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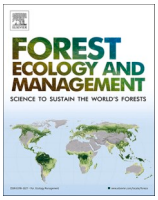

Mortality and growth rates in two populations of ancient oaks over a century

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ABSTRACT

Understanding the long-term performance of large trees is crucial for predicting forest responses to environmental change. We compared oak growth and mortality in two Scandinavian parks over two consecutive 50-year periods spanning nearly a century, with different temperatures and rainfall patterns. Tree diameter at breast height was measured, and survival status was recorded at three points in time. In Dyrehaven, a deer park with scattered and grouped trees, 641 oaks were followed, and annual mortality was 0.386 % per year (CI 0.333; 0.440). In Djurgården, a former deer park now partly covered by forest, 59 oaks were followed, and the annual mortality rate was 0.992 % (0.712; 1.374). Since 1930, growing seasons have lengthened by 9 days in Stockholm (Djurgården) and 15 days at Falsterbo (proxy for Dyrehaven), while precipitation variability has increased only in the latter. Mortality did not differ between time periods. Despite a longer growing period, annual basal area growth was greater in the first period than in the second. Our results show that despite mortality and slower individual growth rates over time, the standing biomass of large oaks in open parkland can continue to rise, underlining their importance as long-term carbon stores. Ensuring the long-term availability of large oaks in these parks will require increased recruitment efforts, forward-looking management, and adaptive conservation strategies.

1. Introduction

Large trees are important for carbon storage and forest resilience due to their disproportionate capacity to produce biomass compared to smaller trees (Stephenson et al., 2014; Norby et al., 2024), while also providing unique biological, historical, and aesthetic values (Gibbons et al., 2008, Lindenmayer et al., 2012, Lindenmayer and Laurance, 2017). Despite their importance, their long-term responses to environmental change remain poorly understood. Current views on old trees are conflicting, with one perspective asserting that they are generally in decline (Weiner and Thomas, 2001, Phillips et al., 2008, Kutsch et al., 2009), whereas others argue that this is not the case (e.g., Johnson and Abrams, 2009, Mencuccini et al., 2014, Stephenson et al., 2014, Piovesan and Biondi, 2021). This lack of consensus stems from limited biomass data for large trees (Calders et al., 2022) and the focus on forest stands rather than individual trees.

Climate change presents conflicting pressures on tree populations. Heat stress and extreme events like fires reduce growth and increase mortality (Anderegg et al., 2019, Andrus et al., 2021, Bauman et al., 2022, Hartmann et al., 2022, Yan et al., 2024, Jääskeläinen et al., 2025), whereas warmer conditions lengthen growing seasons in northern regions (Høgda et al., 2007; Linderholm et al., 2008; Karlsen et al., 2009; Aalto et al., 2022). In northern Europe, pedunculate oak (*Quercus robur* L.) represents an ideal species for studying these dynamics due to its exceptional longevity and size (Drobyshev and Niklasson, 2010; Skarpaas et al., 2017). These ancient oaks also create unique habitats for numerous associated species (Johansson et al., 2009; Thor et al., 2010; Bergman et al., 2012; Milberg et al., 2016; Larrieu et al., 2018; Prevedello et al., 2018; Franzén et al., 2025a), making them keystone species in northern European ecosystems.

Despite several attempts to estimate oak mortality, most studies have focused on younger trees (Drobyshev et al., 2008). The few studies of trees over 200 years old report an average mortality rate of 1.01 % per year, though with wide confidence intervals (Drobyshev et al., 2008). A recent 50-year study of large solitary Danish oaks found lower mortality at 0.43 % per year (95 % CI: 0.354–0.501) (Milberg and Christensen,

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2024). This pattern reflects broader trends among mature oaks: mortality decreases with tree age and size, and increases with forest density (Drobyshev et al., 2008, Rohner et al., 2012, Milberg and Christensen, 2024). Consequently, old oaks in open environments like forest edges or grazed areas may experience the lowest mortality rates of all (Milberg and Christensen, 2024).

Long-lived trees experience multiple climates over their centuries-long lifespans, making them natural experiments for understanding how climate change affects growth and carbon storage. In this context, dendrochronology is an essential tool (e.g., Scharnweber et al., 2011, Andersson et al., 2011; Cailleret et al., 2017), but the method has limitations, including the inability to account for trees lost from a population. Hence, cases where individual trees were mapped long ago allows partly different questions to be addressed (Rohner et al., 2012, Fassl et al., 2024, Finndin and Milberg, 2024, Milberg and Christensen, 2024, Milberg and Strandhag, 2024, Franzén et al., 2025b).

In the present study, we assessed oak growth and mortality over a full century using two contrasting populations: a large cohort in Dyrehaven (Copenhagen), a Danish deer park (Raunkiær, 1934; Milberg and Christensen, 2024), and a smaller cohort in Djurgården (Stockholm), a Swedish former park with higher tree density (Sernander et al., 1935). We tested five hypotheses:

1) Based on previous reports that oak mortality increases with forest density (Drobyshev et al., 2008, Rohner et al., 2012), we hypothesised that the mortality rate was lower in the more open park (Dyrehaven) compared to the one with denser tree cover (Djurgården).
2) As drought stress is generally considered an increasing threat to trees (Bréda et al., 2006; Allen et al., 2015), we hypothesised that mortality rates have increased in the last 50 years due to more variable rainfall under climate change.
3) Based on dendrochronological data showing that oak death can be preceded by extended growth decline (Andersson et al., 2011; Cailleret et al., 2017), we hypothesised that trees with slower growth in the first period (1933–1984) would experience higher mortality in the second period.
4) Greater growth in forest has been attributed to longer growing seasons (Henttonen et al., 2017), so we hypothesised that individual tree growth rates were higher in the second period compared with the first.
5) Total population biomass growth depends on the number of trees, their growth rate, and mortality. If mortality is low, as recently reported (Milberg and Christensen, 2024), growth of the survivors may compensate for tree loss, maintaining biomass accumulation. Based on a newly developed model for calculating total volume of oaks (Moeys et al., 2025), we tested the hypothesis that total volume would continue to accumulate despite tree mortality.

2. Materials and methods

2.1. Study sites

We studied oak populations at two contrasting Scandinavian sites (Fig. 1, Table 1), both with histories as royal deer parks (Birrell, 1992; Liddiard, 2019; Olsson, 2022) but with different current management regimes for two centuries. At both sites, deer populations had been fenced several hundred years ago, with high stocking densities resulting in open, savanna-like landscape with scattered trees or groups of trees.

Dyrehaven, Denmark (55°47'N 12°34'E) is an active deer park approximately 1100 ha in size, located north of Copenhagen. Established around 1670 (Flor, 1941), it maintains a mixed population of fallow, red, and sika deer that continuously graze and browse the landscape. This has created an open, savanna-like environment with scattered individual trees and groups of trees, mainly oaks. The site has

Table 1
Characteristics of the two oak cohorts included in the study.

	Dyrehaven	Djurgården
Trees mapped at start	641	
Trees measured at start	329	59
Average DBH cm (SD)	101.1 (32.3)	176.4 (16.8)
Max DBH cm	237.1	244.1
Min DBH cm	39.4	159.2

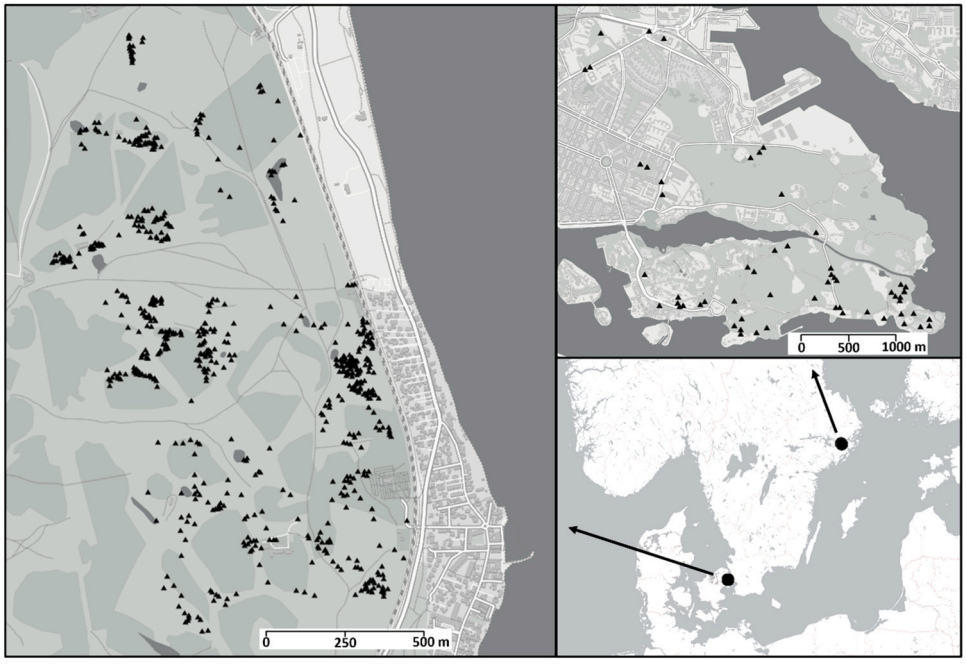

Fig. 1. The study areas are located north of Copenhagen in Denmark and Stockholm, Sweden. The black triangles represent the large oaks included in 1933 and 1930, respectively.

been exempted from forestry since 1844 (Flor, 1941). The park can be traced back to at least 1670, when an area of 1500 ha was fenced off and the farmers were evicted (Flor, 1941). It has been suggested that many of today's oaks were recruited in the years after the siege of Copenhagen (1658–60), when there was extensive felling of trees as well as culling of cattle and deer (Möller, 1938, Nielsen and Frederiksen, 1973). Dyrehaven was declared a recreational forest in 1844 when forestry was banned (Flor, 1941). Since then, some dead trees and trees deemed a safety hazard have been removed. Most oaks in the current study are naturally recruited, with the exception of 32 trees planted around 1830.

Today, it is a popular recreational area of approximately 1100 ha on the outskirts of Copenhagen. Oaks are a prominent feature of the Dyrehaven (Holten, 1998, Milberg and Christensen, 2024).

Djurgården, Sweden (59°20'N 18°05'E) is a former deer park located in central Stockholm and today a popular recreational area. Originally established in 1579 (Brusewitz and Ekman, 1995), deer were removed in 1828 (Tollstorp, 1844), allowing the site to develop into mixed forest with open areas. The site now supports denser tree populations than Dyrehaven, creating a more closed canopy environment in many areas, with oaks as an important feature.

2.2. Long-term surveys and measurement protocols

In 1933, Danish ecologist Christen Christensen Raunkiær (1860–1938), a pioneer of plant ecology, initiated this long-term study (Raunkiær, 1934). Raunkiær was specifically interested in understanding the growth rates of large oaks and believed that better age estimates could be calculated through repeated measurements over time. He mapped and measured large oaks across Dyrehaven, focusing on 17 oak groups containing healthy trees with regular trunk shapes suitable for accurate measurement. From 1796 large oaks identified, he mapped 668 individuals of which 641 were alive, and of which 329 were measured. Raunkiær measured tree circumference at varying heights (70–170 cm, preferably 150 cm) to avoid trunk irregularities, taking five measurements per tree and recording the average, maximum deviation, measurement height, and compass direction (Raunkiær, 1934). Trees were relocated and circumference re-measured in 1984 (Milberg and Christensen, 2024) and 2024 using the original measurement height, creating three census points spanning 91 years. For consistency with historical data, original measurement heights were maintained but with trees being measured twice per visit and averaged. Original bark marks from 1933, reinforced during the 1984 survey, could often be relocated in 2024 and were then reused. Trees were relatively easy to locate with the detailed maps, partly because of the spaciousness of the area. Trees that had died were most often identified as standing or downed trunks, sometimes by a stump (if the stem had been removed). In 2024, no trace could be found of three oaks that had died during the first period (1933–84).

In 1930, Swedish botanist Rutger Sernander (1866–1944), an influential professor of plant ecology and founder of the Swedish Society for Nature Conservation, surveyed Stockholm's large oaks as part of early urban conservation efforts (Sernander, 1926, Sernander et al., 1935). Sernander measured all trees > 500 cm girth in Djurgården, creating a cohort of 59 of the largest oaks present at the time (Sernander et al., 1935). He also measured numerous smaller oaks and other trees in Djurgården, but those data seem to have been lost (Andersson, 1975). He measured diameter at breast height (DBH) at 130 cm height for all trees > 500 cm circumference. Sernander specifically recommended regular re-measurement of these trees to track their long-term dynamics. Trees were re-surveyed in 1975 (Andersson, 1975) and 2025, spanning 95 years total. Tree height was also recorded in 2025. For consistency with historical data, original measurement protocols were maintained, with trees measured twice per visit and averaged.

2.3. Data analysis

2.3.1. Climate analysis

We analyzed growing period length and precipitation patterns using long-term weather station data:

- Dyrehaven: Falsterbo station (55°23'N, 12°49'E, since 1880) - selected to avoid the urban heat island effects for the nearest Danish station.
- Djurgården: Stockholm-Observatoriekullen (59°34'N, 18°05'E, since 1756)

Growing period was defined according to the Swedish Meteorological and Hydrological Institute (SMHI): the part of the year when mean daily temperatures consistently stay above 5°C (start criterion: first occurrence of 5 consecutive days with daily mean temperature ≥5°C after 1 March; end criterion: last occurrence of 5 consecutive days with daily mean temperature ≥5°C before 1 November). Climate variables were compared between the early period (1933–1984 for Dyrehaven, 1930–1975 for Djurgården) and recent period (1984–2024 and 1975–2025, respectively). To analyze differences in growing period between the two study periods, we conducted t-tests. To examine temporal changes in daily precipitation variability, we used Levene's test to assess variance homogeneity, followed by F-ratio variance tests for period-wise comparisons. Wilcoxon rank-sum tests were then used to evaluate monthly significance.

2.3.2. Tree cover

We delineated the two study areas encompassing veteran *Quercus robur* populations in Denmark (668 trees) and Sweden (59 trees). Study area boundaries were defined using minimum convex hull polygons calculated from the outermost tree positions. Land-cover classification data were sourced from the Copernicus Land Monitoring Service CLC+ Backbone product (30 m spatial resolution; Copernicus Land Monitoring Service, 2022), using the 2021 reference year dataset. Forest classes were defined according to CLC+ nomenclature (codes 311–313), with proportional coverage calculated as the sum of fractional forest pixels divided by total polygon area. According to these calculations, trees in Dyrehaven covered 1.6 % of the 936 ha area, the corresponding value for Djurgården was 21.8 % of 2079 ha.

2.3.3. Mortality calculations

Annual mortality rates were calculated using precise time intervals between fieldwork periods:

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

Where C is the number of living trees at the end of the period, N_0 is the original number of living trees, and y is the length of time between samplings. Time intervals were calculated as the difference in days between median sampling dates in each period to better adjust for actual sampling timing (e.g., Dyrehaven was sampled in August 1933, March 1984, and October 2024). Confidence intervals for mortality estimates were calculated by generating 1000 values using a bootstrapping approach based on a binomial distribution, with the 95 % confidence interval defined by the 2.5th and 97.5th percentiles (Arellano, 2019).

2.3.4. Growth calculations

Tree circumference data (including bark) were used to calculate basal area. Basal area increase (BAI) was calculated as the difference between two time points, divided by the number of growing seasons:

- Dyrehaven: 50 seasons (1933–1984), 41 seasons (1984–2024), 91 seasons total
- Djurgården: ~45 seasons (1930–1975), ~50 seasons (1975–2025), 95 seasons total

Annual BAI was analyzed using generalized linear models (normal distributions), fitted separately for each site. For Dyrehaven, where measuring height varied, measurement height was included as an independent variable along with "oak group" to adjust for spatial components. For both sites, tree identity was included to account for repeated measures (two growth periods per tree).

2.3.5. Growth/mortality analysis

To test whether trees with slower growth during the first period were more prone to mortality in the second period, we used generalized linear mixed models (GLMM) with binomial error distribution for each site. The response variable was mortality (dead/alive), and the explanatory variable was annual BAI during the first period (1933–1984 or 1930–1975). For Dyrehaven, oak group was included as a random effect to account for spatial structure.

2.3.6. Population and volume estimates

Dyrehaven includes open areas devoid of trees (including a golf course and areas used to produce winter fodder for deer). Most of Raunkiær's oaks are in the eastern part of Dyrehaven, occurring in an area of approximately 936 ha. Raunkiær measured 329 of the 1796 old oaks that were present in 1933, hence 18.3 % of the oaks (Raunkiær, 1934). From this percentage and 936 ha, we calculated (i) the number of oaks/ha, (ii) the basal area per hectare, and (iii) the total volume per hectare.

Oak volume was calculated using a formula developed for large solitary trees in central and northern Europe (Moeys et al., 2025). The models include both stem and branch volumes. We used a version that does not require the height of trees to be known.

$$\ln V = \beta_0 + \beta_1 * \ln DBH \quad (1)$$

Where V is the total volume (m^3), DBH is the tree diameter (m), and $\beta 0 + \beta 1$ are constants that can be selected according to geographic location. We chose "Lund", 44 km from Dyrehaven.

As the Djurgården data involved only very large oaks and a less well-defined area, it was not meaningful to express it per hectare. Total volumes for the trees that survived the full study were calculated using the geographic location "Linköping", 170 km from Djurgården (Fig. 1).

3. Results

3.1. Growing period and precipitation

The mean growing period increased significantly by 9.7 days for Stockholm ($p = 0.018$, Cohen's $d = 0.49$; Fig. 2a) and 15.0 days for Falsterbo ($p < 0.001$, Cohen's $d = 1.04$; Fig. 2c).

Daily precipitation variance exhibited contrasting patterns between locations (Fig. 2b and d). Falsterbo exhibited a significant overall increase in precipitation variance from 10.3 ± 0.6 mm² to 11.7 ± 0.8 mm² (+13.3 %, $p = 0.004$; Fig. 2d). June showed the largest

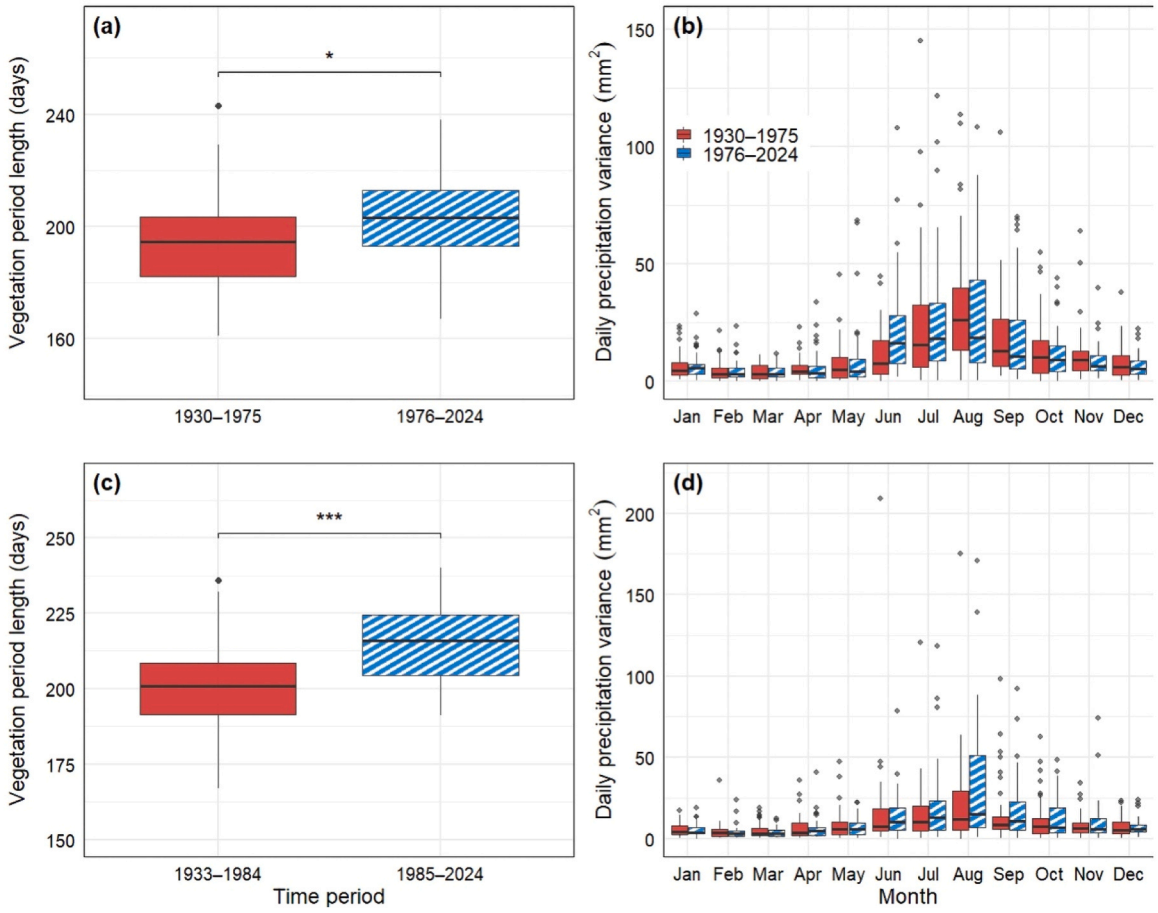

Fig. 2. Differences in growing period and daily precipitation variance for Stockholm (Djurgården) and Falsterbo (a proxy for Dyrehaven) during the two time periods. Box plots show the median (horizontal black line), interquartile range (IQR; coloured box spanning 25th to 75th percentiles), whiskers extending to the most extreme data points within 1.5 × IQR from the box edges, and outliers (black dots) beyond the whiskers. (a) Growing period length in Stockholm. Asterisk (*) indicates a statistically significant difference between periods ($p < 0.05$). (b) Monthly daily precipitation variance (mm²) in Stockholm. Each month shows paired box plots for the two time periods, revealing seasonal patterns in precipitation variability. (c) Growing period length in Falsterbo (Dyrehaven)). Three asterisks (***) indicate a highly significant difference between periods ($p < 0.001$). (d) Monthly daily precipitation variance (mm²) in Falsterbo.

increase (+85.4 %), while several autumn and winter months showed decreases (Fig. 2b). In contrast, the overall variance remained stable between periods (12.3 ± 0.7 mm^2 to 12.5 ± 0.7 mm^2, +1.3 %, $p = 0.894$) in Stockholm, despite substantial monthly variation (Fig. 2b). Both locations exhibited peak precipitation variance during the summer months (June–August) in the recent period, indicating enhanced convective precipitation activity during the growing season.

3.2. Mortality

The annual mortality rate over the entire study was 0.386 % (95 % CI = 0.329–0.440) for the open Dyrehaven and 0.992 % (0.712–1.374) for the more densely covered Djurgården.

Mortality rates did not differ between the two time periods at either site (Fig. 3), contrary to our second hypothesis.

Mortality in period 2 increased with decreasing growth rate in period 1 in both populations (Table 3), i.e. supporting our third hypothesis (Table 3)

On the basis of the mortality rate over the entire study period (1933–2024), 50 % of Raunkiærs oaks will remain by 2112 ($CI_{95\ \%}$ 2090–2143), i.e., after c. 180 years. The cohort of large oaks in Djurgården had a much shorter half-life, reaching 50 % mortality by the year 2000 ($CI_{95\ \%}$ 1980–2027), i.e. after 70 years (Table 1).

3.3. Growth rates

The annual BAI of individual trees that survived the full study did not increase over time, as hypothesised. Instead, it was significantly lower in the second period (Dyrehaven) or unaltered (Djurgården) (Table 2). Basal area growth significantly increased with increasing tree circumference in 1933 but decreased with increasing measuring height (Table 2).

3.4. Population estimates

Despite a declining population density, the sum of basal area of the survivors increased over time in Dyrehaven, as did the total volume estimate (Table 4). In Djurgården, however, basal area and total volume estimates shrank over time (Table 4).

4. Discussion

This study offers a rare century-long perspective on dynamics within oak populations under climate change, tracking individual growth and mortality across 91–95 years (during which deer browsing prevented recruitment at Dyrehaven). Such long-term datasets for large trees are exceptionally scarce (Larrieu et al., 2018), making our three-census approach particularly valuable for understanding how ancient trees respond to environmental change.

We tested five hypotheses examining climate-growth-mortality interactions, addressing critical questions about tree resilience under warming conditions, extreme weather impacts, and the carbon storage role of large trees (Anderegg et al., 2019). Our comparative analysis across two distinct time periods provides empirical evidence for how

Table 2
Parameter estimates with standard errors and p values for the GLMM of basal area increase per year.

Parameter	Estimate	Std. Error	p-value
DYREHAVEN			
Intercept	0.010	0.00030	< 0.001
2nd period (1984–2024)	−0.0024	0.00031	< 0.001
Tree circumference 1933	0.0051	0.00025	< 0.001
Measuring height	−0.00071	0.00022	0.0011
DJURGÅRDEN			
Intercept	0.00778	0.00088	< 0.001
2nd period (1975–2025)	−0.00044	0.00127	0.7272
Tree circumference 1930	0.00219	0.00065	0.000645

Table 3
Parameter estimates with standard errors and p values for the GLMM of mortality probability during the second period (1984–2024).

Parameter	Estimate	Std. Error	p value
DYREHAVEN			
Intercept	−1.8638	0.2127	< 0.001
Annual BAI 1933−1984	−0.5779	0.2729	0.0342
DJURGÅRDEN			
Intercept	−0.4890	0.3734	0.189
Annual BAI 1930−1975	−1.3274	0.5922	0.025

Table 4
Measured oaks, their basal area, and stem volume at the two sites at three points in time.

DYREHAVEN	1933	1984	2024
Number of oaks	1.92	1.73	1.48
Total basal area (m^2)	1.70	2.27	2.52
Total volume (m^3)	46.39	63.19	71.56
DJURGÅRDEN	1930	1975	2025
Number of oaks	59	39	23
Total basal area (m^2)	145.5	104.2	73.3
Total volume (m^3)	4021.1	2889.0	2053.7

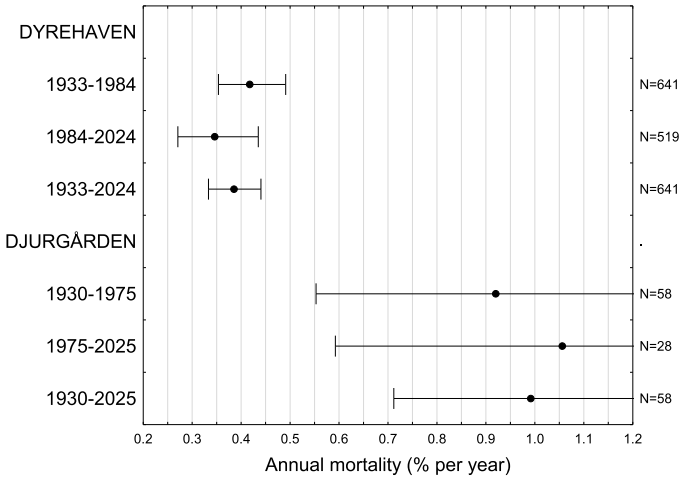

Fig. 3. Annual mortality (95 % CI) among the oaks of Dyrehaven, Denmark, and Djurgården, Sweden, during two time periods and the full study period.

century-scale environmental changes affect forest structure and carbon sequestration (Andrus et al., 2021; Hartmann et al., 2022).

Linking historical datasets from pioneering ecologists (Raunkiær, 1934, Sernander et al., 1935) with contemporary measurements reveals complex responses to climate warming. Despite significantly longer growing seasons at both sites, individual tree growth rates declined or remained unchanged rather than increased as expected. However, population-level volume continued accumulating in the open deer park environment, despite mortality and slower growth, demonstrating that large oaks can maintain their crucial role in carbon storage and ecosystem function even under changing climatic conditions.

4.1. Mortality

Based on previous reports of mortality increasing with forest density (Drobyshev et al., 2008, Rohner et al., 2012), we hypothesised that the more open Dyrehaven would have lower mortality than the more forest-like Djurgården. This was supported by the data as Djurgården had mortality in line with what has previously been reported for old or large oaks (Drobyshev et al., 2008), while Dyrehaven showed lower mortality consistent with a previous estimate for the first 50-year period (Milberg and Christensen, 2024), and from another semi-open environment in southern Sweden (Franzén et al., 2025b). The difference between the two populations was significant, yielding very different projections for the half-lives of the two populations. The more open environment in Dyrehaven, compared to Djurgården, might explain this substantial difference as *Quercus robur* is considered a moderately shade-tolerant species (e.g. Kuehne et al., 2014). It is also possible that exploitation and building activities in Djurgården might have contributed to the mortality. In contrast, Dyrehaven remains unaltered by such activities. Current models predicting rapid declines in large solitary oaks may overestimate their vulnerability, which aligns with evidence that large, older trees can persist far longer than often assumed (Piovesan and Biondi, 2021).

Our second hypothesis, that climate change characterized by greater variation in precipitation, increases mortality among large oaks, was not supported by the data. Mortality remained stable across both time periods at both sites, even as precipitation variance increased at one of the sites. The finding of stable mortality is surprising given the "oak decline" reported from northern Europe (Sonesson and Drobyshev, 2010, Gosling et al., 2024). If drought is the primary driver of oak mortality, increasing precipitation levels might explain the stable or even reduced mortality observed. Additionally, mortality has been reported to decrease with increasing tree size or age (Monserud and Sterba, 1999; Eid and Tuhus, 2001; Shifley et al., 2006; Luo and Chen, 2011; Thomas et al., 2013; Milberg and Christensen, 2024), suggesting that older, well-established populations may better endure periods of climatic stress.

Oak death can be preceded by decades-long decline in growth (Andersson et al., 2011, Cailleret et al., 2017), probably driven by changes in crown architecture and physiological changes (Rust and Roloff, 2002, 2004, Urban and Urban, 2024). Therefore, we hypothesised that trees with slower initial growth had a greater probability of dying later, an outcome supported by our data. This implies a protracted decline of individual trees (Andersson et al., 2011) potentially triggered by earlier extreme drought events, such as those in 1933 (both sites), 1947 (Dyrehaven), and 1955 (Djurgården). These findings underscore the importance of long-term monitoring to detect early indicators of stress in large oaks.

4.2. Growth rate

Our fourth hypothesis, that basal area growth increases under global warming due to an extended growing season, was not supported by the data. Instead, the trees that survived the full study period grew more slowly in the second period. This was noteworthy, as growth rates typically increase with tree size due to larger circumference (Johnson and Abrams, 2009), and both sites experienced approximately two weeks longer growing periods. This suggests that potential benefits from warming climate and extended growing seasons (e.g., Linderholm et al., 2008, Henttonen et al., 2017) were offset by other stressors, such as drought or competition, resulting in overall reduced growth rates.

Despite these declines, our estimates of oak growth rates in both Scandinavian populations align with previous reports from southern Sweden (Blomberg, Billqvist, 2003; Drobyshev and Niklasson, 2010; Andersson et al., 2011).

In temperate oaks (Andersson et al., 2011) and broadleaves in general (Cailleret et al., 2017), sustained growth suppression precedes death by one to three decades, which is in line with our finding that mortality risk in period 2 was higher in trees with lower growth rates in period 1. These findings together with the observed lower growth rates in period 2, may foreshadow an eventual rise in mortality. Hence, heightened vigilance is warranted for individuals now showing chronically low increment.

4.3. Population perspective

The combined effects of reduced individual growth and ongoing mortality had contrasting outcomes between sites. In the Dyrehaven population, basal area and total volume continued to increase, despite mortality and slower individual growth, indicating net biomass accumulation and supporting our fifth hypothesis. This aligns with studies challenging the notion of strict declines in older trees (Castagneri et al., 2013). Even with slower individual growth rates, large solitary oaks continue to contribute significantly to total basal area and volume.

In contrast, the Djurgården cohort of very large oaks experienced higher mortality that resulted in net decreases in basal area and total volume.

4.4. Future projections

Our mortality estimates (Fig. 3) suggest that the oak populations in Dyrehaven and Djurgården could experience halving within 180 and 70 years, respectively. This highlights the vulnerability of long-lived tree populations when regeneration is limited or absent. While such projections come with wide confidence intervals, they emphasize the importance of long-term demographic assessments and the challenges of managing slowly declining populations. Without sufficient recruitment or effective conservation measures, both the oaks and the species strongly associated with them face significant risk of local extinction (Johansson et al., 2013).

Despite decreasing tree numbers, large open-grown oaks continue to contribute substantially to ecosystem structure through their extensive branching architecture rather than trunk biomass alone. Large solitary oaks store much of their aboveground volume as branch biomass (Balboa-Murias et al., 2006, André et al. 2010, Moeys et al., 2025), underscoring the carbon sink potential of old trees. However, the protracted timescales involved—often exceeding 200 years—necessitate forward-looking forest management approaches, including promotion of new oak cohorts. Long-term monitoring and adaptive management strategies will be crucial for sustaining these culturally, economically, and ecologically valuable landscapes.

5. Conclusion

These century-scale data reveal that responses are context-dependent rather than universally positive or negative, underscoring the need for site-specific management. While both populations experienced longer growing seasons, individual growth rates paradoxically declined. However, population-level outcomes differed dramatically: the open Dyrehaven environment maintained low mortality that enabled continued biomass accumulation, while the Djurgården population experienced net losses due to higher mortality.

These contrasting outcomes underscore the critical importance of habitat openness for ancient oak survival and their continued role as carbon sinks under climate change. The projected half-lives of 180 years for Dyrehaven versus 70 years for Djurgården demonstrate how management context shapes population trajectories.

Effective conservation requires protecting existing trees while promoting new generations. For open sites like Dyrehaven, temporary fenced exclosures could protect saplings from browsing. In denser sites like Djurgården, targeted thinning around young oaks may reduce competition and mortality and accelerate development. Given the centuries-long timescales involved, implementing forward-looking management strategies is essential for sustaining these ecologically and culturally valuable landscapes.

CRediT authorship contribution statement

Per Milberg: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kurt Christensen:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Victor Johansson:** Writing – review & editing, Visualization, Software, Methodology, Formal analysis, Conceptualization. **Markus Franzén:** Writing – review & editing, Methodology, Investigation, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

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Data availability

Data is available in the Zenodo repository: 10.5281/zenodo.16945148

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