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Regeneration patterns of native and introduced oak species in Sweden: Investigating the roles of latitude, age, and environmental gradients

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ABSTRACT

Oak species worldwide face substantial challenges in natural recruitment, significantly affecting biodiversity and ecosystem services. Oaks are a keystone species in northern temperate zones, influencing ecosystem dynamics. This study analysed oak regeneration patterns from 29 oak stands (*Quercus* spp.) across southern Sweden up to the species' northern range limit. The study focused on two native species, *Q. robur* and *Q. petraea*, and one introduced species, *Q. rubra*, used in Swedish forestry. We aimed to evaluate whether and how oak regeneration was i) associated with latitude, ii) influenced by ground moisture and nitrogen levels, and iii) correlated with stand age, as well as to iv) compare regeneration rates among the species. Contrary to the hypothesis that oak regeneration should decline towards the range margin, our results did not indicate any latitudinal association. This finding raises the possibility of a future northward range expansion for oaks. We also observed that oak regeneration was positively correlated with stand age, while increasing nitrogen and ground moisture levels were inversely related to regeneration. The positive age-dependent effect on recruitment also indicates that species recruitment dynamics within forests may be modified via age-dependent effects within the tree community, with implications for forestry and conservation management. Notably, the natural regeneration of the introduced *Q. rubra* indicates its successful adaptation to Swedish climate and forests. This study represents Sweden's first large-scale analysis of oak regeneration across multiple oak species. Future research should prioritise longitudinal monitoring, particularly at the northern range limits, and further investigate the expansion of the potentially invasive *Q. rubra*.

1. Introduction

The decline in tree regeneration seriously impacts biodiversity and ecosystem services in temperate regions (Abrams, 2003; Schulze et al., 2014; Petersson et al., 2019). Potential contributors to this decline include climate change, modified land use and variation and change in biotic and abiotic factors that covary with latitude (Hampe, 2005; Zardi et al., 2015; Castro-Insua et al., 2018), and the effect may be further modified by moisture and nutrient availability (Aerts and Honnay, 2011) and species-specific traits (Castro et al., 2004; Svenning et al., 2015; Lutz et al., 2018; Qiu et al., 2021; Zhu et al., 2022). This multitude of influential factors calls for studies that evaluate environmental correlates of tree regeneration in different species and geographic regions. Seed production (fecundity) in trees increases with age or size, subsequently levelling off and decreasing as trees approach senescence (Qiu et al., 2021). This implies that forests of advanced age classes or certain species within these forests should exhibit enhanced recruitment owing to elevated forest-wide seed production.

Oaks (*Quercus* spp.) are particularly interesting, given their ecological importance and utilisation in forestry (Dey, 2014; Gustafsson et al., 2023). Oaks are foundational in temperate ecosystems, serving as critical habitats for endangered species (Ranius and Jansson, 2000; Bernicchia et al., 2008; Tallamy and Shropshire, 2009). However, shifts in land management and herbivore proliferation have adversely affected oak regeneration (Drobyshev et al., 2008; Petersson et al., 2019). While existing literature has delineated tree recruitment dynamics, studies examining how these dynamics differ between core and peripheral areas within species ranges and whether they change depending on the age structure of the trees are relatively rare, particularly in the context of climate change (Parmesan, 2006; Aitken et al., 2008). Yet, understanding recruitment dynamics at the range margins is imperative for predicting shifts in forest ecosystems due to climate change (Pecl et al.,

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2017). For oaks, these dynamics directly inform forestry management practices (López-Tirado et al., 2018) and serve as broader indicators of ecosystem resilience (Millar and Stephenson, 2015).

This study investigates oak regeneration across diverse Swedish oak forests spanning latitude 55° to 61°, the current northern range margin for native oaks. We define 'oak regeneration' as seedlings and saplings up to a height of one meter. Our study also compares two native oak species Pedunculate oak, *Quercus robur* L. and Sessile oak, *Q. petraea* (Matt.) Liebl, against the exotic northern red oak, *Q. rubra* L. since the 1940 s introduced to Sweden for forestry applications (Fahlvik and Johansson, 2021; Rauschendorfer et al., 2022). The objectives are fourfold: i) to evaluate how oak regeneration correlates with latitude; ii) to elucidate the influence of moisture and nitrogen on oak regeneration; iii) to assess the impact of forest stand age on regeneration; and iv) to contrast regeneration rates among the three oak species.

2. Material and methods

2.1. Study area

The study area encompasses southern Sweden (Fig. 1), a 130,000 km^2 region characterised by a mosaic of forests, farmland, and lakes. The area's climate varies, with mean annual precipitation ranging from 600 to 1000 mm and mean temperatures oscillating between −3°C in January and 16°C in July (reference period 1961–1990). Forests dominate the landscape, covering 85,000 km^2, of which 78,000 km^2 are productive (Nilsson et al., 2020). Oaks comprise approximately 1% of this productive (i.e., have an annual increment of 1 m^3 woody biomass per ha or more) forestland and are primarily composed of *Q. robur* L. and *Q. petraea* at their northern range limit. The regional tree composition is influenced by active forest management, which has favoured conifers like Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) over broadleaved species such as birch and oak (Sjörs, 1965; Nilsson et al., 2022).

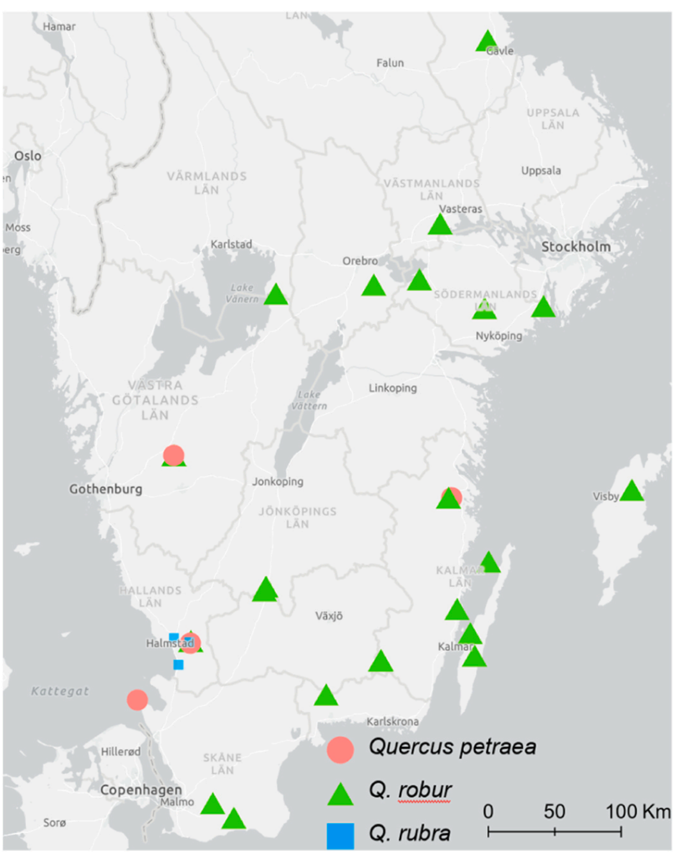

Fig. 1. Geographic distribution of the 29 oak stands sampled in Sweden in 2022. The oak species are differentiated as follows: *Q. rubra* represented by blue quadrats (3 stands), *Q. robur* by green triangles (24 stands), and *Q. petraea* by red dots (4 stands).

2.2. Data collection

In 2022, data were collected from 29 oak stands across the distribution range in Sweden (Fig. 1). These sites predominantly featured *Q. rubra* (3 stands), *Q. robur* (24 stands), and *Q. petraea* (4 stands). Within each stand, we selected 10 of the dominant trees (part of the upper canopy). The selection criteria focused on capturing the site-specific environmental variation and the size distribution of dominant oak trees. This involved choosing trees that represented a range of sizes (diameter at breast height) and positions within the stand to reflect the local environmental heterogeneity and forest structure adequately. We employed dendrochronological techniques to determine the mean age of mature trees within each examined stand. Increment cores, extracted at breast height (approximately 1.3 m above ground) using a 5.15 mm increment borer, were taken from the selected trees. These cores encompassed the tree rings from pith to bark. The tree-ring widths (TRW) were measured using a digital LINTAB positioning table connected to an Olympus stereomicroscope and TSAPWin Scientific software, following the procedures outlined by Bräker (2002). All TRW data series were cross-dated for missing rings and dating errors using COFECHA, as per Holmes (1983). Stand age was calculated as the average age of these ten oak trees per forest stand. The geographical midpoint latitude of each site was recorded. A structured grid of 40 vegetation plots measuring 0.5 m^2 was established for seedling enumeration, with four plots around each of the ten age-identified oaks at each site. Plots were systematically deployed at an 8-metre radial distance from each oak's trunk and aligned with the four cardinal directions (West, East, South, and North). Each plot acted as an independent sampling unit. When oak seedlings were present, they were numerically denoted as '1', and these were aggregated at the stand level. In selecting plots for our study, we aimed to include a representative sample of the understory vegetation typically associated with oak stands. While the vegetation in these plots generally did not exceed a height of 1 metre, this was not a strict selection criterion. Plots were systematically deployed at a 5-metre radial distance from each oak's trunk and aligned with the four cardinal directions. In cases where taller vegetation was encountered, such as shrubs, these were included as part of the natural understory composition of the oak stand. Simultaneously, the vascular plant flora within these plots was identified, and Ellenberg values for nitrogen and moisture were assigned to each plant species, adhering to established protocols (Dengler et al., 2023). Soil moisture was categorised from 0 (species strictly associated with arid conditions) to 10 (species requiring submersion for extended periods). Nitrogen availability was similarly classified, ranging from 0 (species tolerant of oligotrophic conditions) to 10 (species associated with environments high in phosphorus and nitrogen, such as landfills) (Dengler et al., 2023).

2.3. Statistical analyses

We calculated mean nitrogen, mean moisture, mean age, and oak seedling prevalence for one and each of the oak stands. A Generalised Linear Model (GLM) employing a Poisson distribution was constructed. This model examined the relationship between the frequency of oak seedlings and multiple predictor variables: latitude, moisture indicator value, nitrogen indicator value, stand age, and oak species. The statistical analysis were performed in the R programming environment (version 4.3.0) (R Core Team, 2023), utilising the 'glm' function for model fitting. The model's validity was subsequently assessed through a type-II Analysis of Deviance, facilitated by the Anova function from the car package (Fox et al., 2019).

3. Results

The GLM revealed that stand age and plant Ellenberg nitrogen and moisture levels were statistically significant predictors for oak regeneration (for nitrogen $\chi^2 = 35.59$, $p < 0.001$, $df = 1$ and $\chi^2 = 12.40$, $p < 0.001$, $df = 1$ and for moisture $\chi^2 = 5.63$, $p = 0.018$, $df = 1$). Stand age exhibited a strong positive correlation with seedling frequency, whereas moisture and nitrogen were inversely associated with regeneration (Fig. 2, Table 1). In contrast, latitude and oak species were not significantly correlated with oak recruitment ($\chi^2 = 1.79$, $p = 0.181$, $df = 1$ and $\chi^2 = 4.90$, $p = 0.086$, $df = 2$, Fig. 2, Table 1). Among the oak species, *Q. petraea* demonstrated the highest regeneration but had a limited sample size, while *Q. robur* and *Q. rubra* did not significantly differ in their regenerative capacities. Overall, the findings partially corroborate the initial hypotheses, underscoring the importance of stand age and certain environmental variables in oak regeneration while not supporting the presumed influence of latitude and interspecies variations.

Table 1
GLM Poisson regression model presents the coefficients, standard errors (SE), z-values, and associated p-values of the five predictors concerning the frequency of oak seedlings at each studied oak stand across Sweden. *Quercus petraea* is the reference category.

Predictor	Estimate	SE	z value	p-value
(Intercept)	11.789	3.519	3.350	<0.001
Age	0.011	0.002	5.813	<0.001
Moisture	-0.990	0.420	-2.358	0.018
Nitrogen	-0.328	0.094	-3.497	<0.001
Q. robur	0.357	0.187	1.905	0.056
Q. rubra	0.578	0.297	1.945	0.052
Latitude	-0.084	0.063	-1.329	0.183

4. Discussion

The current investigation provides important information on the regeneration patterns of oaks in southern Sweden, an area mainly characterised by coniferous taxa such as Norway spruce (*P. abies)* and Scots pine (*P. sylvestris*). Key determinants of oak seedling prevalence were stand age, nitrogen Ellenberg values, and moisture Ellenberg values, but not latitude or oak species (but with a trend of higher recruitment in *Q. petraea* forests). Surprisingly, oak recruitment did not decrease towards the range margin, in contrast to what could be expected, as abiotic conditions and biotic interactions generally are less favourable for recruitment at range margins (Hawkins et al., 2003). This deviation may point to the oak's inherent adaptive capacities in the face of climatic heterogeneity and merits further scrutiny into local adaptations at the range margin, including the role of plasticity in buffering against environmental variation (Eriksson, 1996; Forsman, 2015). This finding also points towards a future northward range expansion for oaks under current and future climate conditions. While our results indicate that oak recruitment did not decrease towards the species' northern range margin, this finding is only applicable to *Q. robur*, given the distribution and abundance of our study sites.

Contrary to expectations, oak regeneration decreased with increasing moisture and nitrogen Ellenberg values, conflicting with

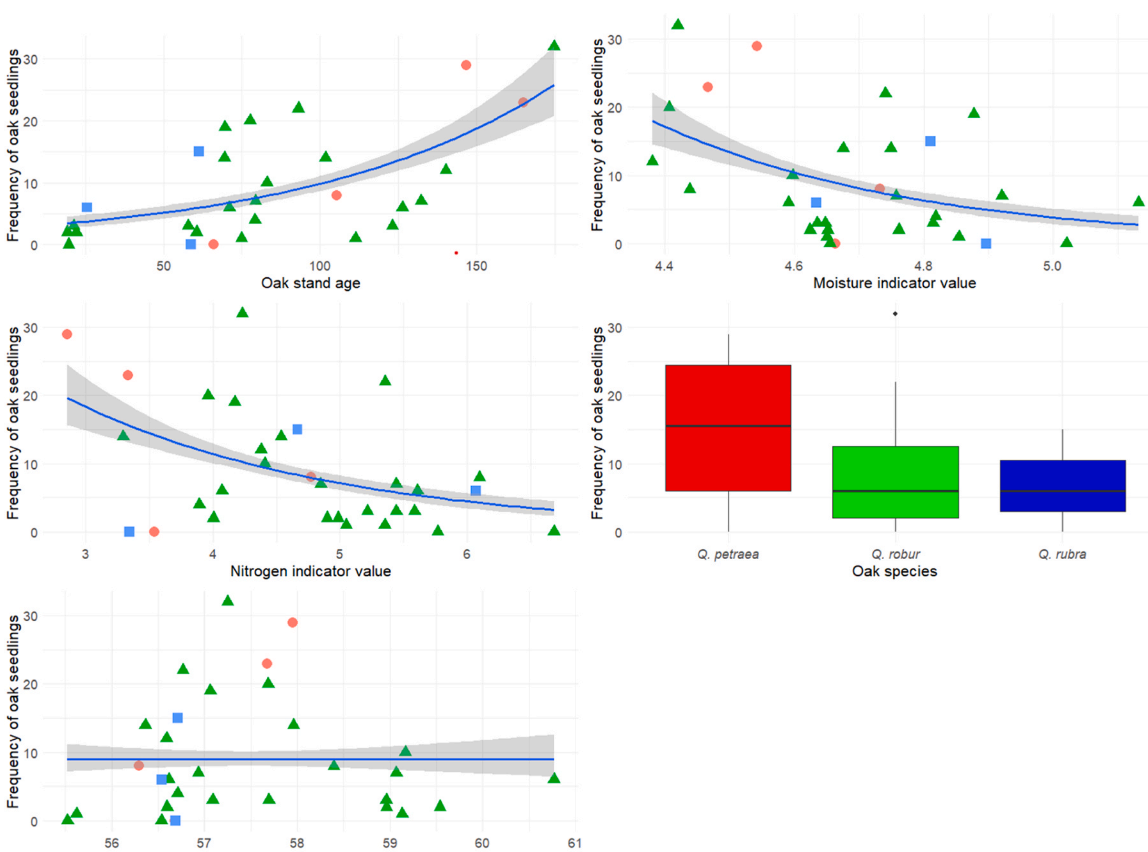

Fig. 2. Illustrating the relationship between five specific predictors and the frequency of oak seedlings, modelled using a generalised linear model (GLM) with a Poisson distribution. Panel A: Depicts the relationship between oak regeneration and stand age. Panel B: Depicts the relationship between oak regeneration and moisture. Panel C: Depicts the relationship between oak regeneration and nitrogen. Panel D: Presents a boxplot detailing the distribution of oak regeneration across different oak species. Panel E: Depicts the relationship between oak regeneration and latitude. Axes are consistently labelled across panels: the x-axis represents the respective predictor variables, and the y-axis represents the frequency of oak seedlings. The oak species are differentiated as follows: *Q. rubra* represented by blue quadrats (3 stands), *Q. robur* by green triangles (24 stands), and *Q. petraea* by red dots (4 stands).

established ecological theories which suggest that plant growth typically increases with increasing nitrogen access (Engelbrecht et al., 2007; Etzold et al., 2020). However, favourable abiotic and biotic conditions for recruitment often differ from those that impact growth and fecundity in later life stages of the trees (Bogdziewicz et al., 2017) and indeed, our present finding is congruent with prior research reporting adverse effects of excessive soil nutrients on oak regeneration (Harpole and Tilman, 2007; BassiriRad et al., 2015; Svensson et al., 2023). This suggests that nutrient-rich soils may be suboptimal for oak regeneration, highlighting the possible adverse effect on seedling recruitment of nutrient augmentation in forest management.

An important consideration in evaluating the factors influencing oak regeneration is the competition from other plant species, particularly in more fertile soils. This competition can significantly impact oak seedling establishment and growth, as other plants may outcompete oak seedlings for light, water, and nutrients. Kolb and Steiner (1990) highlight how shading and grassroot competition can affect the growth and biomass partitioning of northern red oak and yellow-poplar seedlings. Similarly, Jensen et al. (2011) have demonstrated the effects of above- and belowground competition from shrubs on the photosynthesis, transpiration, and growth of *Q. robur*. Further, Löf et al. (2021) discuss how fencing, which limits herbivore access, can influence seedling establishment during the reforestation of oak stands, indirectly pointing to the role of competitive interactions in natural regeneration processes. Other factors, such as light availability, are crucial for oak regeneration (Mölder et al., 2019). However, our forest stands, all within similar light conditions, were not explicitly analysed for this factor. Future studies should aim to include detailed light measurements in forest environments to further elucidate its impact on oak seedlings.

The age of the oak forest was identified as an important predictor of oak seedling abundance. This finding aligns with earlier studies showcasing age or size-dependent recruitment dynamics in trees (Petritan et al., 2007; McEwan et al., 2011). Specifically, older forest stands may offer a more hospitable environment for oak seedling establishment, including factors such as increased organic matter, age-dependent changes in the forest understory and soil-microbiota-fungi-tree interactions, thereby promoting natural regeneration processes (Davis et al., 1999; Petritan et al., 2007). The relationship between regeneration and average stand age might also be driven by age-dependent changes in tree fecundity, with older trees being more fecund (Herrera et al., 1994). Interestingly, two recent studies from Central Poland have elucidated external factors' influence on acorn production, particularly for *Q. rubra*. Gręda et al. (2022) demonstrated that acorn production in *Q. rubra* is more significantly impacted by weather conditions than forest site characteristics. Similarly, Woziwoda et al. (2023) reported high acorn size variability in introduced *Q. rubra*, indicating its effective spread potential in new ranges. While we cannot identify with certainty the underlying mechanisms, our present results demonstrate an age-dependent increase in oak stand regeneration.

While the impact of species identity barely missed the conventional threshold for statistical significance, likely attributable to a constrained sample size, all three species in the study had recruitment within their forests, and with a trend towards higher recruitment in *Q. petraea* forests. One interesting observation was the notably higher frequency of oak regeneration observed on the isolated island site Blå Jungfrun, situated in the Baltic Sea, devoid of regular ungulate and rodent populations. On the island, 32 out of 40 plots demonstrated oak regeneration, a significantly elevated proportion relative to other sites (Table S1). This lends credence to the hypothesis that the absence of common herbivores, such as deer and moose, as well as seed predators like squirrels, can considerably alleviate biotic constraints on seedling establishment and survival (Côté et al., 2004; Hanberry and Abrams, 2019). However, as our study primarily considered oaks below 1 m in height, the direct effect of ungulate browsing, which may keep saplings in a 'browsing trap', but not necessarily decrease their abundance, might be less pronounced (Kuijper et al., 2010). Conversely, the impact of rodent seed predation may be more relevant to seedling density than ungulate browsing in this context. Our results underscore the complex interactions between biotic factors and oak regeneration, particularly in the face of changing seed and seedling predator populations and climate change (Kaul et al., 2023).

We did not find any relationship between oak recruitment and latitude (towards the current range margin), contrary to what could be expected based on the literature that suggests less favourable climate conditions and biotic interactions as a species approaches its range margins (Zardi et al., 2015; Castro-Insua et al., 2018). This indicates that a wide variety of climate and biotic conditions are suitable for oak regeneration or that core-margin populations have local adaptations that sustain recruitment under varying environmental conditions. These results also point towards a potential future northern range expansion of oaks. Furthermore, the latitudinal gradient in our study area is primarily characterized by colder winter temperatures in the north, while mean July temperatures are relatively similar across the region (Andersson et al., 2021). Additionally, the photoperiod at northern latitudes is significantly longer, potentially extending the daily photosynthesis period for oak species in these areas (Bauerle et al., 2012). This could have implications for oak recruitment, as extended daylight hours during the growing season may partially offset the challenges posed by colder winter temperatures.

4.1. Conclusions and future directions

The present study advances our understanding of oak regeneration by revealing the importance of stand age for tree regeneration while also highlighting the roles of soil moisture and nitrogen content in modifying recruitment patterns of oak in southern Sweden's ecosystems. Interestingly, we found no changes in oak regeneration towards the range margin, indicating suitable environmental conditions even in the northernmost localities and the possibility of a future northward range expansion under current and future climate regimes. A noteworthy observation is the presence of *Q. rubra* regeneration in all three stands, raising ecological concerns regarding its invasive capabilities and subsequent impact on native species. This necessitates ongoing surveillance and potentially mitigative action (Vilà et al., 2011). Our findings are also consistent with the hypothesis that the absence of grazing ungulates, such as deer, could influence oak regeneration (Côté et al., 2004; Petersson et al., 2019), although this requires further investigation as Blå Jungfrun has the oldest oaks studied in our study, which could alternatively explain the observed regeneration patterns. Future endeavours should prioritise longitudinal analyses focused on oak regeneration at northern range limits and scrutinise the invasive propensity of *Q. rubra* within these ecosystems.

CRediT authorship contribution statement

Markus Franzén: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Marcus Hall:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Johanna Sunde:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Anders Forsman:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors, Markus Franzén, Marcus Hall, Johanna Sunde, and Anders Forsman, declare that there are no competing interests regarding the publication of this paper titled "Oak regeneration: a multi-species

analysis across latitude, age, and environmental factors." All authors are affiliated with the Department of Biology and Environmental Science, Linnaeus University, SE-391 82 Kalmar, Sweden. No financial, personal, or professional interests could be construed to have influenced the paper.

Data availability

Data will be made available on request.

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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.2024.121871.

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