached historically low levels in this region during the late 19th century due to a combination of climate change, harvesting and deforestation for agriculture (Lindbladh and Foster, 2010), and despite the increase in recent decades, adult oak populations remains relatively sparse today.

The observed decrease in oak sapling density is not unexpected, as the regeneration requirements of these species are best met in semi-open forests, where moderate disturbance maintains relatively high light levels over time (Vera, 2000; Bobiec et al., 2018). During the study period, the wood volume and total basal area increased steadily (SLU, 2017), and our analysis revealed that greater basal area had a negative effect on oak sapling density, as well as increased the probability of not finding oaks saplings in a plot. This strongly suggests that reduced understory light is a crucial driver of the observed oak sapling decline. The overall negative relationship between basal area and understorey light make it a practical and commonly used proxy for light availability (Sonohat et al., 2004; Hale et al., 2009). However, it is important to note that the exact relationship varies depending on e.g. tree species, stand age, stem distribution, and canopy characteristics (Jenkins and Chambers, 1989; Comeau and Heineman, 2003).

The oak sapling population displays distinct trends in conifer- and broadleaf-dominated forests. The initial increase in conifer-dominated forests was likely an effect of the large-scale implementation of clear-cuts in these forests from the 1950s onward, as these created large open areas suitable for oak regeneration (Götmark and Kiffer, 2014). However, between 1985 and 2010 the proportion of middle-aged forest, the successional stage with the darkest understories (Oliver and Larson, 1996), increased from 30% to 40% (SLU, 2015). This period coincides with the observed decline in oak saplings. In contrast, the continuous decline of oak sapling density in broadleaf-dominated forests was likely in part due to secondary succession following abandonment of traditional land-use practices in the early 20th century and a subsequent lack of management or other disturbance. Over time, this process creates dense and dark forests with reduced seedling and sapling growth and increases mortality of light-demanding species (Lorimer et al., 1994; Vera, 2000).

Furthermore, the four deer species in southern Sweden experienced extreme population increases since 1960, largely due to a combination of game management focused toward high animal densities and the large-scale creation of clear cuts that increased food availability (Lavsund et al., 2003). The large peak in roe deer numbers in the early 1990s was due in part to a combination of a diminished fox (*Vulpes vulpes* L.) population following disease and a series of warm winters (Lindström et al., 1994). Despite a subsequent reduction of moose and roe deer numbers following their peak years, population densities have remained at much higher levels than during the 1960s.

Hunting data is a commonly used proxy for changes in deer population number over time, however, it should not be considered an exact estimate. For example, it is influenced by hunting effort, there are often time lags, and it tends to overestimate deer population growth and decline (Pettorelli et al., 2007; Ueno et al., 2014). Nevertheless, at large spatial scales and over long periods it is often the best proxy available for deer population changes. The deer index used in this paper as a proxy for browsing pressure has further limitations. As the metabolic weight is based on average adult body mass, it does not consider population age or sex composition. Furthermore, it is sensitive to species-

specific food requirements. Moose and roe deer are considered browsers, while red deer and fallow deer have a smaller proportion of browse in their diet (Hofmann, 1989). Therefore, red deer and fallow deer might inflate the deer index as a measure of browsing pressure as their populations increase.

Oaks are tolerant of moderate browsing and, even if growth is reduced, they can tolerate such browsing pressure for an extended period (Annighöfer et al., 2015; Leonardsson et al., 2015). However, our analysis revealed that increased deer abundance strongly decreased the probability of finding oak saplings. Furthermore, the initiation of oak sapling decline in conifer-dominated forests, and stronger decline in broadleaf-dominated forests, coincide with the high deer densities. As oak is a preferred food of deer and browsing damage increases with deer population density (Bergquist et al., 2009; Angelstam et al., 2017b), the high browsing pressure since the 1980s has likely had disproportionate impacts on natural regeneration of oak. Rapid increases in deer populations have occurred in most temperate forest ecosystems during the last decades (Rooney and Waller, 2003; Milner et al., 2006; Takatsuki, 2009). As a consequence, high deer densities that limit natural regeneration of palatable tree species have been observed elsewhere in Europe (Kuijper et al., 2010; Angelstam et al., 2017a), North America (Rooney and Waller, 2003; Bradshaw and Waller, 2016), and Asia (Takatsuki, 2009).

This negative relationship between oak saplings and increased deer density was particularly clear on the island of Gotland, where the introduction and subsequent expansion of a roe deer population is associated with a swift decrease in oak sapling density. Similar results have been found for other tree species after introduction of deer to islands previously lacking large wild herbivores (Martin et al., 2010). In our study, the strong negative effect of roe deer was evident in the multiple linear regression, despite a reduction of NFI plots over time that caused increased year-to-year variability in the oak density estimates. The positive year coefficient in the model can probably be partly explained by the early effects of natural succession following abandonment of traditional land-use practices, which occurred later on Gotland than in the rest of southern Sweden (Dahlström, 2006 and references therein). The positive interaction term suggests a slight decrease of the negative effect of deer over time.

This study is limited by the exclusion of saplings under 1.3 m from the NFI data. All deer species in our study mainly browse below this height (Nichols et al., 2015). Therefore, browsing could be expected to mainly affect oaks that are shorter than those registered by the NFI and consequently browsing effects would not be visible in the NFI data until these individuals have grown (or fail to grow) above the height limit. This may increase the time lag before browsing effects appear in the data. It is likely that the browsing pressure has prevented oaks from reaching 1.3 m. These small oaks might be caught in the "browse trap", where chronic browsing does not necessarily kill the trees but rather keep them in small size classes (Staver and Bond, 2014; Churski et al., 2016).

As pre-commercial thinning was introduced on a large scale in the early 1980s, one could expect that this forestry practice would be a major cause of the observed oak sapling decline, as broadleaved saplings are often targeted during these operations to enhance growing conditions for young conifers (Ekelund and Hamilton, 2001). However, our analysis could not find evidence of such an effect.

It is important to keep in mind that the models in this study do not provide a full picture of why oak regeneration is failing. Year was also a statistically significant predictor of sapling density, suggesting that other, unidentified, factors that have changed consistently over time play an additional role, for instance a changing climate. The positive effect of year and deer abundance, although the latter was statistically marginal, on oak sapling density in the conditional model was likely caused by the coarse spatial resolution of these two variables combined with a reduction in NFI sample plots over time. Due to the reduction in total number of sample plots, each plot represented a larger forest area

and thereby a larger fraction of oak saplings over time.

This study has revealed a clear ongoing decrease in natural regeneration of oak in the Swedish forest landscape, despite a substantial increase in mature trees over the same period. Similar demographic changes, with successively ageing populations due to lack of regeneration, have previously been indicated in smaller-scale case studies elsewhere in Europe (Bernadzki et al., 1998; Rohner et al., 2012; Brunet et al., 2014) the United States (Aldrich et al., 2005; Rogers et al., 2008), and Japan (Takahashi et al., 2003). At a stand level, natural oak regeneration could be expected to mainly occur in pulses following disturbance events, followed by a period of low regeneration success as the cohort ages (Peterken and Tubbs, 1965). Whereas at a landscape scale, one would expect a mix of successional stages that would even out such demographic patterns. However, it appears that such disturbance events are very rare in the homogenous forest landscape created by intensive forest management. This would not necessarily be immediately problematic for the oak population itself, due to the long lifespan of individual trees. However, a prolonged period of low regeneration at a landscape scale will eventually cause a large gap in the oak size distribution. This study appears to have revealed the beginning of such a process. Over time, this could hurt the many species dependent on old and large oak trees and thereby have negative effects on biodiversity.

4.1. Management implications

Most of the changes described here can be attributed to changed land use and game-management practices. Intensive forest management has altered tree species compositions, increased wood volumes and forest density over wide areas in temperate oak-rich ecosystems (Gold et al., 2006; Kirby and Watkins, 2015). These changes in stand structure and density have caused a shift towards more shade-tolerant understory species and a decrease in groundcover (herbaceous plants) across Europe (Verheyen et al., 2012; Hedwall and Brunet, 2016). Together with rapidly increasing deer populations across the northern hemisphere (Lavsund et al., 2003; Rooney and Waller, 2003; Takatsuki, 2009), conditions have been created which are not beneficial for natural regeneration of oak or other light-demanding, palatable species.

Active management to restore landscapes with high-light understory patches and moderate browsing pressure therefore seems essential. In broadleaved stands conservation-oriented thinning, i.e. partial cutting as a conservation measure with the objective to increase light and stand complexity, have shown positive results (Götmark, 2013; Leonardsson et al., 2015). Pedunculate and sessile oak seedlings and saplings require a minimum of about 15–20% of full light for sustained growth, however, the light requirement of oak increases with age and size (von Lüpke, 1998; Annighöfer et al., 2015). Such light levels are rarely achieved during standard forest management for Norway spruce (Löf et al., 2007). Therefore, substituting Norway spruce with tree species that create more light-transparent canopies, e.g. Scots pine and broadleaves such as birch, could allow more light for oak regeneration while maintaining a relatively high forest density (Bobiec et al., 2018; Mölder et al., 2019). Considering the dominance of coniferous forests in southern Sweden and how many oak saplings they harbour, oak populations may also be buttressed by favouring oak during pre-commercial and commercial thinning. However, to be effective this may require a substantial oak and broadleaved tree component in the regeneration.

Diversified forest management, including reinstatement of traditional land-use practices such as selective cuttings, would be beneficial by creating more heterogeneous forest landscapes (Mölder et al., 2019; Kirby and Watkins, 2015). By leaving crowns of felled trees, one could further facilitate recruitment of palatable tree species, such as oak, as coarse woody debris creates sheltered refugia in areas with high deer densities (Smit et al., 2012; Chantal and Granström, 2007). Restoration of grazed woodlands, which to a large degree have been transformed

into dense conifer forests, would create habitats with enough light to facilitate oak regeneration (Bobiec et al., 2018; Mölder et al., 2019). However, grazing levels need to be controlled, and preferably combined with protective structures such as downed trees or exclosures, to not supress oak regeneration (Bakker et al., 2004; Leonardsson et al., 2015).

Overall, to favour natural regeneration of palatable tree species, development of strategies that manage both deer populations and their available food across the landscape are needed (Beguin et al., 2016; Apollonio et al., 2017). As forest management often directly influences the landscape's carrying capacity for deer populations, management strategies that integrate the two are necessary. Ungulate populations should be kept at lower levels while simultaneously diluting browsing effects with increased food availability. Such integrated management requires a landscape-oriented approach and greater collaboration between different stakeholders (Beguin et al., 2016).

5. Conclusion

We show that an initially-growing oak sapling population went into a steep and continuous decline after the early 1980s and connect this development to extensive land use and game management changes. These changes have created continuously denser and darker forests with more herbivores, which is likely hindering the palatable and light demanding oak from successfully regenerating at a landscape scale. To our knowledge, our study is the first to link this negative long-term development in oak regeneration to land use change and increased browsing pressure at such a broad scale in this region. Without changes in active management regimes, it is likely that this oak regeneration decline will continue, eventually with consequences for the population of oak trees and the biodiversity that depends on them.

Acknowledgements

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.04.037.

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