Forest Ecology and Management 582 (2025) 122560

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Evaluating the performance of mainstream Swedish growth models in uneven-aged forestry systems

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ARTICLE INFO

Keywords:
Boreal forestry
Continuous cover forestry
Growth models
Heureka system
Model assessment
Uneven-aged forest

ABSTRACT

Continuous Cover Forestry (CCF) practices are increasingly recognized for their potential in climate change adaptation and biodiversity conservation. Selection cutting, a key method within CCF, presents unique challenges for forest growth modelling due to its complex structure and distinct growth dynamics. Current models, largely developed from data obtained from even-aged stands, may exhibit lower accuracy when applied to uneven-aged stands. This study assessed the short-term (i.e., up to 15 years) predictive accuracy of the Swedish Heureka Decision Support System for stands managed with selection cutting. It assessed growth models for tree recruitment, growth, and mortality using data from 27 CCF field experiments covering a broad latitudinal and environmental range across Sweden. A linear mixed-effects modelling approach was used to analyse differences between observations and model predictions. Findings revealed potential species-specific biases, with an average underestimation of volume growth by 2 m^3 ha^{-1} yr^{-1} after ten years of simulation, driven predominantly by underestimations in Norway spruce growth. While mortality predictions were generally accurate, they exhibited slight underestimation after recent cutting and overestimation otherwise. Ingrowth density predictions demonstrated minor biases, with spruce being underestimated and birch overestimated, but displayed high residual variability. Sensitivity analysis revealed correlations of residuals with stand variables, including site index, proportion of spruce, and stand basal area. The study faced limitations due to data scarcity and the short observation periods. Although most observed biases were not statistically significant, the findings underscore potential discrepancies when applying current Swedish models to selection cutting stands.

1. Introduction

In Nordic countries, the rotation forestry system, which involves creating even-aged and single-storied stands, remains the dominant form of forest management (Mason et al., 2022). This system is well-established, with extensive research backing its methods, and best practices are widely disseminated among forestry professionals. In contrast, alternative silvicultural methods are less common, with relatively limited guidelines and tools available for their implementation. However, interest in these methods is growing, driven by heightened public awareness of climate change and concerns regarding the ecological impact of forestry practices, as well as compliance with forest certification requirements, and adherence to national and international policies (Ekholm et al., 2023; Fahlvik et al., 2024; Puettmann et al., 2015). These alternative methods, collectively referred to as continuous cover forestry (CCF), encompass various approaches that avoid large clear-cuts and emphasize the multifunctional role of forests (Pommerening and Murphy, 2004). While there is no universal agreement on what qualifies as CCF, the single-tree and group selection methods are the most widely accepted practices (Mason et al., 2022). Lundqvist (2017) defines the selection system as a silvicultural system aimed at preserving a forest's full-storied and uneven-aged structure by periodic partial cutting of the overstory trees. Such forests are characterized by the dominance of shade-tolerant species and an inverted J-shaped diameter distribution, which persists largely unchanged as removed trees are replaced by smaller ones over time.

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https://doi.org/10.1016/j.foreco.2025.122560
Received 10 December 2024; Received in revised form 31 January 2025; Accepted 12 February 2025

The selection system, with its capacity to create structural diversity, is considered a viable method to emulate the natural dynamics of boreal forests (Drössler et al., 2015; Ekholm et al., 2023; Kuuluvainen et al., 2012), where small-scale disturbances and gap dynamics play an important role (Drössler et al., 2015; Kuuluvainen, 2009). This system is believed to better preserve late-successional species assemblages compared to even-aged management, enhance forest resilience to natural disturbances, and is more visually appealing to the public (Ekholm et al., 2023; Felton et al., 2024; Kuuluvainen et al., 2012). However, research on productivity and economic returns has yielded mixed results, hampered by a scarcity of empirical data from field experiments and uncertainties regarding the accuracy of growth models (Ekholm et al., 2023; Kuuluvainen et al., 2012; Lundqvist, 2017). Despite increasing societal pressure and the potential advantages of the selection system, its adoption in Nordic countries remains limited (Hertog et al., 2022; Mason et al., 2022). This reluctance is attributed, among other factors, to insufficient knowledge about the consequences of large-scale application and a lack of experience in managing this type of forest (Hertog et al., 2022; Mason et al., 2022; Puettmann et al., 2015).

Forest decision support systems (DSS) are computer-based tools that utilize models and analytical methods to assist in management planning and multi-objective analysis (Lämås et al., 2023). These systems provide valuable information on long-term yield potential, the large-area consequences of alternative forest management strategies, and play a crucial role in examining the effects of forest policy changes (Bergseng et al., 2014; Kurttila et al., 2014; Lämås et al., 2014). Extensively used by both state-owned and private forest enterprises, DSSs aid in planning, optimization, and updating forest inventories (Bergseng et al., 2014; Kurttila et al., 2014; Lämås et al., 2014). Beyond their practical applications in forest management, DSS also support academic research and teaching (Lämås et al., 2023). They facilitate studies comparing growth (Lundqvist, 2017; Ekholm et al., 2023), economic returns (Ekholm et al., 2023; Wikström, 2007), ecological (Ekholm et al., 2023; Felton et al., 2017) and social impacts (Eggers et al., 2018), and carbon balance (Lundmark et al., 2016) between management strategies, and are used in investigating the effects of forest conversion (Drössler et al., 2014; Fahlvik et al., 2024) and optimizing silvicultural practices (Pukkala et al., 2012).

The backbone of each forest DSS is a set of tree- and/or stand-level models. Consequently, the validity of analyses and research outcomes depends heavily on the accuracy of these models (Lämås et al., 2023). However, given the long history of rotation forestry in the Nordic countries, many models have been developed using data primarily from homogeneous, even-aged and single-species forests (Kuuluvainen et al., 2012). This may reduce their performance for the selection system, which involves more complex forest structures and distinct growth dynamics (Kuuluvainen et al., 2012).

Uneven-aged forests display more variable competition that largely affects tree growth (Bianchi et al., 2020a). The response to competition depends on tree species and size (Canham et al., 2006; Pukkala et al., 2013), species composition (Canham et al., 2006; Pukkala et al., 2013), and site potential (Pretzsch and Biber, 2010). Suppressed trees may respond to selection cutting with a delay (Koistinen and Valkonen, 1993; Metslaid et al., 2007; Myllymäki et al., 2024), and the peak of stand growth due to competition release appears later (Hynynen et al., 2019; Øyen et al., 2011; Valkonen et al., 2017) than in even-aged stands (Elfving, 2010). The growth recovery after treatment is further influenced by the size of the created openings (Hökkä and Mäkelä, 2014). Selection cutting also induces more pronounced changes in tree stem form, leading to inaccurate volume estimation when using functions based on homogeneous forests (Lundqvist et al., 2007). Additionally, selection cuttings may increase mortality in the remaining stand due to damages from harvesting (Myllymäki et al., 2024; Pretzsch et al., 2017).

In uneven-aged forests, ingrowth is essential to maintaining long-term production but tends to be highly variable (Ekholm et al., 2023; Lundqvist, 2017; Pukkala et al., 2009). Newly regenerated trees take decades to reach the ingrowth threshold, defined by a specific height or diameter, at which they are considered part of the main canopy or established stand (Eerikäinen et al., 2014; Ekholm et al., 2023; Lundqvist, 2017). The spatial distribution of regeneration is uneven and clustered (Drössler et al., 2015; Eerikäinen et al., 2007; Valkonen et al., 2017), influenced by variation in local conditions (Coates and Burton, 1997; Kuuluvainen, 1994), and characterized by high early mortality rates (Leemans, 1991; Lundqvist, 2017). Therefore, the amount of ingrowth is not directly related to current stand conditions and recent treatments but largely depends on historical legacies.

Determining site quality (i.e., the production potential) in selection forests is challenging. Site quality is described by site index (e.g., the expected height of the 100 thickest trees ha^{-1} at a predetermined age) (Skovsgaard and Vanclay, 2008) and together with age, are essential predictors in many empirical-based forest growth models (Elfving, 2010). However, these variables are not readily applicable to uneven-aged forests. Stand age is challenging to estimate in practice, and site index from dominant height is affected by the removal of dominant trees and difficulties in age estimation (Fagerberg et al., 2022; Pukkala et al., 2009). An alternative approach that avoids reliance on dominant height and age involves deriving the site index from site variables (e.g., climate, field vegetation, soil properties, etc.) (Hägglund and Lundmark, 1977). However, this method may inadequately reflect the actual site quality due to the changes in ground vegetation following canopy opening during harvest operations (Lundqvist, 2017).

The distinct characteristics of silvicultural rotation and selection systems, combined with the complexities of modelling uneven-aged stands, indicate that models developed for one system are unlikely to reliably represent the growth dynamics of the other (Bianchi et al., 2020a; Lundqvist, 2017). These discrepancies and the widespread use of DSSs underscore the need for thorough model evaluation. Studies have shown that models calibrated with even-aged forest data often exhibit biases when applied to selection systems. For instance, Lee et al. (2024) found that the Finnish MOTTI DSS overpredicted diameter and height growth in Norway spruce stands, with a shift to underprediction for larger trees. Bianchi et al. (2023) assessed two general, age-independent models and found substantial overestimation of Scots pine basal area growth, increasing with stand's annual increment, and variable results for Norway spruce. Similarly, studies conducted in Norway also showed biased results when applying models based on even-aged stands to the selection system (Maleki et al., 2022; Øyen et al., 2011). Ekholm et al. (2023) compared results on annual volume growth in the selection system from experimental studies and simulations using Finnish and Norwegian models, finding that simulations generally tend to overestimate growth rates.

In Sweden, the primary decision support system for forest management is the Heureka DSS developed by the Swedish University of Agricultural Sciences. It integrates forest development models (see 2.3 Heureka DSS), optimization techniques, multi-criteria decision analysis, and GIS tools to support large- and small-scale forestry planning (Lämås et al., 2023; Wikström et al., 2011). The performance of the basal area growth models implemented in the Heureka DSS has been examined using extensive datasets for even-aged monocultures (Fahlvik et al., 2014) and mixed-species forests (Aldea et al., 2023), and the results indicate a good agreement between observed and the predictions. However, only two studies have examined the performance for selection systems, both using limited data from southern Sweden (Drössler et al., 2015; Fagerberg et al., 2022). The empirical data in these studies covered growth periods of 8 and 28 years, respectively, during which the Heureka DSS was found to underestimate basal area growth in uneven-aged stands. Elfving (personal communication, October 29, 2023) investigated the accuracy of the Heureka ingrowth functions (Wikberg, 2004), showing lower than observed densities in both unthinned layered primeval forests and stands thinned from above. To the best of our knowledge, no studies have examined the accuracy of models for height growth or mortality for uneven-aged stands in

Sweden.

Considerable knowledge gaps remain regarding the application of Heureka DSS to uneven-aged stands. Therefore, this study aims to evaluate the short-term performance of height and basal area growth, mortality, and ingrowth models of the Heureka DSS for stands managed by selection cutting. The examination is based on data from field experiments distributed throughout Sweden. The study includes an assessment of the overall accuracy of the Heureka DSS as well as of its individual components for growth periods up to 15 years. In addition, a sensitivity analysis was made in an attempt to identify sources of the potential uncertainty and their impacts.

2. Material and methods

2.1. Study material

Data for evaluation of the predictive performance of the Heureka DSS, comprising 23,456 tree-level observations, were obtained from 73 experimental plots located at 27 sites across Sweden, covering a latitudinal range from 56° to 67° N, though most sites were located up to 64° N (Fig. 1). Plot selection was based on the classification by Goude et al. (2022), which considered the experiments' objectives and the treatments applied. The plots varied in size from 0.04 to 0.52 ha and exhibited differences in stand density, species composition, average tree size, site potential, and mean age (Table 1). Overall, Norway spruce (*Picea abies* (L.) Karst., henceforth spruce) accounted for 62 % of the total tree-level basal area in the dataset, followed by Scots pine (*Pinus sylvestris* L., henceforth pine) at 31 % and birch species (*Betula pendula* Roth and *Betula pubescens* Ehrh., henceforth birch) at 4 %. Other species, accounting collectively for 3 % of the dataset, were excluded from the analysis. Measurements were conducted 2–4 times, with intervals ranging from 4 to 7 years, and in some cases extending from 8 up to 13 years. The duration of all but one experiment was between the years 2000 and 2023, with data being well-balanced within this timeframe. In terms of structural characteristics, the plots showed two primary patterns in diameter at breast height (DBH) distribution: 56 plots displayed the inverted J-shaped distribution typical of full-storied forests, while 17 plots showed a bimodal distribution, indicating a transition from even-aged to uneven-aged stands (Figs A1-A2). Preliminary analysis revealed no statistically significant differences in predictive accuracy between full-storied stands and transitional stands, though predictions were slightly more accurate for the latter. Excluding transitional stands from the analysis did not substantially alter observed biases (Fig. A5). As both structure types represent potential applications for models designed for continuous cover forestry, and to maintain statistical power given the limited data, the plots were pooled for analysis.

The experimental plots differed in terms of the treatments performed. In 40 plots, selection cutting was applied at the beginning of the experiment, 25 plots underwent selection cutting during the study period, while the remaining 17 plots had not been treated for at least 5 years prior to the experiment's commencement. Selection cutting intensities ranged from 14 % to 62 % of the basal area removed. Due to difficulties in distinguishing between natural mortality and harvesting in the dataset, plots that were harvested during the experiment were excluded from the mortality analysis. In one case, only the last revision was excluded. Additionally, preliminary analysis revealed elevated mortality rates in two other plots, with losses exceeding 25 % of the total stand basal area, which suggested unrecorded selective cutting or major disturbance. These revisions were likewise excluded. This resulted in a final dataset of 57 plots at 19 sites (19,133 tree-level observations) for the mortality assessment (Fig. 1). For other analyses, the entire dataset was utilized, and all trees not marked as alive were collectively considered removed, regardless of the cause of mortality.

A detailed description of the experiments can be found in the compilation by Goude et al. (2022) and on the metadata base for forest field trials (www.silvaboreal.com). Graphs illustrating the DBH and height distribution for each experimental plot are provided in Supplementary material A.

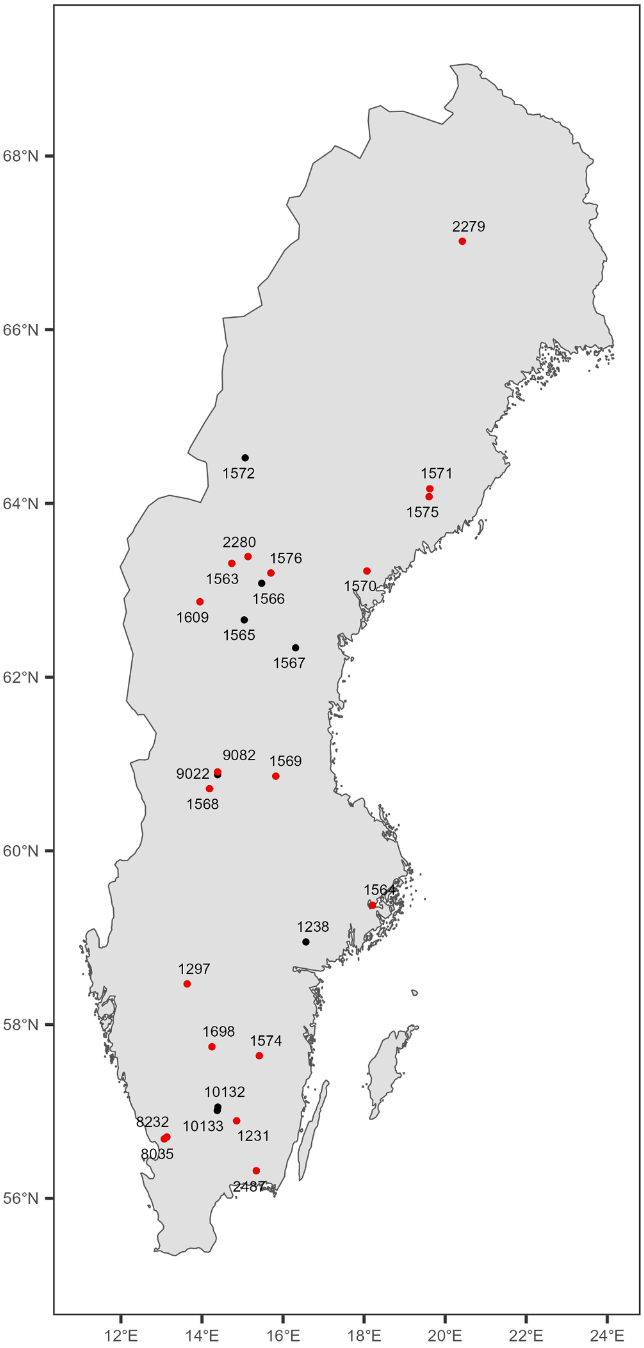

Fig. 1. Locations of experimental sites in Sweden used for model assessment, with identification numbers corresponding to those on www.silvaboreal.com. All points represent sites included in evaluating basal area, height, and ingrowth models, while points highlighted in red indicate sites included in the assessment of mortality models.

2.2. Data management

Given that height measurements were only available for sample trees in the dataset, a nonlinear mixed-effects modelling approach was employed to estimate the height for the remaining trees. This step was essential, as the simulation software required height data for all trees. Additionally, the sampling procedure (Karlsson, 2003) resulted in an overrepresentation of the largest trees, while small, temporarily

Table 1
Characteristics of the residual stand at the time of the first revision, along with ingrowth density and volume increment observed during the subsequent first between-revision period.

Variable	Mean	Std Dev.	Minimum	Maximum
Density, trees ha^{-1}	751	286	200	1520
Basal area, $m^2\ ha^{-1}$	21.2	5.8	4.5	34.0
Quadratic mean diameter, cm	19.9	5.9	10.6	42.6
Proportion of spruce[a], %	63.7	30.9	1.9	100.0
Stand mean age[b], years	108.9	25.1	78.0	197.0
Site index[c], m	22.8	4.0	13.0	33.0
Volume increment, $m^3\ ha^{-1}\ year^{-1}$	5.6	2.8	0.9	17.0
Ingrowth density, trees ha^{-1}	96	83	8	329

[a] The ratio of the total tree-level spruce basal area to the total basal area in each plot.

[b] The arithmetic mean age derived from 10 trees of the dominant species by counting annual growth rings on the stumps or wood cores, accounting for the time required to reach the measurement height.

[c] The expected height of the 100 dominant trees ha^{-1} at age 100 estimated from site variables (Hägglund and Lundmark, 2004); pine SI values were converted to spruce SI (Leijon, 1979).

numbered trees (as described below) were not included in the sample.

Models based on the height-diameter function by Näslund (1936) were fitted for each tree species (or species groups), with random effects specified to reflect the hierarchical structure of the data. The models were applied using predicted random effects. In cases where random effect predictions for the lowest level of grouping were not available, predictions for higher grouping levels were utilized. The models were fitted using the R statistical software (R Core Team, 2024) and the "nlme" package (Pinheiro et al., 2023). The detailed modelling procedure is provided in Supplementary material B.

In field experiments, it has been a standard practice to assign temporary numbers to trees below a specified ingrowth threshold during inventory. In these instances, trees did not receive permanent tags with numbers. Instead, the temporary numbers were solely used for recording measurements in the database. Consequently, the growth of smaller trees often has not been possible to track between revisions. To address this issue, such trees were manually matched using the following assumptions: 1) trees are matched in descending order of diameters, 2) a tree in a subsequent revision must be at least the same size as in the previous revision, and 3) trees that cannot be matched according to assumptions 1) and 2) are considered dead. To limit potential bias on stand growth, this procedure was applied only to trees below 10 cm DBH, which constituted 1.8 % of observations. Experimental plots or revisions where this procedure could not be applied were excluded.

Due to measurement errors and wood shrinkage due to drying following tree death, some diameters of permanently numbered trees appeared to decrease between revisions. Such discrepancies could result in an underestimation of observed mortality. To address this issue, smaller recorded diameters were replaced with the values measured in the previous revision. This correction was applied to 1.4 % of observations.

In the Heureka DSS, the ingrowth threshold is set at 4 cm DBH (Wikberg, 2004). Since temporarily numbered trees were measured in 1 cm classes, in this study the ingrowth threshold was adjusted to 4.5 cm, representing the boundary between the 4 cm and 5 cm classes. Consequently, the correction of numbers and diameters, along with all subsequent analyses, excluded trees with diameters smaller than 4.5 cm.

2.3. Heureka DSS

The Heureka system consists of four software components, three of which – StandWise, RegWise, and PlanWise – utilize the same forest development models to predict stand growth at various spatial scales (Lämås et al., 2023; Wikström et al., 2011). This set of models includes single-tree and stand basal area growth models working in tandem (Elfving, 2010), top-height development functions (Elfving, 2003; Elfving and Kiviste, 1997; Eriksson et al., 1997), and four-step ingrowth models (Wikberg, 2004). From the available mortality models, the two most recent were selected for assessment and are henceforth referred to as "Elfving" (Elfving, 2014) and "SNS" (Siipilehto et al., 2020), following Heureka's naming convention. Basal area growth is adjusted using thinning response functions (Elfving, 2010). Single-tree age, an essential variable for most models, can be estimated from variables such as tree diameter, mean stand age, and site index using a set of empirical models developed for different forest structure types (Elfving, 2010). Although the growth models predict the development of individual trees, the lowest unit in Heureka DSS is the stand or sample plot (Wikström et al., 2011).

Simulations were performed using the Heureka PlanWise software, a tool designed for simulations and planning at scales larger than individual stands (Lämås et al., 2023; Wikström et al., 2011). Two methods were employed: (M1) a regular simulation at 5-year intervals (Lämås et al., 2023), and (M2) a model validation procedure (Fahlvik et al., 2014; Heureka Wiki, 2011). The key difference is that the second method disables mortality models, allowing users to manually specify which trees were removed or had died, while adjusting simulation intervals to reflect actual measurement periods via nonlinear interpolation. For M1, harvested trees were manually removed before the start of the simulation, and to activate the thinning response functions within the simulator, the thinning intensity for selectively cut plots was set to 0.01 % of basal area removal. This prevented the system from selecting harvested trees through its algorithms, while retaining the information about selective cutting having occurred. Default settings were used for all other parameters, except that in M2, the management system was set to "Uneven-aged (CCF)", while in M1, it was changed to "Unmanaged", and the mortality model was configured as either "Elfving" or "SNS". A graphical representation of the simulation methods used is presented in Fig. 2.

Method M2 was employed for evaluating basal area, height, and ingrowth models, whereas method M1 was used for assessing mortality models. Given that measurement intervals were seldom exactly 5 years, predicted cumulative mortality volume loss after t years since the first revision (CM_t) was interpolated linearly using the following formula:

$$CM_t = \begin{cases} \sum_{n=1}^{N} M_{5n} + \frac{1}{5} M_{5(n+1)} \times (t - 5N) & (t > 5) \\ \frac{1}{5} M_{5(n=1)} \times t & (t \leq 5) \end{cases} \tag{1}$$

where N represents the number of 5-year simulation periods and $5N < t < 5(N + 1)$. M_{5n} denotes the stand volume loss due to mortality during the n-th simulation period.

2.4. Results analysis

The analysis of results was conducted by comparing observed and predicted values. The differences were computed as follows:

$$\text{Tree} - \text{level residuals}: \quad RT_{ijkl} = y_{ijkl} - \hat{y}_{ijkl} \tag{2}$$

$$\text{Stand} - \text{level residuals}: \quad RS_{jkl} = y_{jkl} - \hat{y}_{jkl} \tag{3}$$

where y and $\hat{y}$ are observed and predicted values, respectively, for tree i in plot j, and site k at time l, and for plot j in site k at time l. Eq. 2 was used to analyse tree-level variables such as DBH, height, and volume, whereas Eq. 3 was applied to stand-level variables, including annual stand volume increment, mortality volume loss, and ingrowth density. Table 2 provides an overview of the tree- and stand-level variables included in the analysis and the associated models.

Due to variations in area, species composition, density, and growth conditions among experimental plots, the arithmetic mean could be biased towards plots with more observations or extreme values. To

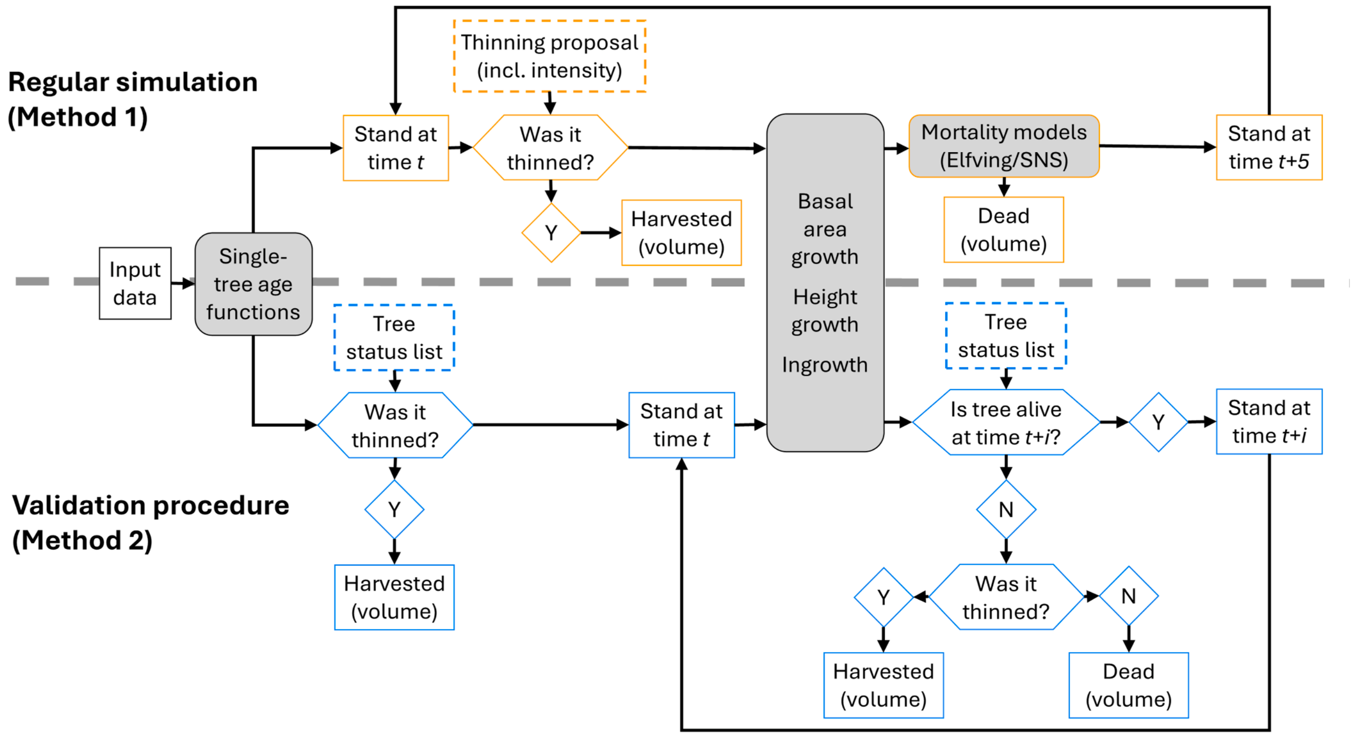

Fig. 2. Graphical representation of the simulation methods used in the study. Panels with a grey background represent models implemented in the Heureka DSS. Elements exclusive to the regular simulation (Method 1) are outlined in orange, while those specific to the validation procedure (Method 2) are outlined in blue. Shared elements are marked with a black outline. Dashed outlines denote additional data provided for the simulation. The letter *i* in the expression $t + i$ signifies that growth was nonlinearly interpolated to match the actual time between revisions.

Table 2
Output variables generated in Heureka DSS simulations, their units, associated models, and corresponding references to the literature.

Output variable	Unit	Model	References
Tree-level variables			
Diameter at breast height (DBH)	cm	Single-tree and stand basal area growth models (tandem)	Elfving, (2010)
Height	dm	Top-height development models	Elfving, (2003); Elfving and Kiviste, (1997); Eriksson et al., (1997)
Volume	dm^3	Derived from height and DBH using volume functions	Elfving, (2010)
Stand-level variables			
Volume increment	$m^3\ ha^{-1}\ year^{-1}$	(Derived from single-tree volumes)	
Volume loss	$m^3\ ha^{-1}$	Mortality models	Elfving, (2014); Siipilehto et al., (2020)
Ingrowth density	trees ha^{-1}	Ingrowth models	Wikberg, (2004)
Ingrowth mean DBH	cm	Ingrowth models	Wikberg, (2004)
Ingrowth mean height	dm	Ingrowth models	Wikberg, (2004)

isolate the overall mean difference from site-specific effects, linear mixed-effects models were employed. For each combination of variable, species, size class, and simulation duration (denoted thereafter as group *g*), an intercept-only model was fitted (e.g., a model for the height difference of Norway spruce with a DBH of 10–15 cm after 10 years of simulation). The fixed intercept in this model represented the mean value of the difference, while the estimated standard error of the intercept indicated the variability within that group. The models were fitted using the "nlme" package (Pinheiro et al., 2023), and were specified in the following forms:

$$RT_{ijkg} = \beta_{0g} + b_{kg} + b_{jkg} + + \varepsilon_{ijkg} \tag{4}$$

$$RS_{jkg} = \beta_{0g} + b_{kg} + \varepsilon_{jkg} \tag{5}$$

Where β_{0g} is a fixed intercept for group *g*, RT_{ijkg} and RS_{jkg} are the residuals for tree *i* in plot *j*, site *k* and group *g* (Eq. 2), and for plot *j* in site *k* and group *g* (Eq. 3), respectively, b_{kg} and b_{jkg} are corresponding random components, and ε_{ijkg} and ε_{jkg} are residual error terms. Note that the time *l*, a grouping level present in Eqs. 2 and 3, was not included explicitly as it is incorporated into group *g*.

P-values for the fixed intercepts were used to assess whether the mean difference for each group significantly deviated from zero. To account for multiple comparisons, the base significance threshold of 0.05 was adjusted using the Holm-Bonferroni method (Holm, 1979). Detailed tables containing model estimates, p-values, and adjusted significance thresholds are provided in Supplementary material C.

2.5. Sensitivity analysis

To detect potential trends in the residuals, the results were plotted against several stand and tree variables, including the basal area of larger trees, the basal area of living trees, the proportion of spruce, time since selection cutting, and site index. Trends in the residuals were also examined over time to exclude the potential influence of annual weather variations.

The Heureka DSS models are largely based on data from the Swedish National Forest Inventory, which uses measurement plots of 0.03 ha (Elfving, 2010). In contrast, the experimental plots used in this study range from 0.04 to 0.52 ha. Given the diverse structure and uneven tree distribution in uneven-aged stands, aggregating data from larger plots may obscure spatial differences, particularly in terms of competition, potentially increasing bias in model predictions. To investigate this hypothesis, the experimental plots at two locations (see Lundqvist et al., 2007), where tree coordinates were available, were divided into five 10 m radius (0.03 ha) subplots (Fig. D20). The average predictions from the subplots treated separately were compared to those from the aggregated subplots.

Furthermore, using the same subplots, the impact of potential errors in determining the average stand age on predictions was analysed. This was done by randomly altering the average age by ± 20 and ± 40 years on four out of five subplots and comparing the outcomes with simulations using the unaltered stand age. Results of sensitivity analysis are available in Supplementary material D.

3. Results

3.1. Stand volume increment

The simulated stand volume increment was consistently lower than the measured values in uneven-aged stands across all simulation periods, with the magnitude of this bias increasing during the initial two simulation periods (Fig. 3). After 10 years of simulation, the underestimation reached its peak, with the simulated stand volume increment being, on average, 1.96 m^3 ha^{-1} $year^{-1}$ ($p = 0.013$) lower than the observed values (Table C1). Factors such as higher stand basal area and higher site fertility were associated with a more pronounced underestimation of stand volume increment (Figs D1, D3), while a slight reduction in bias was observed with an increasing proportion of spruce in the stand (Fig. D2). The time since the last thinning did not have a substantial influence on the residuals (Fig. D4).

3.2. Tree growth

Norway spruce, the most abundant species in the dataset, showed the most pronounced trends in growth prediction residuals for DBH, height, and volume with increasing tree size and simulation length. DBH and volume were notably underestimated in larger size classes, with peak DBH biases of 0.54 cm, 2.44 cm, and 2.95 cm (Fig. 4, panels a-c), and volume biases of 53 dm^3 , 216 dm^3 , and 242 dm^3 per tree (Fig. 4, panels g-i) after 5, 10, and 15 years of simulation, respectively. Height growth was consistently underestimated across nearly all size classes, with peak residuals of 3.54 dm, 10.48 dm, and 12.80 dm for the same simulation periods (Fig. 4, panels d-f). Height growth residuals also showed a slight arcuate trend after 10 and 15 years of simulation, with a greater bias for medium-sized trees compared to small and large trees. DBH and height underestimation was consistent across stand basal area values (Fig. D5, panels a-b), but both DBH and height biases decreased with the higher proportion of spruce (Fig. D7, panels a-b). In contrast, underestimation increased with higher site fertility for DBH, height, and volume growth (Fig. D9).

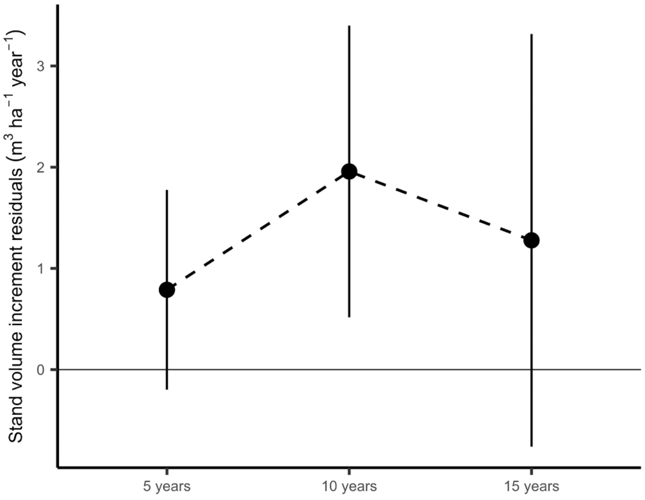

Fig. 3. Average differences between observed and predicted stand annual volume increments (m^3 ha^{-1} $year^{-1}$) across simulation lengths (years). Points represent the fixed intercept estimates for each simulation length, with lines indicating ± 2 standard errors. These estimates were derived from intercept-only linear mixed effects models with sites included as a random component.

Scots pine exhibited less consistent trends compared to spruce. DBH growth for trees under 35 cm was slightly overestimated after 10 and 15 years of simulation (Fig. 4, panels b-c), while height growth was generally underestimated and showed high variability (Fig. 4, panels d-f). DBH residuals were negatively correlated with stand basal area, shifting from slight underestimation in low basal areas stands to overestimation in high basal areas stands (Fig. D5, panel a). Height underestimation increased in denser stands (Fig. D5, panel b) and with the higher proportion of spruce (Fig. D7, panel b). Site fertility increased DBH overestimation but did not affect height predictions (Fig. D9, panels a-b).

Birch showed slight DBH underestimation after 5 and 10 years of simulation, although residuals were near zero after 15 years (Fig. 4, panels a-c). Volume followed a similar pattern, with slightly positive residuals after 5 and 10 years, turning somewhat negative after 15 years (Fig. 4, panels g-i). Height growth was slightly overestimated after 10 and 15 years, with peak residuals of −9.32 dm and −15.16 dm (Fig. 4, panels e-f). DBH residuals were negatively correlated with stand basal area (Fig. D5, panel a), but no clear trends were observed for height residuals (Fig. D5, panel b). Similar to spruce, underestimation of DBH growth decreased with higher spruce proportion, although the effect was less pronounced (Fig. D7, panel a). Site fertility had no clear impact on DBH, height, or volume growth residuals (Fig. D9).

Across all species, no consistent trends were observed in prediction residuals relative to the basal area of larger trees, indicating that this variable was adequately accounted for in the model (Fig. D6). Likewise, the timing of thinning had no substantial impact on residuals for any species (Fig. D8). Despite some notable trends, particularly for Norway spruce, statistical analysis showed that most of these biases were not statistically significant (Table C5).

3.3. Ingrowth

Spruce ingrowth density was underestimated by an average of 21 trees ha^{-1} , while birch density was overestimated by 6 trees ha^{-1} (Fig. 5, panel a), with the latter being statistically significant (Table C4). DBH was slightly underestimated for both spruce and birch by 0.29 cm and 0.27 cm, respectively (Fig. 5, panel b), while height showed no major bias (Fig. 5, panel c). Pine ingrowth density and DBH were predicted without bias, though height was overestimated (Fig. 5, panels a-c). However, pine regeneration was sparse, resulting in limited data for this species. Stand basal area had no substantial effect on density predictions but was negatively correlated with birch height and DBH residuals, as well as slightly negatively correlated with spruce DBH residuals (Fig. D10, panels a-c). Spruce ingrowth density was more underestimated in stands with a lower proportion of spruce, though this was not observed for birch and pine, and little effect was seen on DBH and height residuals (Fig. D11, panels a-c). Spruce ingrowth density was slightly more underestimated on more fertile sites, whereas site fertility had no effect on birch and pine (Fig. D13, panel a). DBH underestimation for spruce and birch decreased with increasing site fertility, eventually shifting to overestimation, though site index had little effect on height residuals (Fig. D13, panels b-c). Timing of thinning had minimal impact on the density of ingrowth and spruce height and DBH but did influence the bias in height and DBH predictions for birch (Fig. D12, panels a-c).

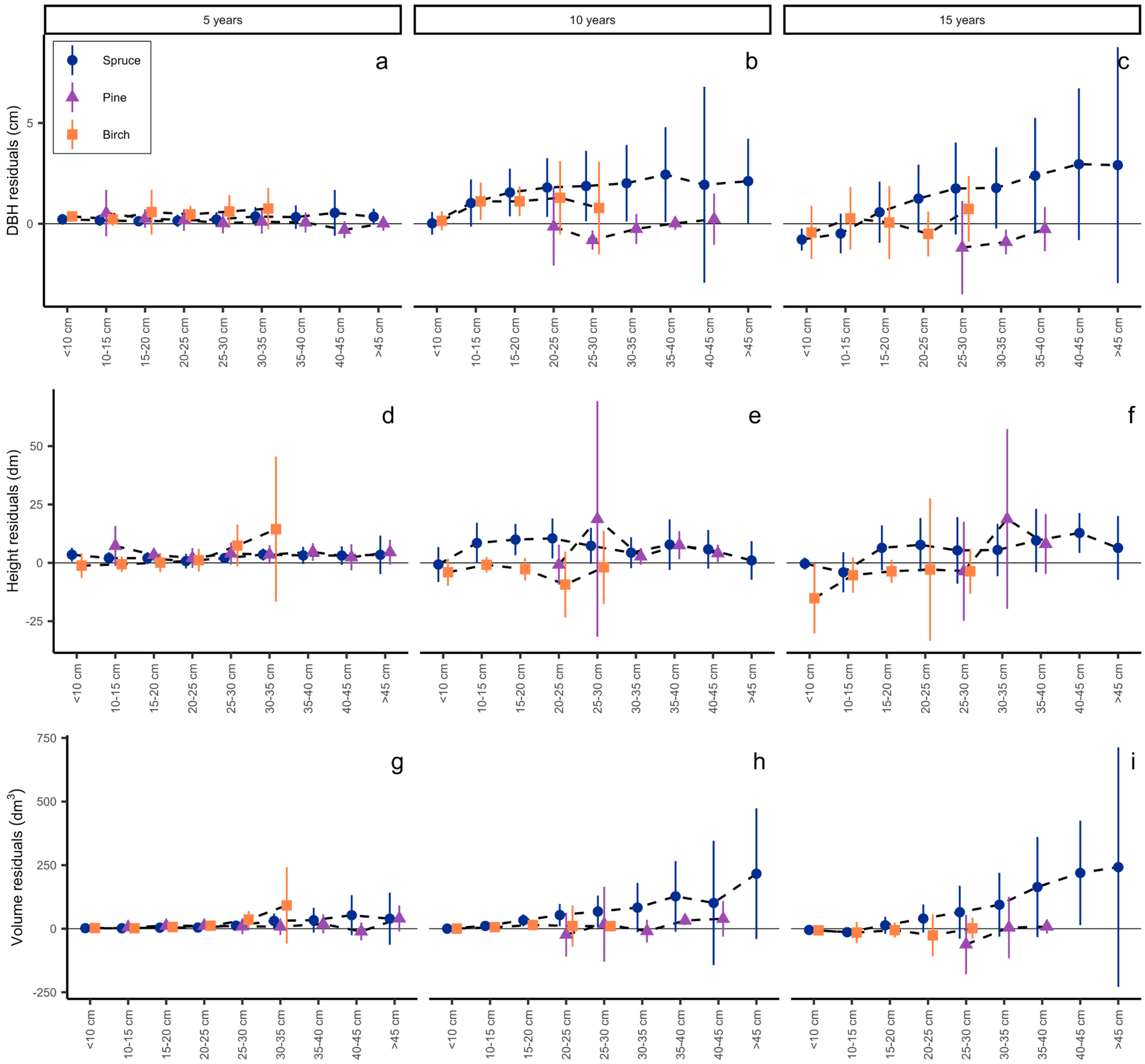

Fig. 4. Average differences between observed and predicted values for tree (a-c) DBH (cm), (d-f) height (dm), and (g-h) volume (dm^3) across DBH classes (cm) and simulation lengths (years). Points represent the fixed intercept estimates for each species, size class, and simulation length, while lines indicate ± 2 standard errors. These estimates were derived from intercept-only linear mixed effects models with sites and plots within sites included as random components.

3.4. Mortality

In terms of mortality, both models demonstrated similar accuracy in predicting volume loss (Fig. 6, panels a-b), with no values significantly different from zero, except for the combined residuals of the SNS model after 5 years of simulation (Table C3). Both models tended to slightly overpredict mortality in stands that had been thinned more than 5 years before the experiment's establishment, while they underpredicted mortality in recently thinned stands (Fig. 6, panels c-d). Pine volume loss residuals from both models were positively correlated with stand basal area, although no clear bias was observed for spruce and birch (Fig. D14, panels a-b). Underestimation of mortality increased with site fertility for pine in the Elfving model and for pine and spruce in the SNS model (Fig. D16, panels a-b). Additionally, pine and, to a lesser extent, spruce residuals were negatively correlated with the proportion of spruce in the stand (Fig. D15, panels a-b).

3.5. Model sensitivity

The model sensitivity analysis revealed temporal variation in residuals around the mean, but no clear trends were observed, particularly after excluding data from before 2005, which comprised only one experimental site (Fig. D17). Comparing the average predictions from subplots treated separately versus aggregated subplots showed similar patterns, with differences between these predictions being negligible (Fig. D18). However, altering the mean stand age had a more pronounced impact on predictions, particularly for height models (Fig. D19). Specifically, a lower mean stand age resulted in a disproportionately large increase in growth predictions compared to the reduction in predicted growth associated with a higher mean age (Fig. D21). This nonlinear response contributed to larger overall growth predictions when averaged over subplots with altered age.

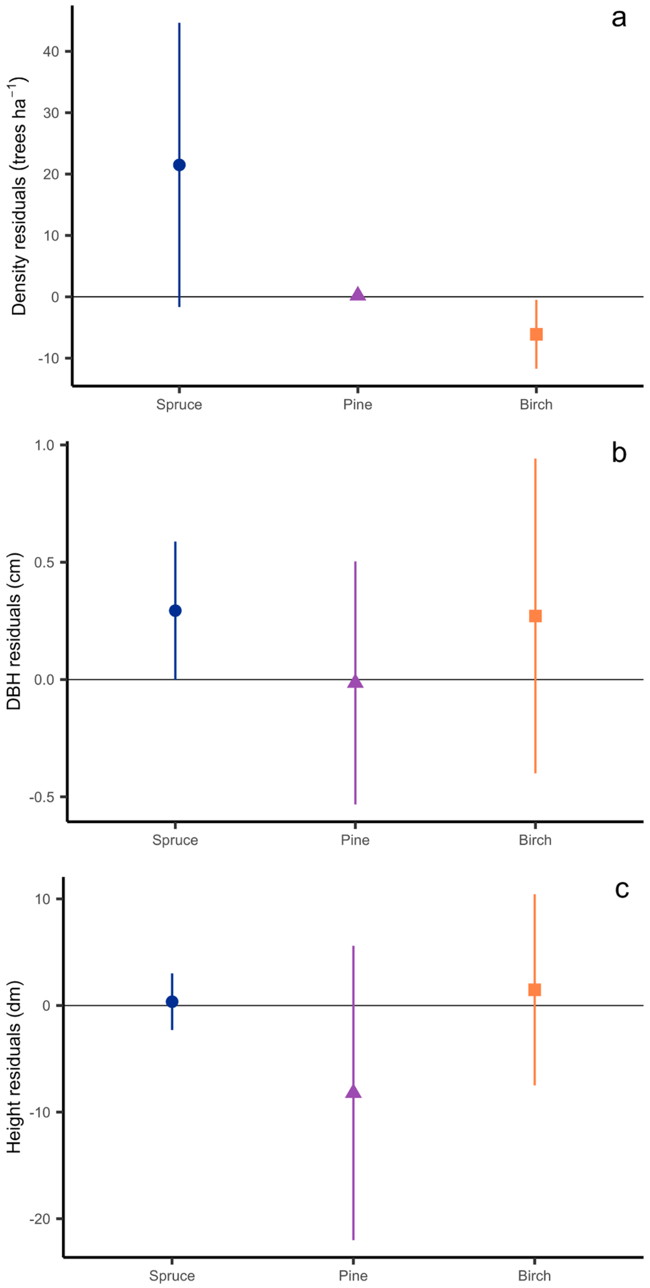

Fig. 5. Average differences between observed and predicted values for ingrowth (a) density (trees ha^{-1}), (b) initial DBH (cm), and (c) initial height (dm). Points represent the fixed intercept estimates for each species, with lines indicating ± 2 standard errors. These estimates were derived from intercept-only linear mixed effects models with sites included as a random component.

4. Discussion

4.1. Overall evaluation

This study aimed to evaluate the short-term performance (i.e., 15 years) of current Swedish models for tree recruitment, growth, and mortality in uneven-aged stands using data from field experiments. The dataset covered a broad latitudinal gradient across Sweden and encompassed a wide range of site conditions. It included both full-storied, uneven-aged stands and those in transition, reflecting potential applications for models designed for continuous cover forestry. Although this dataset provided a valuable basis for assessment, it is limited by the number of sites and the duration of experiments.

The analysis of differences between predicted and observed values was conducted using a linear mixed-effects modelling approach. This method accounted for variability in stand area, species composition, density, and growth conditions across different sites. It facilitated the isolation of general residual patterns from site-specific variation and addressed the hierarchical structure of the data, thereby avoiding pseudoreplication in the statistical analysis. Despite the constraints in data availability, the observed trends are deemed reliable, particularly for Norway spruce during the first two simulation periods, which had the most comprehensive dataset. The consistent direction of biases and residual patterns across various simulation lengths suggests that these results reflect the potential behaviour of current models when applied to uneven-aged stand conditions.

4.2. Model performance

The results revealed a tendency for current models to underestimate stand volume increment, with an average bias of 2 m^3 ha^{-1} $year^{-1}$ after 10 years of simulation. This underestimation corresponds to approximately 35 % of the observed growth in the studied plots, where the annual increment was 5.6 m^3 ha^{-1} $year^{-1}$ on average. The effect of underestimation was larger for spruce. Similar trends have been observed in other local studies from Sweden (Drössler et al., 2015; Fagerberg et al., 2022). Research from other Nordic countries also reported biases when models developed for even-aged stands were applied to uneven-aged conditions, although the direction and magnitude of bias varied (Lee et al., 2024; Maleki et al., 2022; Øyen et al., 2011). For example, Øyen et al. (2011) found that stand-level models tended to overestimate growth, while individual-tree models produced the opposite effect. Similarly, Maleki et al. (2022) observed that overestimation in stand-level models increased with actual volume, a pattern consistent with the findings in this study, where bias magnitude increased with higher stand basal area. In addition to differences in growth dynamics between even-aged and uneven-aged stands, the underestimation of volume increment could also be attributed to gradual changes in growth conditions over time (Sterba and Monserud, 1997), especially since the basal area growth models were developed using data from the 1980s.

After the first simulation period, DBH across all tree size classes was slightly underestimated. However, this pattern changed in subsequent periods. The most pronounced bias was noted for Norway spruce, which showed a positive, nearly linear relationship between DBH residuals and size classes for the two longest simulation periods. This finding aligns with Fagerberg et al. (2022), who reported that the Heureka basal area increment models tend to overestimate the growth of small trees while progressively underestimating the growth of larger trees in stands where selective cutting was applied. However, in the current study, overestimation of the smallest size classes was only observed after 15 years of simulation. A similar pattern was observed by Lee et al. (2024) in the Finnish MOTTI DSS, although the DBH residual pattern was not strictly linear and DBH predictions for trees in the 15–30 cm range were largely unbiased. The bias in spruce DBH predictions may stem from distinct growth dynamics between uneven-aged and even-aged stands. In even-aged stands, tree growth rates increase more rapidly with age, and the culmination of mean annual increment occurs earlier compared to uneven-aged stands (Rossi et al., 2009). This delayed growth culmination in uneven-aged stands might explain the stronger-than-predicted growth of larger trees, which can grow more vigorously compared to trees of the same age in even-aged stands. Consequently, the growth of smaller trees would be expected to be overestimated, however, it was only evident after 15 years of simulation and with rather low magnitude.

Contrary to expectations of error accumulation from the sequential use of nonlinear basal area growth models (Kangas, 1997), a noticeable change in DBH prediction bias was observed only between the first and second simulation periods. However, the standard errors of residuals increased sharply after the first period, aligning with Kangas (1997), who noted that prediction variability rises rapidly initially but stabilizes

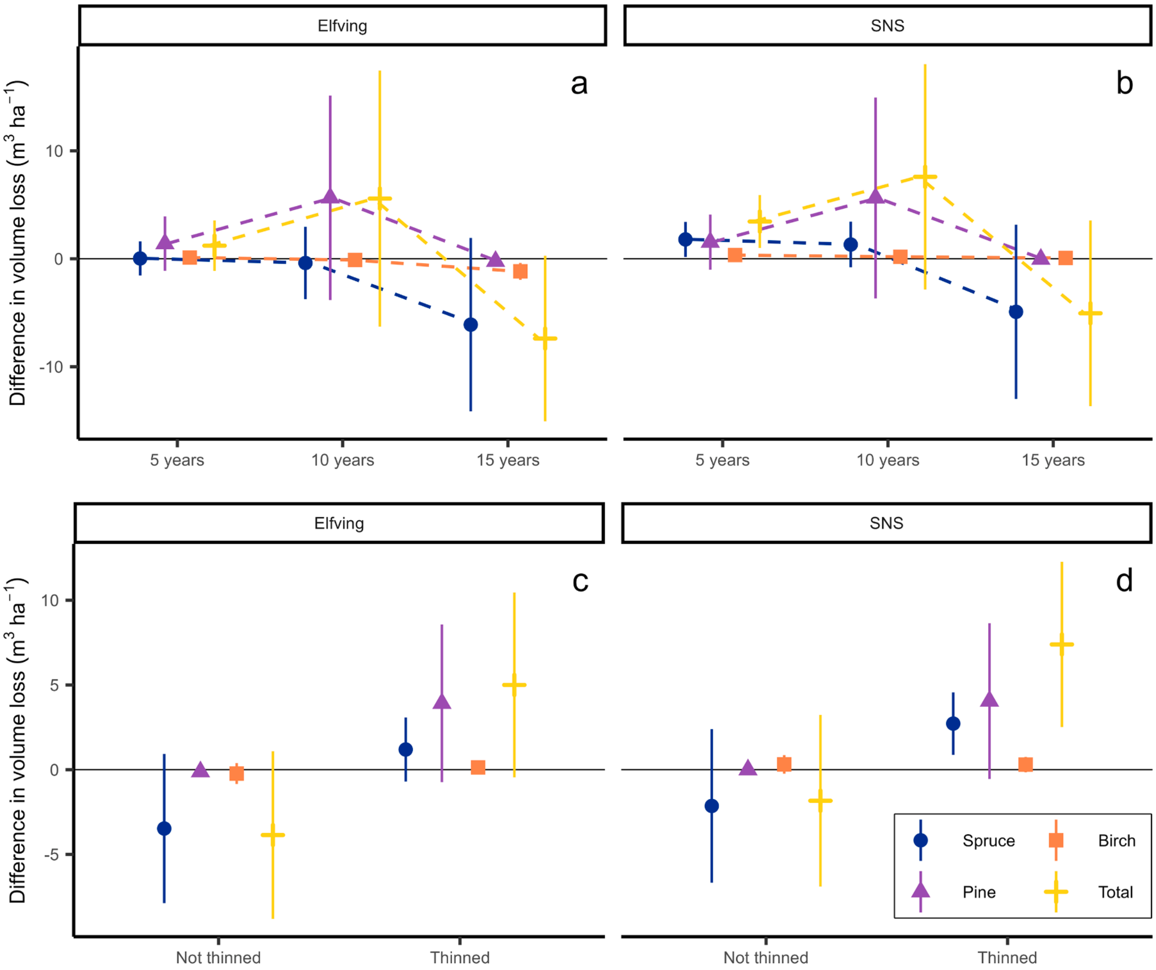

Fig. 6. Average differences between observed and predicted volume loss due to mortality (m^3 ha^{-1}) in relation to (a, b) simulation length (years) and (c, d) time since the last selection cutting. Points represent the fixed intercept estimates for each species, mortality model and either simulation length or time since the last selection cutting, with lines indicating ± 2 standard errors. These estimates were derived from intercept-only linear mixed effects models with sites included as a random component. "Not thinned" refers to stands where selection cutting occurred more than 5 years before the start of the between-revision period, while "Thinned" indicates stands where selection cutting was performed at the beginning of the between-revision period.

after about 25 years of simulation. It is important to note that in this study fewer sites were included in the later simulation periods, which could have influenced the results and particularly the estimated variation. A consistent dataset across all 15 years of simulation might have revealed different patterns.

Height residuals did not exhibit clear trends relating to tree size, and the magnitude of errors remained stable throughout the simulation, with the exception of a shift between the first and second periods. Additionally, the variability of the residuals remained relatively low. The slight arcuate pattern observed in the spruce height residuals, resembles the findings of Lee et al. (2024), although it is less pronounced. This may be attributed to the fact that most tree heights were estimated using models that smoothed out natural variation, particularly for smaller trees, as temporarily numbered trees (see 2.2. Data management) were excluded from height measurements. The height-diameter functions used for estimating heights in this study may overlap with the site index equations applied in the height growth simulations, given that tree size and age share a similar relationship to height. Including the full range of variability could potentially reveal more pronounced trends.

Thinning had a less pronounced effect on growth predictions than expected. Previous studies indicate that uneven-aged stands respond more slowly to selection cutting than even-aged stands do after thinning, with peak growth occurring later (Hynynen et al., 2019; Lee et al., 2024; Øyen et al., 2011). Suppressed trees may also experience delayed responses as they acclimate to new conditions after competition release (Metslaid et al., 2007). It was expected that thinning response functions developed for even-aged stands would overestimate growth in uneven-aged stands, especially in the initial period after selection cutting. However, this study found similar biases regardless of whether selection cutting occurred. That aligned with Bianchi et al. (2020a), who observed no substantial growth delay after tree removal in uneven-aged stands. Nonetheless, limitations in this study should be considered. The compared groups were unbalanced, with most stands being cut at the beginning of the experiment. Additionally, the observation periods were often too short to effectively assess the accuracy of thinning response and basal area growth models, given the duration of thinning effect included in these models (Elfving, 2010).

Prediction residuals for ingrowth did not show substantial deviation from zero, although variation was high, particularly for spruce ingrowth density. High variability is a well-known characteristic of ingrowth, with many studies highlighting its stochastic nature (Drössler et al., 2015; Eerikäinen et al., 2007; Valkonen et al., 2017). This high level of randomness makes accurate modelling of ingrowth particularly challenging. While residuals for the number of spruce ingrowth trees were statistically insignificant, the mean bias accounted for a substantial proportion of the ingrowth density recorded in the experiments. The observed underestimation of spruce ingrowth aligns with Elfving (personal communication, October 29, 2023), though the discrepancy was larger in that study. This underestimation could have major implications for studies on the long-term feasibility of CCF using simulations, where ingrowth is considered crucial for sustaining productivity (Ekholm et al., 2023; Wikström, 2007). Biased ingrowth predictions may substantially affect study results and conclusions.

Predictions of mortality showed no significant bias or time trends in this study, even though a cumulative volume loss was tested. Both models assessed demonstrated similar accuracy, suggesting the potential use of the simpler SNS model, which has lower data requirements. The SNS model does not include detailed variables on soil conditions or require site index estimates. However, both models still require age for predictions, which is an unsuitable variable for uneven-aged stands. While no major discrepancies were found in the general time-wise assessment, treatment-related trends emerged. Both models tended to underestimate mortality in recently selectively cut stands and overestimate it in stands treated more than five years prior to the start of the between-revision period. The increased volume loss after harvesting could be linked to damage from frequent harvesting of large trees (Myllymäki et al., 2024; Pretzsch et al., 2017). Although both models account for thinning effects, selection cutting may differ from standard thinning from below, where smaller, outcompeted trees are removed, which reduces the potential for damage. Wind damage is another factor that could influence the observed bias. However, studies suggest that uneven-aged stand structure reduce wind disturbance risk compared to even-aged stands (Hanewinkel et al., 2014; Pukkala et al., 2016), implying this factor likely mitigates rather than contributes to underestimation. The overestimation of mortality in untreated stands could be explained by the lower competition levels maintained through regular selection cutting, keeping the density below the self-thinning threshold. Additionally, the selective removal of the largest and oldest trees, which are more prone to disturbances due to declining physiological functions (Luo and Chen, 2011), may contribute to the observed discrepancies. Density-dependent mortality also varies with species composition and the vertical structure of the forest (Trifković et al., 2023). The results suggest that, after the initial negative effects of selective cutting subside, mortality in uneven-aged stands may be lower than in even-aged stands.

4.3. Sensitivity analysis

Sensitivity analysis revealed temporal variations in residuals that can potentially be linked, to e.g., annual weather fluctuations, biotic damages, etc. However, no distinct temporal trends in residuals were found, as observed in other studies (e.g., Mensah et al., 2023), potentially due to the relatively short study periods. Several dependencies were identified between prediction residuals and stand variables, suggesting that the models did not adequately account for the influence of these factors. This highlights differences in the relationships between stand variables and response variables in uneven-aged versus even-aged stands. For instance, Bianchi et al. (2020a) demonstrated that competition indices exert a stronger negative impact on growth in uneven-aged stands compared to even-aged ones. Among the stand variables assessed, the proportion of spruce and site index showed the largest and most consistent impact on simulation results. Generally, a higher proportion of spruce led to reduced bias in growth predictions. This could be attributed to the greater uniformity observed in pure spruce stands, as opposed to mixed forests, where interspecific interactions introduce additional complexity and uncertainty. Notably, shade-tolerant species tend to exhibit better growth when overtopped by shade-intolerant species than when exposed to intraspecific competition (Laiho et al., 2014; Oboite and Comeau, 2019; Pukkala et al., 2013). Furthermore, the admixture of pine and birch can enhance ingrowth by promoting the growth of saplings (Laiho et al., 2014; Pukkala et al., 2013) and reduce the mortality rates of small trees (Pukkala et al., 2013). On the other hand, the underestimation of mortality in stands with lower proportions of spruce might be linked to dominant pine trees in these mixtures. The loss of a single large pine would have a substantial impact on overall volume loss, amplifying the mortality bias.

Site index exhibited the opposite effect on residuals, with higher site index increasing prediction errors. This could be related to more dynamic stand development on fertile sites, where the differences between even-aged and uneven-aged growth patterns become more pronounced. Moreover, Lundqvist (2017) noted that the Swedish system for estimating site index from site characteristics may underestimate site potential, particularly on fertile sites. Overall, site index is widely considered an inadequate measure of site productivity in uneven-aged stands (Fagerberg et al., 2022; Pukkala et al., 2009; Skovsgaard and Vanclay, 2008), and its ability to accurately capture growth potential is limited. For example, Myllymäki et al. (2024) found that random plot effects better explained growth differences than site index. Given these shortcomings, we echo the conclusion of Bianchi et al. (2020b) and emphasize the need for better metrics to describe site potential in uneven-aged stands.

4.4. Limitations and future research

This study was clearly constrained by a scarcity of empirical data, particularly a low number of pine and birch trees, incomplete DBH class ranges, and limited data for the longest simulation periods. The lack of high-quality, long-term empirical data is a well-known challenge in evaluating and developing growth models for CCF (Hynynen et al., 2019; Lee et al., 2024). The marginalization of silvicultural systems other than rotation forestry during the second half of the 20th century resulted in a very limited number of field trials, especially older, long-term experiments (Kuuluvainen et al., 2012). Consequently, due to data limitations and high site variability, most results in this study were not statistically significant despite observable trends. Nevertheless, the outcomes provide an indication of potential discrepancies when applying current Heureka models to selection cutting stands.

The short duration of the experiments also limited the study's ability to investigate the development of ingrowth, which is crucial for accurate long-term simulations, as ingrowth will eventually constitute the majority of the simulated growing stock. Additionally, this study was unable to assess how individual tree ages are assigned. The sensitivity analysis supported findings by Fagerberg et al. (2022) that errors in estimating mean stand age can substantially affect predictions, but the accuracy of assigning age to individual trees by implemented functions remains unknown.

There is a clear need for further investigation into model accuracy, particularly in long-term simulations, as this study was limited to short-term assessments and could not provide definitive conclusions. Future research should also focus on better representation of birch and pine and assess the simulated development of ingrowth. In addition to model evaluation, the development of new stand development models tailored specifically to CCF systems is necessary, as this study suggests that using models developed for even-aged stands may lead to biased results. These findings are consistent with other studies from Nordic countries. To support these efforts, it is crucial to maintain existing field trials and establish new ones. This would not only enhance modelling efforts but also facilitate further research into the economic feasibility, ecological benefits, and societal impacts of CCF systems.

5. Conclusions

In conclusion, this study provided valuable insights into the short-term performance of current Swedish models for tree recruitment, growth, and mortality in uneven-aged stands. Despite limitations stemming from the scarcity of empirical data, the results consistently revealed an underestimation of volume increment, particularly for Norway spruce. The biases observed in growth predictions, along with model inaccuracies found in other studies from Nordic countries, highlight the challenges of applying models developed for even-aged systems to uneven-aged forestry. While most results were not statistically significant due to data limitations and high variability across sites, they indicate potential discrepancies when using Heureka models in selection cutting systems.

Greater discrepancies are expected in more productive stands with high site index and basal area, as well as in mixed-species stands. Caution is also advised when estimating stand age, which is challenging in practice but substantially influences model predictions, particularly for height. Long-term simulations are not recommended, as the Heureka DSS remains untested over extended periods. Although no progressive accumulation of errors due to the sequential use of nonlinear models was observed between last two simulation periods, this possibility cannot be ruled out.

To improve predictive accuracy, the development of new models specifically tailored to CCF systems is necessary to address the unique growth dynamics and stand structures characteristic of uneven-aged forests. These models should be age-independent and incorporate a more suitable alternative to site index for assessing site fertility. Accurately accounting for competition is also crucial but requires balancing model complexity, accuracy, and practical usability. Expanding and maintaining long-term field trials is vital for enhancing model reliability, with particular emphasis on monitoring small trees, including regeneration. Currently, ingrowth models are largely based on the assumption of an existing sapling pool, while little is known about the dynamics within the seedling and sapling layers. Additionally, unified field inventory guidelines greatly facilitate data pooling and improve modelling efforts.

CRediT authorship contribution statement

Ståhl Göran: Writing – review & editing, Supervision, Methodology, Conceptualization. **Trubins Renats:** Writing – review & editing, Supervision, Conceptualization. **Eggers Jeannette:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Goude Martin:** Writing – review & editing, Data curation. **Mensah Alex Appiah:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Grzeszkiewicz Mateusz:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT (GPT-4o) to improve readability and language of the article. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Declaration of Competing Interest

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

Acknowledgements

This research was carried out under the E-tools (Evidence-based knowledge and decision support for alternative management strategies) project and was funded in Sweden by Svenska Forskningsrådet Formas (Grant No. 2022–02112), the Strategic Research Area “Trees for the Future” (T4F), and the SLU Future Forests.

This study was performed based on the empirical data provided by the Unit for Field-based Forest Research of the Swedish University of Agricultural Sciences (SLU). We gratefully acknowledge the efforts of all team members involved in fieldwork and data maintenance.

The authors also wish to thank Magnus Ekström for his valuable advice.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122560.

Data availability

Data will be made available on request.

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