

Long-term woody species dynamics following meadow abandonment in a strictly protected area

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ABSTRACT

Over the last century, the abandonment of agricultural land has led to significant changes in traditionally managed landscapes and their associated species across Europe. The reserve, Vessers Udde, in southern Sweden, was protected in 1923 when mowing ceased and the area was fenced; no further management of any kind has been conducted since then. Over the century, the wooded meadow has evolved into a mixed forest. We studied how two woody species characteristic of wooded meadows, pendunculate oak (*Quercus robur*) and common hazel (*Corylus avellana*), changed over 87 years by analysing tree numbers, basal area, and size distribution since their first mapping in 1937. Over nearly nine decades, oak and hazel have exhibited diverging population trends. Oak density declined by 61 % (from 217 to 84 trees ha⁻¹), yet total basal area increased by 26 %, reflecting selective mortality among smaller trees (87 % mortality at ~10 cm DBH vs 20 % at >50 cm). This size-dependent process, combined with minimal oak recruitment (19.46 trees ha⁻¹ over 87 years), resulted in a marked shift toward larger stems and a more fragmented canopy. In contrast, hazel abundance expanded by 168 % since 1920, with crown cover increasing by 84 % since 1937. Despite substantial differences in demography, spatial analyses show no strong competitive exclusion between oaks and hazel. These findings underscore how the cessation of traditional management reshapes stand structure, favouring hazel proliferation while limiting oak regeneration.

1. Introduction

European agricultural landscapes have undergone dramatic changes over the past century, with land abandonment being one of the most significant transformations (Stoate et al., 2009). Such abandonment is not new historically, nor unique to Europe (Lagerås, 2007; Rey Benayas et al., 2007; Ramankutty, Heller and Rhemtulla, 2010; Queiroz et al., 2014). In northern Europe, this process has particularly affected traditionally managed meadows and pastures, which historically were maintained through mowing, grazing, and selective tree management with typically 10–30 % tree cover, many of which have transitioned into forests (Veen et al., 2014). These wooded meadows were often left to natural succession following abandonment (Milberg et al., 2019), leading to profound changes in vegetation structure and composition (Nilsson, Franzén and Jonsson, 2008). Wooded meadows traditionally harbour tree species valuable to biodiversity, with *Quercus robur* (pedunculate oak) and *Corylus avellana* (hazel) being characteristic (Tedersoo et al., 2006). Oaks were maintained as open-grown specimens that are now recognised for their high conservation value (Sebek et al.,

2016),

hazel was preserved for nut production and its role in traditional agriculture (Silvestri et al., 2021). These species represent contrasting growth forms as well as shade tolerances: oak is considered light-demanding and sensitive to competition, while hazel is a shade-tolerant understory shrub capable of regeneration under shaded conditions (Fitter and Fitter, 2002) and reaching a height of 6 m, and occasionally higher (Hicks, 2022).

In Sweden, agricultural land use peaked in the 1920s, after which significant areas were progressively abandoned due to traditional management practices (Karlsson et al., 2010). This transformation from managed agrarian land to forest represents a slow but profound landscape change with far-reaching consequences for biodiversity and ecosystem structure (von Oheimb and Brunet, 2007). The decline of traditionally managed grasslands, particularly those used for mowing or grazing, has been especially dramatic in northern Europe (Nilsson et al., 2008). This trend is likely to accelerate, driven by increasing costs of traditional management and declining availability of grazing animals for maintaining species-rich grasslands (Metzger et al., 2010). The

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challenge is particularly acute for protected areas and sites receiving management subsidies, where understanding succession processes becomes crucial for informed conservation decisions (Kindvall et al., 2022).

While secondary succession on abandoned agricultural land has been extensively studied (Kardell and Fiskesjö, 1999; Götmarm, 2013; Vinogradovs et al., 2018), key questions remain about species-specific responses to abandonment and their implications for conservation management. Understanding which species benefit or decline during forest regeneration and at what rates these changes occur requires long-term monitoring data that are rarely available (Brunet et al., 2014). Such information is essential for projecting future vegetation changes and developing effective management strategies for maintaining biodiversity in these transitioning landscapes.

The progressive development of closed forest canopies in formerly open habitats, described as the "darkening of the landscape", poses significant challenges for species adapted to open and semi-open agricultural habitats, as well as for conservation managers tasked with maintaining habitat openness. In southern Sweden, substantial areas of current forest growth occur on former hay meadows that were abandoned and allowed to undergo natural succession. Despite the widespread nature of this transformation, surprisingly few studies have examined how this overgrowth affects the woody species characteristic of Scandinavian wooded meadows and pastures (Hytteborn et al., 2017; Finndin and Milberg, 2024). While conservation funding exists in Sweden for maintaining open conditions around particularly valuable oak individuals, most oaks must cope with increasing competition as tree and shrub canopies close (Krajicek et al., 1961). Similarly, hazel, another woody species characteristic of Scandinavian wooded meadows, faces changing environmental conditions as these historically open habitats transition to closed forests (Birks, 1988).

We aimed to gain a better understanding of the long-term consequences of management cessation on oak and hazel populations, using data from Vessers Udde. This former wooded meadow was protected in 1923 and subsequently left to natural succession. Originally characterised by dominant oaks, including several veteran trees (Julin, 1948), the site has transformed into a dense mixed forest over the past century. Through four comprehensive surveys (1937, 1988, 1991/92 and 2024), we tracked changes in the oak population, with a particular focus on size-class-specific mortality rates—information crucial for the conservation management of oaks in abandoned agricultural landscapes. While oak mortality is generally lower in farm settings compared to forests and decreases with tree size (Drobyshev et al., 2008; Johnson et al., 2019; Milberg and Christensen, 2024), few studies have documented these patterns during the transition from open to closed canopy conditions. We hypothesised increased mortality rates during succession, particularly among smaller trees. Additionally, we examined oak recruitment under increasing shade conditions to empirically test the common assumption that oak regeneration is poor in shaded environments (Bobiec et al., 2018). Finally, we tested the widespread belief that oaks perform poorly under increasing competition by analysing changes in the basal area throughout the succession period since 1937. While mature oaks with established canopies may dominate the upper strata, their growth can still be constrained by below-ground competition for resources and by crown competition from neighbouring trees (Jensen and Löf, 2017). Additionally, increased stand density can lead to changes in stem architecture and reduced vigour even in dominant trees (Vera, 2000), potentially affecting their long-term survival despite their initial height advantage.

2. Methods

2.1. Study site

Vessers Udde Nature Reserve (58°15'34.5"N 15°43'45.5"E, Fig. S1) is located in the province of Östergötland, southern Sweden, within the

hemiboreal vegetation zone (Julin, 1948). The 3.43 ha study area (excluding a 0.06 ha island) is found on clay-rich till with numerous stones and boulders (Kardell and Fiskesjö, 1999). A lake-lowering project in the 1850s reduced water levels by approximately 1.8 m, creating new land that now forms part of the reserve (Svahn and Nordholm, 2001).

2.2. Historical management

Prior to protection, the site was managed as a wooded meadow for several centuries, with regular hay harvests maintaining an open canopy dominated by oak and scattered hazel. The reserve was formally protected in 1923 to study vegetation development following the cessation of active management, particularly focusing on the natural succession of southern Swedish wooded meadows (Julin, 1948). The last hay harvest took place in 1922, coinciding with the installation of perimeter fencing on the landward side. Since protection, a no-access policy has prevailed.

2.3. Current conditions

Although human access has been restricted since 1923, wildlife still frequents the area. Large herbivores, including roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), and moose (*Alces alces*), enter either over the fence or via the unfenced shoreline, especially during periods when the lake is frozen. These ungulates may exert browsing pressure on woody vegetation, particularly affecting tree seedlings and saplings. Regional ungulate populations, historically low, have increased markedly since 1980 (Bergstedt et al., 2017). Wild boars (*Sus scrofa*), first documented in Östergötland during the 1990s (Bergqvist et al., 2024), have been present in the reserve since at least 2014, as observed personally by the author, PM.

2.4. Tree surveys and measurements

2.4.1. Historical data (1920–1992)

A comprehensive tree survey was first conducted in 1937 as part of doctoral research (Julin, 1948). This baseline effort mapped all oak and hazel. The latter is a shrub that forms distinct bouquets of thin branches reaching 6 m and occasionally more. We refer to bouquets that can reach considerable age and size (Hæggström, 2000) as genets, although we cannot exclude that large bouquets might have originated from more than one hazel nut. In the 1937 dataset, oaks of height greater than 1.3 m were recorded only in categorical 10-cm diameter classes (1–9 cm, 10–19 cm, 20–29 cm, etc.), rather than as precise measurements. In contrast, the subsequent surveys (1979, 1991, and 2024) recorded exact diameter at breast height (dbh) for all trees taller than 1.3 m. To enable temporal comparisons, we converted the recent precise measurements into the same diameter classes used in 1937. Crown projections were recorded for each oak tree and hazel genet on the 1937 maps (Julin, 1948). Historical data for hazel from 1920 were extracted from the 1937 maps, which noted the presence of genets at the reserve's establishment. The 1937 maps were later digitised and georeferenced using reserve boundaries and permanent landscape features. Subsequent surveys in 1979 and 1991/92 recorded DBH measurements but did not include spatial positions (Kardell and Fiskesjö, 1999). These data, archived at the Swedish University of Agricultural Sciences (SLU), provided information on population sizes and size distributions of oak in both periods and hazel in 1991/92.

2.4.2. Surveys in 2024

In 2024, a comprehensive survey of both oak and hazel was conducted, using 1937 maps as reference. For *Q. robur*, trees with DBH were measured using two perpendicular diameters, which were then averaged. For larger trees, the circumference was recorded and converted to DBH. All 2024 measurements were subsequently categorised into 1937 classes, enabling direct temporal comparisons. All hazel genets were

counted regardless of size, and crown coverage was quantified by measuring radial distances north, south, east, and west from the stem. Crown coverage was calculated based on these values. Crown projections were mapped in both 1937 and 2024 to assess changes in spatial coverage, facilitating reliable comparisons of population sizes, basal areas, and distributions over the 87 years.

2.5. Mortality

Annual mortality from 1937 to 2024 was calculated as follows:

$$\text{annual mortality rate} = 1 - (C/N_0)^{1/y} \quad (1)$$

where C is the number of living trees in 2024 that existed in 1937, N_0 is the original number of living trees in 1937, and y is the length of time between samplings (87 years). Confidence intervals for mortality estimates were calculated by generating 1,000 values using a bootstrapping approach based on a binomial distribution, reflecting the initial tree count and survival percentage. Mortality rates were computed for each value, and the 2.5th and 97.5th percentiles defined the 95% confidence interval (Arellano, 2019).

To explore potential competition between *Q. robur* and *C. avellana*, we overlaid a 25 m × 25 m grid across the study area. We counted the number of oak trees in each cell in both 1937 and 2024, as well as the number of hazel genets present in 2024. This grid-based approach allowed us to analyse spatial associations between the species and test specific hypotheses about their competitive interactions. Details of the statistical analysis using this grid system are provided in the "Statistical analyses" section below.

2.6. Statistical analyses

All statistical analyses were conducted in R version 4.4.3 (R Core Team, 2024). Data on oak and hazel (1937–2024) were analysed in terms of (i) tree density, (ii) basal area, and (iii) size class distributions. Basal area was computed as $\pi \times (\text{dbh}/2)^2$, and size classes were grouped into 10 cm intervals.

The relationship between initial diameter (1937) and mortality was analysed using logistic regression (GLM with binomial error and logit link). For surviving trees, absolute basal area change was calculated as basal area in 2024 subtracting the basal area in 1937. Oaks reaching above DBH were analysed in their size classes as described above. Size-dependent growth patterns were analysed using ANOVA with post-hoc analyses using Tukey-adjusted comparisons, emmeans version 1.8.5 (Lenth, 2022).

We used Pearson correlation analyses to examine temporal trends in population density for hazel and oak across four census years (1937, 1979, 1991 and 2024).

We subdivided the site into 74 grid cells (25 m × 25 m), quantified the net change in oak density from 1937 to 2024, and recorded current hazel abundance (in 2024) per cell. To examine potential competitive effects between oaks and hazel, we fitted generalised linear models with a negative binomial distribution (using glm.nb from the MASS package). To assess whether oak recruitment influences hazel abundance, we regressed hazel abundance in 2024 on the net change in oak density from 1937 to 2024. The null hypothesis posited that changes in oak density are independent of hazel abundance in 2024. This model enabled us to determine whether hazel competition might limit oak recruitment, as evidenced by a negative relationship, or whether oak recruitment is associated with hazel presence. We then investigated whether oak abundance affects hazel abundance by regressing hazel abundance in 2024 on oak abundance, using 1937, 2024, or both, depending on the specific question. The null hypothesis proposed that hazel abundance in 2024 is independent of oak abundance in the same cells. This test evaluated whether established oaks outcompete or otherwise influence hazel (indicated by a significant relationship) or

whether hazel abundance occurs independently of oak density. By implementing these models separately, we determined whether oak recruitment is suppressed by hazel (or vice versa) and whether current hazel abundance is shaped by oak presence (Fig. 1)

3. Results

3.1. Population and structure changes since abandonment

The total number of oak individuals recorded decreased from 743 in 1937 to 288 in 2024. Oak population dynamics showed substantial changes over the 89-year study period. Total stem density declined dramatically from 217 trees/ha in 1937 to 167 in 1979, 104 in 1991 and 84 in 2024 (-61 %) (Fig. 2a). Despite this marked reduction in tree numbers, the total basal area per hectare increased from 14.1 m²/ha to 17.8 m²/ha (+26 %). Size-class distributions shifted dramatically over the 87-year study period (Fig. 3a). In 1937, the population exhibited a reverse J-shaped distribution, with 52 % of trees in the smallest size class (0–9 cm dbh) and 7 % exceeding 50 cm dbh. By 2024, this pattern had reversed, with 35 % of trees exceeding 50 cm dbh. Notably, recruitment was severely limited, with the density in the smallest size class dropping from 137 to 15 trees ha⁻¹.

The total number of hazel genets recorded across all surveys was 3490 and the crown area of hazel genets exhibited considerable variation across the study (n = 1393). The mean crown area per genet was 14.8 ± 0.43 m² (SE), with a median of 9.8 m² and crown areas ranged from 0.001 to 143.5 m² (Fig. S2). The population dynamics of *C. avellana* were dramatic: from 151.3 genets/ha in 1920, the density increased to 206.9 genets/ha by 1937, then to 253.1 genets/ha in 1991, and further expanded to 406.1 genets/ha by 2024 (a total increase of 168 % since 1920). This population increase was accompanied by an 84 % expansion in crown coverage, from 7509 m² to 13,788 m², between 1937 and 2024 (Fig. 2b,c).

Hazel genet density showed a positive tendency with the year ($r = 0.941$, $p = 0.059$, $n = 4$), while oak stem density exhibited a significant negative relationship ($r = -0.972$, $p = 0.028$, $n = 4$) (Fig. 3b).

3.2. Mortality and recruitment patterns

Over the 87 years (1937–2024), 198 of the 743 oaks recorded in 1937 survived, corresponding to an annual mortality rate of 1.70 % (95 % CI, 1.65–1.75 %). Additionally, 90 oaks germinated and reached DBH (i.e. 130 cm in height) by 2024, reducing the net loss of DBH trees to 455, which is equivalent to 5.23 oaks lost per year since 1937.

The initial tree size had a significant impact on both mortality and growth patterns over the 87-year period. Mortality probability decreased significantly with increasing stem diameter (GLM: $\beta = -0.048 \pm 0.006$, $z = -8.504$, $p < 0.001$; Fig. 4a), declining from 0.87 for 10 cm trees to 0.20 for trees > 50 cm. Among survivors, absolute basal area increment differed significantly between size classes (ANOVA: $F_{3194} = 39.72$, $p < 0.001$; Fig. 4b). Larger trees showed greater absolute growth, with mean basal area increment increasing from 714 ± 101 cm² in the 10–19 cm class to 3517 ± 330 cm² in trees > 40 cm. Post-hoc tests revealed significant differences between all size classes ($p < 0.05$).

3.3. Competition effects

The spatial pattern analysis showed no significant relationship between local changes in oak abundance (1937–2024) and current hazel density across the 25 m × 25 m grid cells. Despite substantial variation in both oak dynamics (range: -8 to +4 trees per cell) and hazel abundance (0–31 genets per cell), the negative binomial model indicated no systematic effect of oak population changes on hazel occurrence ($\beta = -0.016 \pm 0.015$, $z = -1.099$, $p = 0.272$). Within 74 (25 × 25 m) sampling grids, oak counts in 2024 were not correlated with hazel coverage in 2024 ($r = 0.209$). By contrast, *C. avellana* counts in 2024 showed a

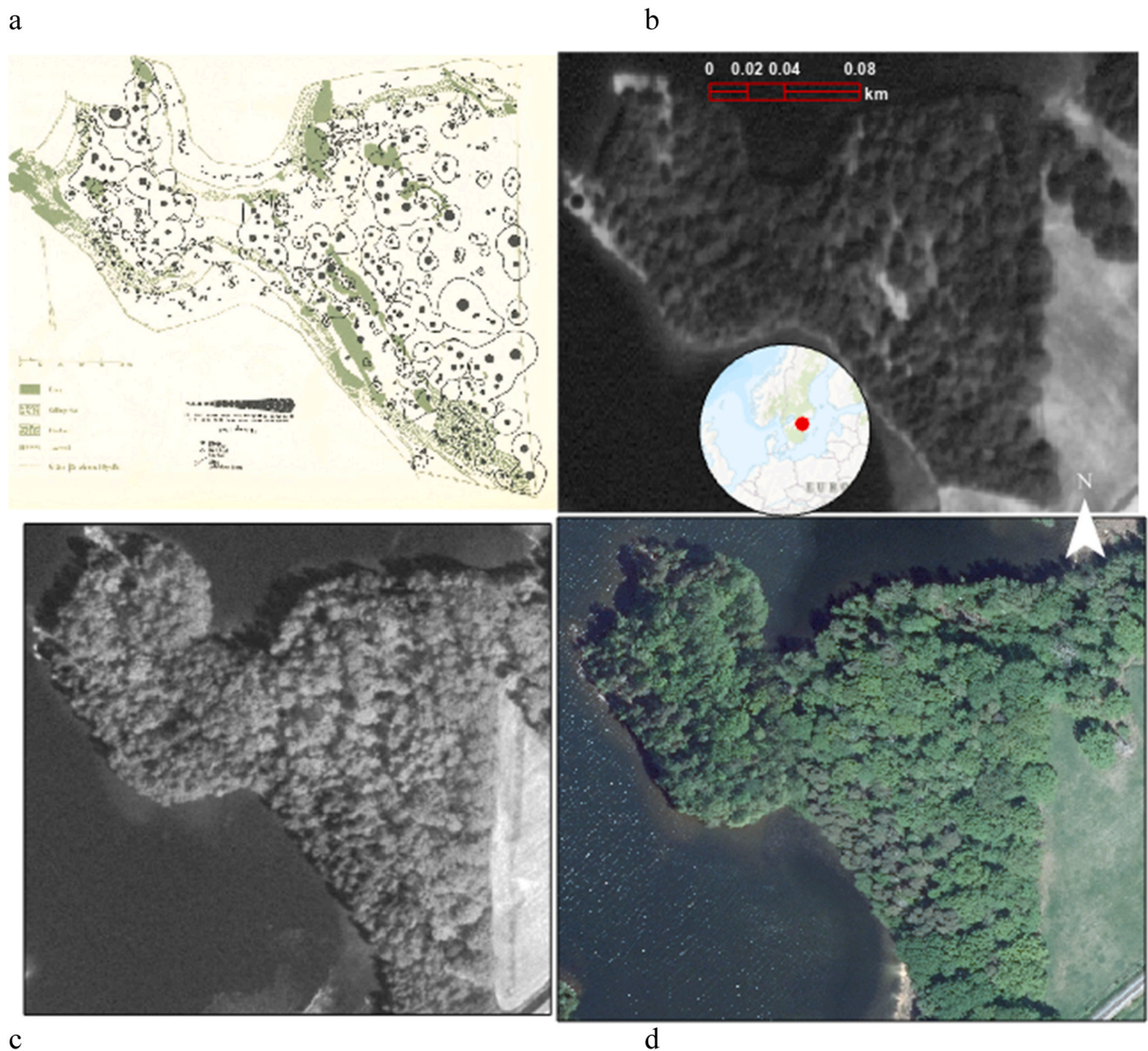


Fig. 1. Long-term vegetation changes in Vessers Udde Nature Reserve, southern Sweden. (a) Oak distribution and canopy cover map from the first systematic survey in 1937 (redrawn from [Julin, 1948](#)). (b) Aerial photograph from 1941, (c) from 1960 and (d) satellite image from 2017 depicting current forest cover. Inset: The location of Vessers Udde (red dot) in southern Sweden.

correlation with the 1937 *Q. robur* coverage ($r = 0.520$, $p < 0.001$).

3.4. Recruitment patterns

Between 1937 and 2024, oak recruitment was minimal, averaging 1.22 ± 0.32 new trees per grid square ($SD = 2.73$), with 60.8 % of grids ($n = 45$) lacking any new oaks. Across the entire study area, only 90 new oak individuals were recorded (19.46 trees ha^{-1} over 89 years; 0.22 trees $ha^{-1} yr^{-1}$). During the same period, the hazel cover increased by 152.2 %, from $7500 m^2$ in 1937 to nearly $19,000 m^2$ in 2024. Mean coverage per plot rose from $101 m^2$ to $256 m^2$, with 85.1 % of grid squares showing an increase, 5.4 % showing a decrease, and 9.5 % unchanged ($n = 74$). There was no significant correlation between oak recruitment and hazel cover change ($r = -0.157$, $p = 0.183$, $n = 74$).

4. Discussion

4.1. Dramatic structural changes following abandonment

Our unique 87-year dataset from a nature reserve that has been allowed to develop naturally over a century reveals profound structural reorganisation in woody vegetation following the cessation of meadow management. Oak (*Q. robur*) and hazel (*C. avellana*) exhibited divergent trajectories: oak density declined by 68 %, but total basal area increased by approximately 25 %, reflecting a shift from numerous small trees to fewer, larger individuals ([Brunet et al., 2014](#)). Hazel, in contrast, expanded substantially, more than doubling its population size and increasing canopy cover by 84 %. These contrasting outcomes highlight the divergent species responses set in motion once traditional management ceases ([Oldén et al., 2017](#)). Our findings mirror broader patterns of vegetation densification recorded across European wooded meadows, where abandonment typically triggers increased woody biomass and

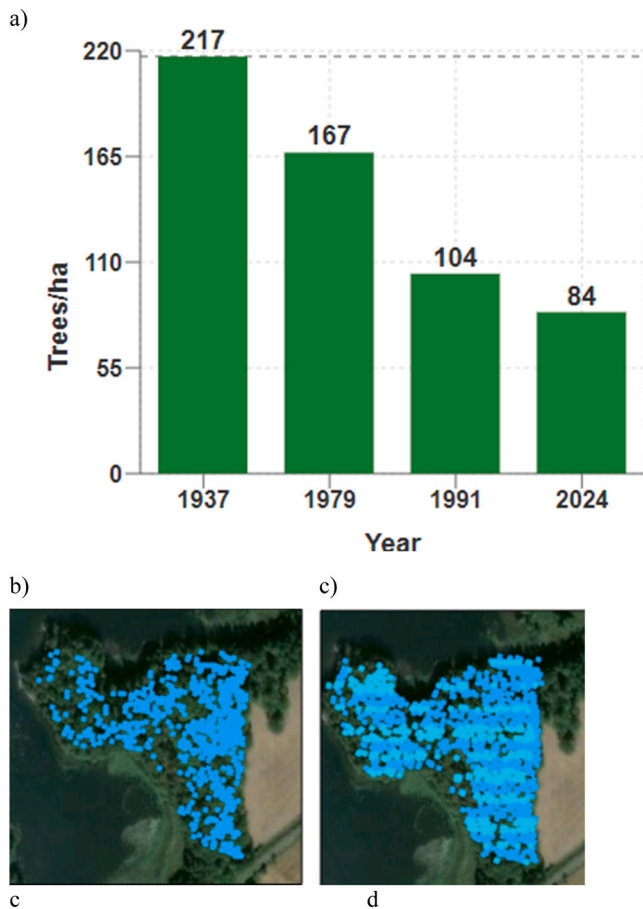


Fig. 2. Spatial distribution of oak (*Quercus robur*) and hazel (*Corylus avellana*) across 87 years of succession. (a) Oak density from 1937 to 2024, (b) Hazel distribution in 1937, including crown projections and (c) in 2024.

closure of the canopy (Milberg et al., 2017; Milberg and Tälle, 2023). Our findings align with Hytteborn et al. (2017), who also documented increases in oak basal area despite initial mortality. While hazel may compete with oaks, its limited height prevents encroachment on mature oak crowns and might actually benefit oaks by impeding the establishment of more competitive trees like beech and elm. This protective dynamic was observed in Dalby Söderskog (southern Sweden), where elm initially outcompeted both species until Dutch elm disease reversed this trend (Brunet et al., 2014). However, oak saplings only survive near hazel when they grow beyond its shade (Brunet and Larsson, 2022), indicating fine-scale spatial interactions.

In eastern North America, old-field succession also often exhibits initial oak dominance, followed by increasing competition from more shade-tolerant species (Flinn and Vellend, 2005). In the more dark forests emerging, oak regeneration fail (Abrams, 2003; Nowacki and Abrams, 2008) while at the same time, species like shade-tolerant red maple thrive (Hart et al., 2012). These similarities to our study system suggest that management approaches developed for North American oak forests may also be relevant for former European wooded meadows (Brose et al., 2013).

Our results contribute to a growing body of literature documenting woody expansion in abandoned agricultural landscapes (Cramer et al., 2008). While many studies emphasise overall biomass accumulation (Meyfroidt et al., 2010), our long-term dataset underscores the more nuanced dynamics that can unfold between canopy and understorey species. For instance, the substantial loss of smaller oaks, coupled with growth in larger size classes, follows patterns observed in other long-term studies of abandoned wooded meadows (von Oheimb and

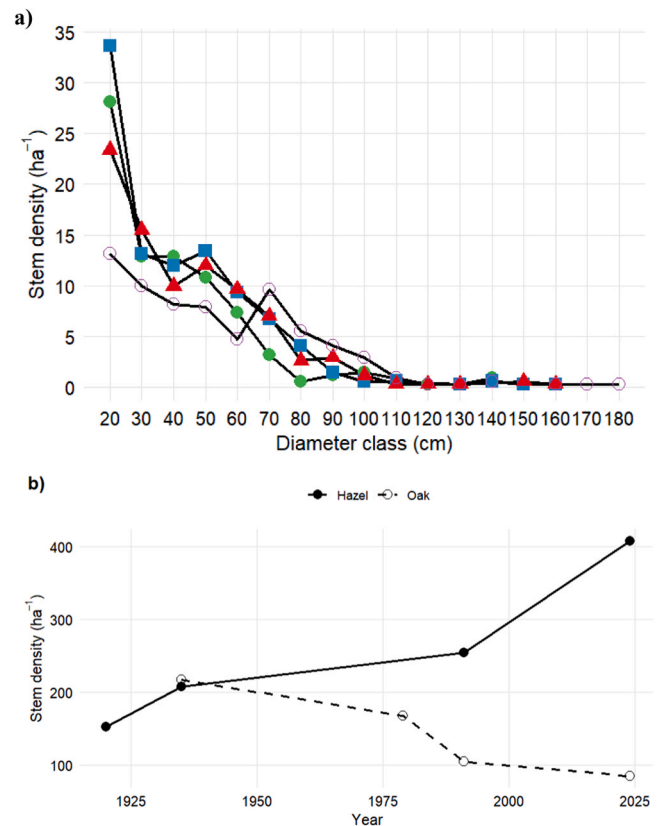


Fig. 3. Population dynamics of oak and hazel from 1937 to 2024.

(a) Size-class distribution changes of oak over time, illustrating the shift toward larger oak size classes and hazel understory expansion. 1937- green circles, 1979- blue squares, 1991/92- red triangles, 2024- rings. Size classes < 20 cm not shown. (b) Changes in population density (stems ha⁻¹) for both species across four survey periods (1923, 1937, 1979, 1991/92, 2024). For Hazel, it is the number of genets—years missing: 1923 oak and 1979 hazel.

Brunet, 2007). The persistence of oak alongside the expansion of hazel suggests that these species can coexist despite changing conditions. This coexistence likely reflects the advantages of established oaks' size and canopy position combined with hazel's shade tolerance and ability to thrive in the understory (Kajtoch et al., 2012; Paulssen et al., 2024).

4.2. Mortality, growth, and recruitment

Our observed annual mortality rate of oaks (1.70 %) at Vessers Udde is higher than reported from Dyrehaven in Denmark, an open savanna-like deer park (approximately 0.39 %, Milberg and Christensen, 2024), underscoring the capacity of oaks to persist for extended periods, even under changing climatic conditions (Piovesan and Biondi, 2021). These differences in mortality rates are noteworthy but require careful interpretation when comparing these contrasting environments. Vessers Udde has undergone significant encroachment, while Dyrehaven remains predominantly open (Milberg and Christensen, 2024). The mortality rates suggest factors beyond canopy closure may influence oak longevity, and differences in initial oak populations affect direct comparability. The relatively low mortality rates contrasts with more pessimistic estimates reported elsewhere (Drobyshev et al., 2008). Notably, both the current study site and Dyrehaven site exhibit poor recruitment, primarily due to ungulate browsing pressure (Dyrehaven) on seedlings and increased shade conditions that inhibit establishment (Vessers Udde), suggesting a common vulnerability despite the resilience of established trees. Overall, these results suggest that established solitary oaks may exhibit greater resilience than is often assumed, although future shifts in climate could still pose challenges.

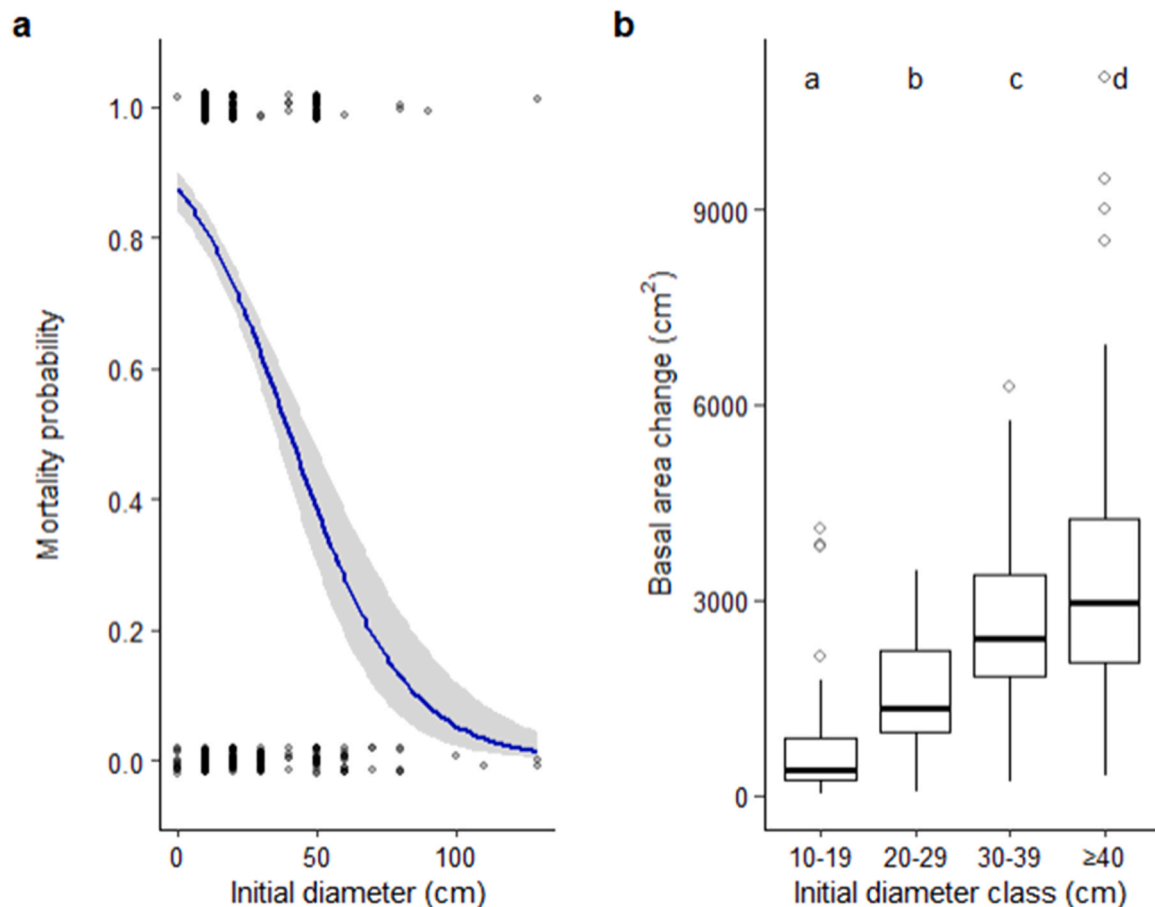


Fig. 4. Oak (*Quercus robur*) performance over 87 years (1937–2024) in an abandoned wooded meadow. (a) Logistic regression of mortality probability in relation to initial stem diameter (dots represent individual trees that either died (1) or survived (0), blue line shows predicted probability, shaded area shows 95 % CI). (b) Absolute basal area change (cm²) of surviving trees by initial diameter class. Boxplots show the median (central line), interquartile range (box), range excluding outliers (whiskers), and outliers (open circles). Different letters indicate significant differences between diameter classes (Tukey's HSD, $p < 0.05$).

Our analysis uncovered strong size dependence in oak mortality. The probability of dying from 1937 to the present declined sharply with increasing tree size, ranging from nearly 90 % among smaller oaks (<20 cm DBH) to < 20 % for the largest trees (>50 cm DBH). This pattern aligns with studies in other temperate forests, where larger individuals enjoy increased survival, likely due to superior light interception and more extensive root systems (Körner, 2005; Pommerening and Meador, 2018). Correspondingly, basal area increment was greatest in larger size classes, driving overall gains in oak basal area despite the decline in total stem density. Reduced recruitment of oak in closed-canopy conditions contributed to a strongly right-skewed size distribution, reflecting an initial recruitment pulse in the early abandonment phase (pre-1937) followed by self-thinning (Peet and Christensen, 1987). While hazel's expansion likely suppresses oak seedling establishment through shade, our findings suggest minimal competitive effects on mature oaks. This aligns with ecological theory - once oaks reach the canopy, their primary limiting resources are accessed above the hazel understory. Any potential belowground competition for water or nutrients appears insufficient to significantly affect established oak trees, whose extensive root systems and canopy position provide competitive advantages despite increasing hazel density beneath them.

Despite the presence of considerable herbivore populations, the recruitment of 90 new oaks reaching measurable diameter at breast height by 2024 demonstrates functional natural regeneration of oaks. This regeneration, occurring at approximately 0.30 trees per hectare per year, suggests that spatial heterogeneity in browsing intensity creates sufficient 'refugia' for seedling establishment (Kuijper et al., 2010),

whilst most years likely produce seed satiation effects that overwhelm predator populations (Szymkowiak et al., 2024). These findings challenge deterministic models predicting complete regeneration failure under high browsing pressure (Palmer et al., 2004; Götzmark et al., 2005) and support the 'shifting mosaic' concept of cyclical oak recruitment in specific temporal and spatial windows (Vera 2000). However, with a low mature tree mortality annually and insufficient recruitment over the past century to compensate for this loss, the long-term viability of the population remains a concern, particularly given the hands-off management approach at this site. This agrees with long-term studies from Białowieża National Park, which also document declining tree populations under strict protection (Brzeziecki et al., 2016, 2020).

4.3. Hazel's expansion without apparent suppression of larger oaks

Our spatial analysis indicates that, while hazel rapidly increased in density and cover, it exerted no evident negative effect on oak performance at local scales. Larger oak trees (diameter >40 cm) maintained robust growth (mean basal area increment 3517 ± 2331 cm² per tree over the entire study period, 1937–2024, within the 3.43 ha study area; $n = 50$, and we detected a minimal correlation between hazel density and oak crown development. While understory hazel may suppress oak regeneration through light competition, our results suggest that established oaks with well-developed root systems remain relatively unaffected by the presence of hazel (Wallraf and Wagner, 2019). This indicates that belowground competition for soil moisture and nutrients between hazel and mature oaks is not a significant limiting factor for

canopy dominants, and oak dominance in the canopy can persist even under dense hazel cover. However, the near-absence of oak recruitment in recent decades (<10 saplings ha^{-1} in the 10–19 cm size class) foreshadows potential long-term declines if no new individuals replace the current veterans (Götmark, 2009; Milberg and Christensen, 2024).

4.4. Implications for stand development and conservation

Contrary to straightforward successional models predicting competitive displacement, our study reveals a more complex structural reorganisation in abandoned wooded meadows, featuring parallel growth trajectories for canopy and understorey species. Large oaks show little evidence of senescence, indicating an ongoing capacity for habitat provisioning and carbon sequestration. However, the lack of oak regeneration suggests that stand dynamics could lead to fewer, albeit larger, canopy individuals over time. Without disturbance or management practices that create sufficient light gaps, oak recruitment may remain low, reflecting conclusions from Dalby Söderskog (Lindquist, 1938). In contrast, hazel is likely to retain or even increase its dominance in the understory (Lindquist, 1938; Alder et al., 2023), at least given the current tree canopy species at this site.

These findings bear important implications for conservation strategies throughout Europe's abandoned wooded meadows (Garcia, 1992). Maintaining long-term regeneration of oak may require targeted interventions, such as selective clearing or controlled grazing, to enhance light availability for seedlings. On the other hand, moderate hazel expansion does not necessarily conflict with oak conservation, given that hazel and large oaks appear capable of coexistence (Lindquist, 1938). Yet, as veteran oaks eventually senesce, a key priority will be ensuring that sufficient recruitment occurs to sustain oak populations in these historically managed landscapes (Bobbie et al., 2018).

Overall, our long-term analysis highlights the complexity of successional outcomes following abandonment. The observed shift towards fewer but larger oak trees, coupled with substantial expansion of hazel, underscores the importance of size-dependent demographic processes and varying competitive interactions. These findings refine our understanding of how formerly managed meadows develop once management ceases and can inform evidence-based strategies to maintain or restore ecological and cultural values in similar wood-pasture systems across Europe.

Finally, the strictly protected status of this particular reserve, with access forbidden, offers a unique opportunity to observe natural successional processes in the near-absence of human disturbance in Europe. The dynamic changes documented here emphasise the need for continued monitoring and research to determine whether the resulting stand trajectories should be left to evolve naturally or guided by targeted interventions to maintain a balance between canopy oak populations and understorey hazel. This decision will be crucial for conserving the ecological and cultural legacies associated with wood-pasture landscapes, particularly in an era of accelerating environmental change.

CRediT authorship contribution statement

Franzen Markus: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Johansson Victor:** Writing – review & editing, Visualization, Validation, Resources, Project administration, Funding acquisition, Conceptualization. **Milberg Per:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122837.

Data availability

Data will be made available on request.

References

- Abrams, M.D., 2003. Where has all the white oak gone? *BioScience* 53, 927–939.
- Alder, D., Edwards, B., Poore, A., Norrey, J., Marsden, S., 2023. Irregular silviculture and stand structural effects on the plant community in an ancient semi-natural woodland. *For. Ecol. Manag.* 527, 120622.
- Arellano, G., 2019. Calculation of narrower confidence intervals for tree mortality rates when we know nothing but the location of the death/survival events. *Ecol. Evol.* 9, 9644–9653.
- Bergqvist, G., Kindberg, J., Elmhagen, B., 2024. From virtually extinct to superabundant in 35 years: establishment, population growth and shifts in management focus of the Swedish wild boar (*Sus scrofa*) population. *BMC Zool.* 9, 14.
- Bergstedt, J., Axelsson, A.-L., Karlsson, J., Lönnander, J., Törnqvist, L., Milberg, P., 2017. Förändringar i Eklandskapet 1927 till 2013: i den första Riksskogstaxeringens fotspår. *Sven. Bot. Tidskr.* 111, 331–343.
- Birks, H.H., 1988. The cultural landscape: past, present and future. Cambridge University Press.
- Bobbie, A., Reif, A., Öllerer, K., 2018. Seeing the oakscape beyond the forest: a landscape approach to the oak regeneration in Europe. *Landscape Ecol.* 33, 513–528.
- Brose, P.H., Dey, D.C., Phillips, R.J., Waldrop, T.A., 2013. A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in eastern North America? *For. Sci.* 59, 322–334.
- Brunet, J., Bukina, Y., Hedwall, P.-O., Holmström, E., von Oheimb, G., 2014. Pathogen induced disturbance and succession in temperate forests: evidence from a 100-year data set in southern Sweden. *Basic Appl. Ecol.* 15, 114–121.
- Brunet, J., Larsson, J., 2022. Ekens dynamik i naturvårdsskogar—Ekbeståndets demografi i Dalby Söderskog 2011–2021. Arbetsrapport Sver. Lantbr., Inst. F. öR. Sydsvensk Skogsvetenskap.
- Brzeziecki, B., Pommerening, A., Miścicki, S., Drozdowski, S., Żybyra, H., 2016. A common lack of demographic equilibrium among tree species in Białowieża National Park (NE Poland): evidence from long-term plots. *J. Veg. Sci.* 27, 460–469.
- Brzeziecki, B., Woods, K., Bolibok, L., Zajaczkowski, J., Drozdowski, S., Bielak, K., Żybyra, H., 2020. Over 80 years without major disturbance, late-successional Białowieża woodlands exhibit complex dynamism, with coherent compositional shifts towards true old-growth conditions. *J. Ecol.* 108, 1138–1154.
- Cramer, V.A., Hobbs, R.J., Standish, R.J., 2008. What's new about old fields? Land abandonment and ecosystem assembly. *Trends Ecol. Evol.* 23, 104–112.
- Drobyshev, I., Niklasson, M., Linderson, H., Sonesson, K., Karlsson, M., Nilsson, S.G., Lanner, J., 2008. Lifespan and mortality of old oaks—combining empirical and modelling approaches to support their management in Southern Sweden. *Ann. For. Sci.* 65, 1.
- Finndin, M., Milberg, P., 2024. The population development of small trees and shrubs after 100 years of free succession of a wooded meadow in southern Sweden. *Silva Fenn.* 58, 23071.
- Fitter, A., Fitter, R., 2002. Rapid changes in flowering time in British plants. *Science* 296, 1689–1691.
- Flinn, K.M., Vellend, M., 2005. Recovery of forest plant communities in post-agricultural landscapes. *Front. Ecol. Environ.* 3, 243–250.

- Garcia, A., 1992. Conserving the species-rich meadows of Europe. *Agric., Ecosyst. Environ.* 40, 219–232.
- Götmark, F., 2009. Experiments for alternative management of forest reserves: effects of partial cutting on stem growth and mortality of large oaks. *Can. J. For. Res.* 39, 1322–1330.
- Götmark, F., 2013. Habitat management alternatives for conservation forests in the temperate zone: Review, synthesis, and implications. *For. Ecol. Manag.* 306, 292–307.
- Götmark, F., Berglund, Å., Wiklander, K., 2005. Browsing damage on broadleaved trees in semi-natural temperate forest in Sweden, with a focus on oak regeneration. *Scand. J. For. Res.* 20, 223–234.
- Hæggström, C., 2000. The age and size of hazel (*Corylus avellana* L.) stools of Nåtö Island, Åland Islands, SW Finland. In: *Methods and approaches in forest history. Papers selected from a conference held in Florence, Italy in 1998*. CABI Publishing Wallingford, UK, pp. 67–77.
- Hart, J.L., Buchanan, M.L., Clark, S.L., Torreano, S.J., 2012. Canopy accession strategies and climate-growth relationships in *Acer rubrum*. *For. Ecol. Manag.* 282, 124–132.
- Hicks, D., 2022. Biological Flora of Britain and Ireland: *Corylus avellana*: No. 302. *J. Ecol.* 110, 3053–3089.
- Hyttborn, H., Svensson, B.M., Kempe, K., Press, A., Rydin, H., 2017. Century-long tree population dynamics in a deciduous forest stand in central Sweden. *J. Veg. Sci.* 28, 1057–1069.
- Jensen, A.M., Löf, M., 2017. Effects of interspecific competition from surrounding vegetation on mortality, growth and stem development in young oaks (*Quercus robur*). *For. Ecol. Manag.* 392, 176–183.
- Johnson, P.S., Shifley, S.R., Rogers, R., Dey, D.C., Kabrick, J.M., 2019. The ecology and silviculture of oaks. Cabi.
- Julin, E., 1948. Vessers udde: mark och vegetation i en igenväxande löväng vid Bjärka-Säby. *Acta Phytogeogr. Suec.* 23.
- Kajtoch, Ł., Żmihorski, M., Bonczar, Z., 2012. Hazel Grouse occurrence in fragmented forests: habitat quantity and configuration is more important than quality. *Eur. J. For. Res.* 131, 1783–1795.
- Kardell, L., Fiskesjö, A., 1999. Vessers udde 1921–1992: skog, vegetation och mark efter 70 års fridlysning. Inst. för skoglig landskapsvård, SLU, Uppsala.
- Karlsson, H., Emanuelsson, M., Segerström, U., 2010. The history of a farm-shieling system in the central Swedish forest region. *Veg. Hist. Archaeobotany* 19, 103–119.
- Kindvall, O., Franzén, M., Askling, J., Forsman, A., Johansson, V., 2022. Subsidized common agricultural policy grazing jeopardizes the protection of biodiversity and natura 2000 targeted species. *Anim. Conserv.* 25, 597–607.
- Körner, C., 2005. An introduction to the functional diversity of temperate forest trees. *For. Divers. Funct.: Temp. Boreal Syst. Springer* 13–37.
- Krajicek, J.E., Brinkman, K.A., Gingrich, S.F., 1961. Crown competition—a measure of density. *For. Sci.* 7, 35–42.
- Kuijper, D.P., Cromsigt, J.P., Jędrzejewska, B., Miścicki, S., Churski, M., Jędrzejewski, W., Kwieczlich, I., 2010. Bottom-up versus top-down control of tree regeneration in the Białowieża Primeval Forest, Poland. *J. Ecol.* 98, 888–899.
- Lagerås, P., 2007. The ecology of expansion and abandonment: medieval and post-medieval agriculture and settlement in a landscape perspective. *Riksanantikvarieämbetet*.
- Lenth, R., 2022. emmeans: estimated marginal means, aka least-squares means. R. Package Version 1 (7), 2 (In).
- Lindquist, B., 1938. Dalby Söderskog: en skånsk lövskog i forntid och nutid. *Acta Phytogeogr. Suec.* 10.
- Metera, E., Sakowski, T., Stoniewski, K., Romanowicz, B., 2010. Grazing as a tool to maintain biodiversity of grassland—a review. *Anim. Sci. Pap. Rep.* 28, 315–334.
- Meyfroidt, P., Rudel, T.K., Lambin, E.F., 2010. Forest transitions, trade, and the global displacement of land use. *Proc. Natl. Acad. Sci.* 107, 20917–20922.
- Milberg, P., Bergman, K.-O., Jonason, D., Karlsson, J., Westerberg, L., 2019. Land-use history influence the vegetation in coniferous production forests in southern Sweden. *For. Ecol. Manag.* 440, 23–30.
- Milberg, P., Christensen, K., 2024. Raunkjær's oaks: mortality and growth among old oaks in a Danish deer park. *Scand. J. For. Res.* 39, 421–425.
- Milberg, P., Tälle, M., Fogelfors, H., Westerberg, L., 2017. The biodiversity cost of reducing management intensity in species-rich grasslands: mowing annually vs. every third year. *Basic Appl. Ecol.* 22, 61–74.
- Milberg, P., Tälle, M., 2023. Maintaining an open landscape: comparison of management methods for semi-natural grasslands: a Swedish multi-site study. *Glob. Ecol. Conserv.* 48, e02721.
- Nilsson, S.G., Franzén, M., Jonsson, E., 2008. Long-term land-use changes and extinction of specialised butterflies. *Insect Conserv. Divers.* 1, 197–207.
- Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and “mesophication” of forests in the eastern United States. *BioScience* 58, 123–138.
- von Oheimb, G., Brunet, J., 2007. Dalby Söderskog revisited: long-term vegetation changes in a south Swedish deciduous forest. *Acta Oecologica* 31, 229–242.
- Oldén, A., Komonen, A., Tervonen, K., Halme, P., 2017. Grazing and abandonment determine different tree dynamics in wood-pastures. *Ambio* 46, 227–236.
- Palmer, S., Mitchell, R., Truscott, A.-M., Welch, D., 2004. Regeneration failure in Atlantic oakwoods: the roles of ungulate grazing and invertebrates. *For. Ecol. Manag.* 192, 251–265.
- Paulsen, J., Brunet, J., Cousins, S.A., Decocq, G., De Frenne, P., De Smedt, P., Hedwall, P.O., Lenoir, J., Liira, J., Lindgren, J., 2024. Patterns of local plant diversity and community saturation in deciduous forests in Europe. *J. Veg. Sci.* 35, e13318.
- Peet, R.K., Christensen, N.L., 1987. Competition and tree death. *Bioscience* 37, 586–595.
- Piovesan, G., Biondi, F., 2021. On tree longevity. *N. Phytol.* 231, 1318–1337.
- Pommerening, A., Meador, A.J.S., 2018. Tamm review: tree interactions between myth and reality. *For. Ecol. Manag.* 424, 164–176.
- Queiroz, C., Beilin, R., Folke, C., Lindborg, R., 2014. Farmland abandonment: threat or opportunity for biodiversity conservation? A global review. *Front. Ecol. Environ.* 12, 288–296.
- R Core Team, 2024. R: A Language and Environment for Statistical. R version 4.4.3, Vienna, Austria.
- Ramankutty, N., Heller, E., Rhemtulla, J., 2010. Prevailing myths about agricultural abandonment and forest regrowth in the United States. *Ann. Assoc. Am. Geogr.* 100, 502–512.
- Rey Benayas, J.M., Martins, A., Nicolau, J.M., Schulz, J.J., 2007. Abandonment of agricultural land: an overview of drivers and consequences. *CABI Rev.* 14.
- Sebek, P., Vodka, S., Bogusch, P., Pech, P., Tropek, R., Weiss, M., Zimova, K., Cizek, L., 2016. Open-grown trees as key habitats for arthropods in temperate woodlands: the diversity, composition, and conservation value of associated communities. *For. Ecol. Manag.* 380, 172–181.
- Silvestri, C., Bacchetta, L., Bellincontro, A., Cristofori, V., 2021. Advances in cultivar choice, hazelnut orchard management, and nut storage to enhance product quality and safety: an overview. *J. Sci. Food Agric.* 101, 27–43.
- Stoate, C., Baldi, A., Beja, P., Boatman, N., Herzon, I., Van Doorn, A., De Snoo, G., Rakosy, L., Ramwell, C., 2009. Ecological impacts of early 21st century agricultural change in Europe—a review. *J. Environ. Manag.* 91, 22–46.
- Svahn, W., Nordholm, B., 2001. Kinda kanal: vattenväg och insjövägar. Gullers.
- Szymkowiak, J., Bogdziewicz, M., Marino, S., Steele, M.A., 2024. Community-wide masting improves predator satiation in North American oaks. *For. Ecol. Manag.* 569, 122172.
- Tedersoo, L., Suvi, T., Larsson, E., Kõljalg, U., 2006. Diversity and community structure of ectomycorrhizal fungi in a wooded meadow. *Mycol. Res.* 110, 734–748.
- Veen, P., Jefferson, R., De Smidt, J., Van der Straaten, J., 2014. Grasslands in Europe: Of high nature value. BRILL.
- Vera, F., 2000. Grazing ecology and forest history. CABI Publishing. Oxon, UK.
- Vinogradovs, I., Nikodemus, O., Elferts, D., Brūmelis, G., 2018. Assessment of site-specific drivers of farmland abandonment in mosaic-type landscapes: a case study in Vidzeme, Latvia. *Agric., Ecosyst. Environ.* 253, 113–121.
- Wallraf, A., Wagner, S., 2019. Effects of initial plant density, interspecific competition, tending and age on the survival and quality of oak (*Quercus robur* L.) in young mixed stands in European Russia. *For. Ecol. Manag.* 446, 272–284.