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New individual tree models of basal area increment confirm decline of Norway spruce growth in Southern Sweden

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ABSTRACT

Recent analyses of Swedish National Forest Inventory (NFI) data have reported changes in forest growth, including indications of declining increment for some tree species. To examine whether such trends are detectable at the level of individual tree, we developed new functions and applied residual analysis across major biogeographical regions of Sweden. We developed new individual-tree basal area increment models for Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) Karst.), and birch (*Betula* spp.) using Swedish NFI data from permanent plots measured between 1983 and 2022. Weighted nonlinear regression was applied with a limited set of tree-, stand-, and site-level predictors to simplify model validation and application. Model performance was evaluated against an independent NFI subset, existing functions implemented in the Heureka decision support system, and long-term thinning experiments (for Scots pine only). Overall predictive accuracy was comparable to established models, with slightly reduced bias at the stand level. No consistent long-term decline was detected for Scots pine or birch in residual analysis. In contrast, Norway spruce exhibited a systematic decline in basal area increment during the last decade in central and southern regions, indicated by increasingly negative residuals. These findings support recent inventory-based evidence of reduced spruce growth and suggest species-specific responses to changing climatic conditions in Sweden.

1. Introduction

In forestry practice, stand-level models of tree growth provide necessary updates for operational management and planning silvicultural treatments such as thinnings (Goude et al., 2022; Maleki et al., 2022). Individual tree growth models have been applied mostly in the context of decision-support systems (DSS), bringing crucial details for simulating basal area and height increment, recruitment and mortality (Fridman and Ståhl, 2001). By integrating such models, DSS can project stand structural development and economic outcomes under alternative management scenarios. For example, Heureka, a Swedish forest management simulator for long-term planning, predicts changes in diameter at breast height (DBH) distributions and evaluates the economic consequences of different treatments (Lämås et al., 2023).The National Forest Inventory (NFI) data has been a universal data source for calibrating individual tree growth models both in Sweden (Elfving, 2010) and other countries (Lessard et al., 2000; Sharma et al., 2011; Jevsenak and Skudnik, 2021; Mehtätalo et al., 2025). The ultimate reasons for that were an unbiased design of NFI and a sufficient number of long-term observations on permanent plots (McRoberts et al., 2010; Bianchi et al., 2023). For instance, Elfving (2010) developed functions for Sweden's main tree species using early observations of basal area growth on the plots established in 1983–1987. These models included traditional plot-level variables such as stand age, basal area of larger trees (*BAL*), quadratic mean diameter, occurrence of thinning event in the last period. Additionally, functions contained many site-related predictors such as distance to the coast, soil wetness, annual sum of temperatures, and occurrence of nitrogen fertilization treatment.

In these empirical models, time is represented only indirectly through repeated measurements, which introduces two major challenges for calibrating reliable individual-tree growth functions. First, due to ongoing climate change and shifts in forest management, models calibrated using data from earlier periods may perform poorly when applied to observations collected several decades later (Gilson et al., 2025). An evaluation of the Elfving (2010) models by Fahlvik et al. (2014) revealed a small (3%) bias in predictions for validation data from later re-measurements (i.e., early 2000s), highlighting the importance of calibration data spanning longer time periods. Second, although NFI

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data sets appear sufficiently large for empirical growth modeling, they often contain critical measurement errors. NFI plots are established in a quasi-anonymous manner, with locations unknown to landowners and trees remaining unmarked (McRoberts et al., 2010). The absence of permanent stem marks for repeated DBH measurements can lead to subjective relocation of "breast height" during subsequent inventories, typically five or more years after the previous measurement. As a result, NFI data commonly include negative basal area growth estimates, which must be corrected or removed prior to modeling (Elfving, 2010). Additionally, NFI data highlights common silvicultural practices but can deliver insufficient insights into less popular forest management options such as continuous cover forestry (Bianchi et al., 2023; Grzeszkiewicz et al., 2025).

Individual tree growth models can be either distance dependent or distance independent. For distance dependent models, the spatial position of individual trees needs to be known which is rarely the case in practical use of the models. Therefore, distance independent models simplify use of the models, model design and facilitates validation since long-term experiment data with accurate re-measurements often do not have record of tree coordinates (Fahlvik et al., 2014). Thus, distance-independent competition indices such as plot-level basal area or basal area of larger trees (*BAL*) are frequently used (e.g., Bianchi et al., 2023). Meanwhile, a rapid advance of high-density laser scanning measurements in forestry has allowed accurately mapping tree locations, heights, and often other parameters such as DBH and tree species (Quiennec et al., 2021; Shao et al., 2024). Accordingly, many studies have developed alternative models for individual tree growth, capitalizing on distance-based competition indices, e.g., basal area or density of all trees in a specific radius around the target tree (e.g., Pretzsch, 2022). However, validations did not show a significant superiority of these functions over traditional models with plot-level competition indices (Kuehne et al., 2019).

Information from permanent NFI plots in Sweden has successfully celebrated 40 years in 2023 and reports on forest growth trends significantly impact the decision making at governmental level (Skogsdata, 2025). Recent analysis suggested that growth of Swedish forests overall declined in the last decade (Mensah et al., 2023; Laudon et al., 2024). These findings have been related to a negative impact of climate-related drought, calculated through the proxies of vapor pressure deficit at pan-European level (Shekhar et al., 2024). However, new findings published at Forest Statistics Report (Skogsdata, 2025) suggest again a positive trend of tree volume growth across Sweden, based on NFI data from the last five years of measurements. However, the continuation of decline for Norway spruce (*Picea abies* L.), unlike for Scots pine (*Pinus sylvestris* L.) was also highlighted by the same report. It may suggest that each tree species responds differently to climatic stressors over varying biogeographical zones of Sweden. This phenomenon was studied through the combination of growth modeling and residual analysis in Finland, the country with similar climate, forest management, and tree species composition (Henttonen et al., 2024).

In this study we used Swedish NFI data collected on permanent inventory plots since 1983 to fit new individual tree basal area growth models. Our research aims were **i**) to fit new functions using a limited set of easily computable predictors and **ii**) to uncover temporal patterns in tree basal area growth per biogeographical region. We harnessed residual analysis as our main technique to compare species-specific growth trajectories between the last decade (until 2022) and observations before. In this way, we followed the approach of Henttonen et al. (2024), i.e. considering systematic residual patterns occurring in the last decade as a direct sign of changing growth trends. Thus, we focused on decreasing average value of model residuals, which may indicate overestimation of the growth prediction and simultaneously decline in the real increment of tree basal area.

2. Methods and data

2.1. Calibration data

We used Swedish NFI data collected on permanent inventory plots ($r = 10$ m) in 1983–2022. These data cover the entire country except north-western montane area on the border with Norway and is often grouped into four main biogeographical regions: Northern north (Norra Norrland), Southern north (Södra Norrland), Central (Svealand), and South (Götaland). We used these regions for exploring temporal patterns in residual analysis.

Each tree on the plot had its diameter at breast height (DBH), species, and coordinates recorded if their DBH exceeded 10 cm. It means that trees thinner than 10 cm were not measured in previous inventories unless those fell within central sub-plot (of varying radius over NFI campaigns). To account for plot-level competition, we simulated DBH of these trees outside the central sub-plot during the previous measurement using simple linear equations and then imputed them into data set. Trees from central sub-plots with DBH 4–10 cm were used to calibrate these equations. Imputed trees were not used to calibrate tree-level basal area growth models but participated in calculating the plot-level quadratic mean diameter (QMD), basal area (BA), and basal area of larger trees (BAL) predictors. Other plot-level predictors included proportions of basal area occupied by other (than target tree) species, site index (from site factors), dummy variable for thinning treatment in the last period, and annual sum of positive temperatures (above 5 ^{0}C). Main tree-level predictors were basal area and estimated (using species-specific DBH-based functions) age (estimates derived by NFI data).

We organized data in growth pairs with five-year difference between measurements (Fig. 1). If time difference deviated from this period, we recalculated change in tree basal area to fit estimate for five years. We excluded data on plots after stand-replacing tree harvest and plot parts not belonging to the main plot area. We also filtered out measurements with negative growth change (but used them to derive plot-level predictors). All remaining growth pairs except validation data set were used to fit species-specific individual tree growth models: 277,857 observations for Scots pine, 299,222 for Norway spruce, and 90,823 for birch (Fig. 2).

2.2. Model fitting

For each tree species (Scots pine, Norway spruce, and *Betula* spp.) we fitted weighted non-linear regression models following Elfving (2010) approach. We used an exponential form to calibrate tree-level basal area growth:

$$\Delta BA_{i,5} = \exp\left(\beta_0 + \sum_{k=1}^{K}\beta_k x_{ki}\right) + \varepsilon_i$$

where $\Delta BA_{i,5}$ denotes the five-year increment in squared DBH (cm^2) between two successive observations of tree *i*. β_0 is the intercept, x_{ki} is the *k*-th tree-, plot-, or site-level predictor for tree *i* and β_k are the corresponding regression parameters. *K* is the number of predictors in the model. The error term ε_i represents unexplained variation. To account for heteroscedasticity, we applied weighted regression, using tree DBH as a proxy for measurement error. Specifically, larger trees were assigned linearly smaller weights.

We transformed tree-level and plot-level variables using logarithmic, quadratic, or other transformations (e.g., dividing annual sum of positive temperatures by 1000) with aim to normalize the data and reduce the range of numerical values (Table 1). After fitting initial models, we removed variables that introduced too much multicollinearity (with variance inflation factor > 5). Final functions did not include predictors, which were not significant at 95% level (i.e. with *p*-value > 0.05).

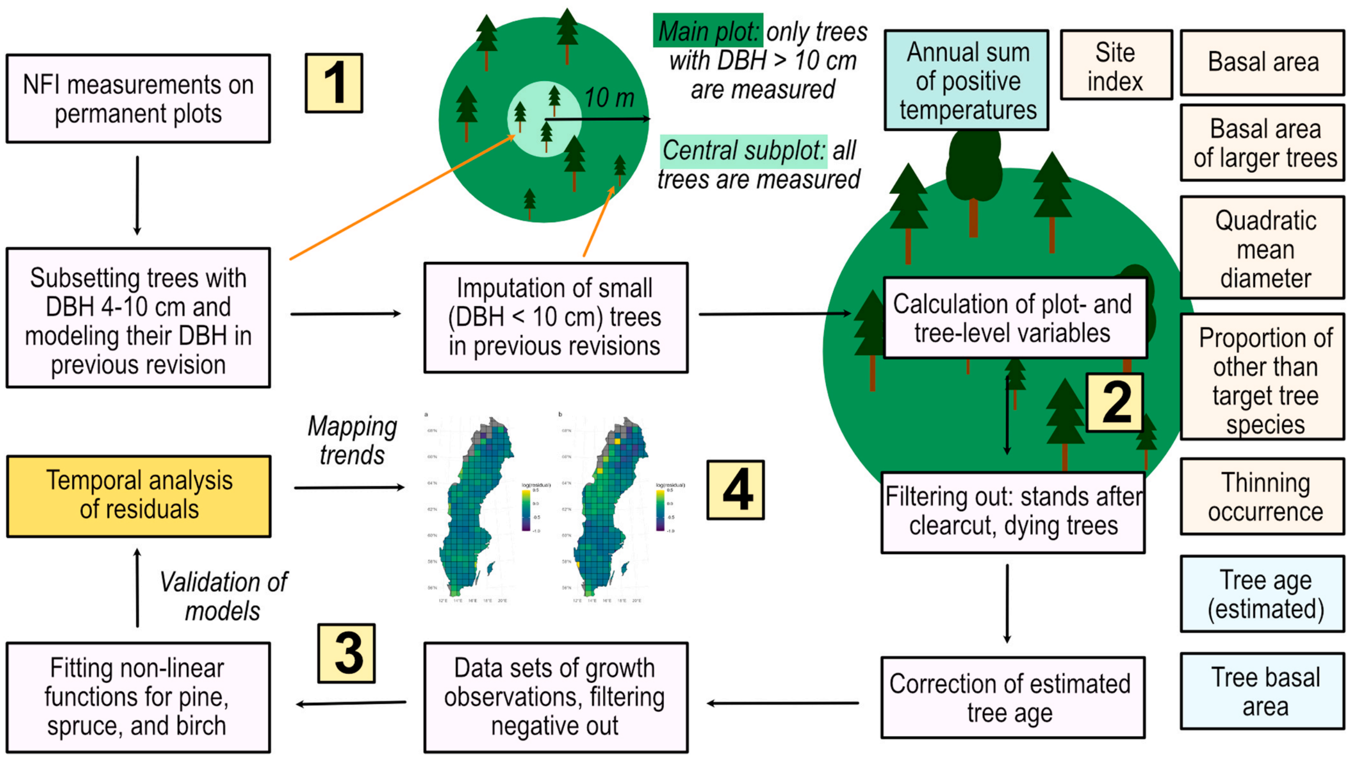

Fig. 1. Flowchart of data processing pipeline: raw data (1) is used to calculate variables including plot-level competition (2). Filtered data (3) is used to calibrate non-linear functions. Finally, temporal analysis of their residuals is applied for detecting changes in growth trends (4).

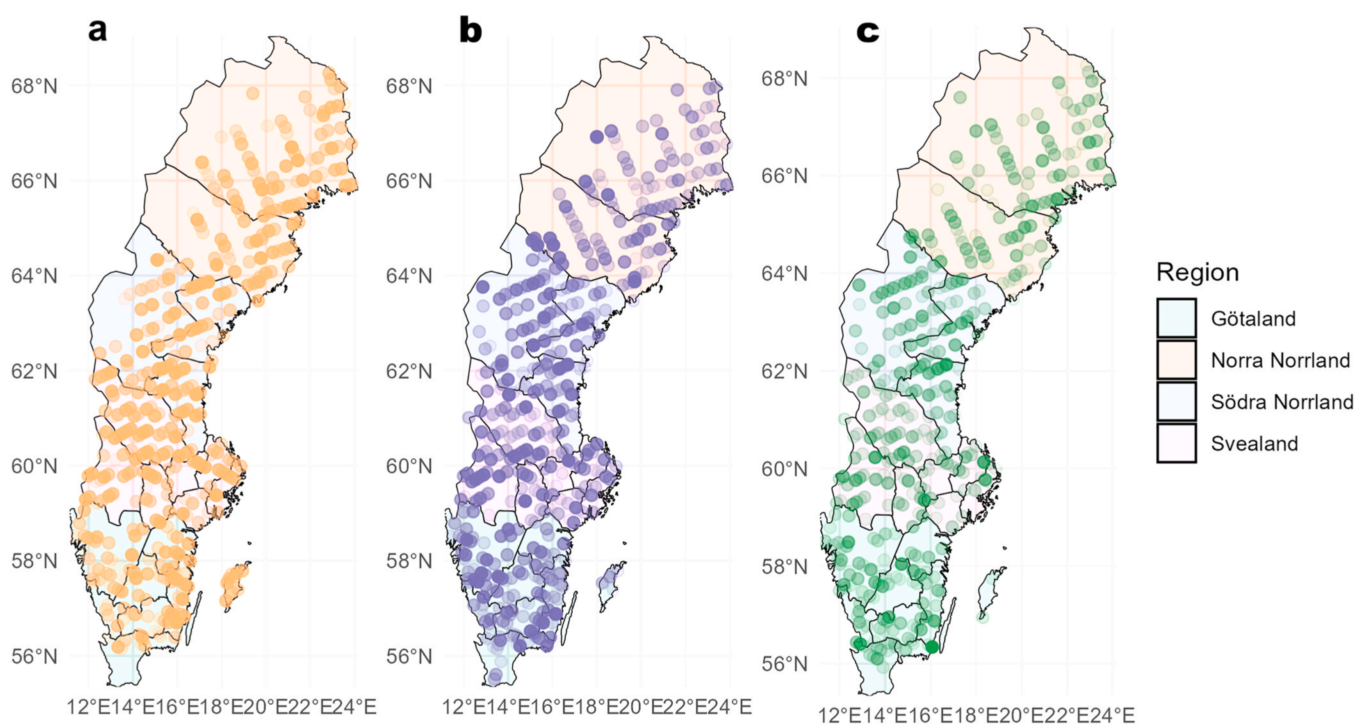

Fig. 2. Permanent NFI plots used to calibrate growth models: (a) Scots pine; (b) Norway spruce; (c) birch. More transparent dots represent less total plot basal area for a given tree species.

2.3. Validation data

We randomly selected around 10% of plots in NFI data to carry out independent model validation: 31,152 observations for Scots pine, 35,063 for Norway spruce, and 10,872 for birch. This random selection was stratified among all Swedish administrative counties to meet uniform spatial distribution over the country. We compared real growth observations with our predictions and simulations provided by Heureka decision support system. Individual tree-level growth models in this system are developed by Elfving (2010) using initial set of NFI

Table 1
Model predictors.

Variable name	Transformation	Description
Tree DBH, cm	log(DBH + 1)	Logarithmic transformation of tree DBH.
Tree age, yr	log(age + 20)	Logarithmic transformation of estimated (based on DBH, provided by NFI data) tree age, which was corrected by year of inventory.
Site index, m	site index / 10	Dominant height at 100 yr divided by 10.
Quadratic mean diameter (QMD), cm	QMD / 10	Quadratic mean diameter (plot level) divided by 10.
Plot basal area (BA), cm^2	log(BA + 3)	Logarithmic transformation of plot basal area.
Plot basal area of larger trees (BAL), cm^2	NA	Basal area of larger trees on the plot (no transformation).
Temperature sum,^{0}C	Tsum / 1000	Annual sum of temperatures above 5^{0}C and divided by 1000.
Thinning occurrence	NA	Binary variable for thinning in last inventory period (1 – thinning, 0 – no thinning).
Proportion of BA (plot) of other tree species	NA	Proportion of total plot BA that is occupied by other (than target tree) species (ranges from 0 to 1).

observations on permanent plots (1983–1997). These functions used substantially more variables (14 for birch, 18 for Scots pine, 20 for Norway spruce) and relied on measurement error corrections.

Simulations were carried out using the PlanWise module of Heureka DSS with default settings, whereby tree-level basal area increment was projected through the combined use of tree- and stand-level basal area growth models (Lämås et al., 2023; Wikström et al., 2011). Each revision of each NFI plot was projected independently rather than sequentially, such that every observation was treated as a separate stand. In addition to the required and optional site variables (Heureka Help, n.d.), information on time of the last thinning and individual tree ages was supplied in the input data. Simulations were performed in 5-year steps, and simulated outputs were directly compared with observed values after adjustment for differences in growth interval length.

In addition, we used data from a long-term thinning and fertilization experiment (GG-data, "Gallring och Gödsling" in Swedish) in Scots pine (Nilsson et al., 2010; Fahlvik et al., 2014) to validate model for Scots pine. This set of high-quality measurements includes observations since 1966 in pine-dominated stands treated with thinnings and fertilization at different intensity levels and repetition intervals. We removed all growth pairs from GG-data after fertilization and filtered out negative growth measurements. Also, we removed all growth observations for those trees which were recorded dead at the end of growth period.

Predictions for individual trees in validation data sets were summarized within plots to derive plot(stand)-level basal area growth estimates. We calculated Pearson correlation, R-square, and relative root mean square error (RMSE%) for both tree- and plot-level estimates. As supplementing metrics, we used agreement coefficients between 1:1 line (observed vs. fitted values) and a line of geometric mean functional regression (GMFR, Ji and Gallo, 2006). The latter was also fitted between observed and fitted values and used to derive specific agreement coefficients: systematic AC_{sys} (shows how well GMFR line corresponds to 1:1 line) and unsystematic AC_{uns} (shows the variance of fitted values around GMFR line). To calculate these coefficients, we followed Ji and Gallo (2006) in deriving first sum of square difference (SSD) and sum of potential difference (SPOD):

$$SSD = \sum_{i=1}^{n} (X_i - Y_i)^2$$

$$SPOD = \sum_{i=1}^{n} (|\overline{X} - \overline{Y}| + |X_i - \overline{X}|)(|\overline{X} - \overline{Y}| + |Y_i - \overline{Y}|)$$

where $\overline{X}$ and $\overline{Y}$ are mean values of observation and predicted data, respectively. Then, we calculated unsystematic sum of product difference (SPD_u) and its systematic variant (SPD_s) using formulas:

$$SPD_u = \sum_{i=1}^{n} (|X_i - \widehat{X}_i|)(|Y_i - \widehat{Y}_i|)$$

$$SPD_s = SSD - SPD_u$$

where $\widehat{X}_i$ and $\widehat{Y}_i$ are derived by GMFR line. Finally, AC_{sys} and AC_{uns} are calculated as:

$$AC_{sys} = 1 - \frac{SPD_s}{SPOD}$$

$$AC_{uns} = 1 - \frac{SPD_u}{SPOD}$$

where values of AC_{sys} closer to 1 illustrate better correspondence between 1:1 line and GMFR fit (lower bias), and higher values AC_{uns} of indicate lower scatter around GMFR line and thus lower variance.

2.4. Residual analysis

First, we plotted residuals (net difference between natural logarithm of observed value and natural logarithm of fitted value) against selected predictors (tree age, site index, annual sum of temperatures, proportion of basal area of larger trees of other species). Second, we plotted residuals through the time (1985–2019, as 2019–2024 constituted the last growth period in available NFI data) across four main biogeographical regions in Sweden. We used a generalized additive model for smoothing the average and visual examination.

Additionally, we applied regime shift analysis (RSA, Rodionov 2005) technique to observe statistically significant differences (at 95% level) in residuals over time. RSA applies *t*-tests within a specific temporal moving window (five years in our case) to uncover relevant changes in the trend. Initially developed for analyzing climatic time series, this technique can be applied for any temporal data with a reasonable time span. We plotted mean residual values within temporal 'regimes' automatically defined by RSA. This approach allowed us to understand which tree species and in which regions could have experienced overestimation of fitted growth (i.e., downward trend towards negative residual values) in the last decade of NFI observations.

3. Results

3.1. Model performance

For Scots pine and Norway spruce, new NLS functions slightly outperformed models implemented in Heureka system (Elfving, 2010) in terms of R^2 and %RMSE when validated on independent NFI data subset (Table 2). For the birch, these were equal. Same pattern could be observed for plot (stand)-level summaries. When comparing variance around GFMR line (AC_{uns}), old models were slightly better than new functions for Norway spruce and birch, but not for Scots pine. In terms of GMFR correspondence to 1:1 line (AC_{sys}), which can be used as an indicator of bias, new models had equal or superior (Norway spruce) performance. If considering GMFR validation at plot level, AC_{uns} values were slightly higher for old models. However, stand-level summaries showcased lower bias of new functions: AC_{sys} reached the value of 0.99 for all tree species, compared to 0.92 for Heureka models. Residuals were distributed evenly across the gradients of site index, stand age, annual sum of temperatures, and proportion of basal area of tree species other than target at plot level (Fig. 3, Supplementary Information Fig. S1-S3).

Model coefficients (Table 3) underlined the limiting power of plot basal area as distance-independent competition factor on individual tree growth (Fig. 4b). While combined with basal area as a classic

Table 2
Performance of models on NFI validation subset (new – NLS developed in this study, old – by Elfving 2010 and used in Heureka).

Individual trees												
Tree species	R		R^2		RMSE, $cm^2 \cdot yr^{-1}$		%RMSE		Ac_{sys}		Ac_{unc}	
	new	old	new	old	new	old	new	old	new	old	new	old
Scots pine	0.62	0.62	0.38	0.35	6.52	6.69	62.8	64.4	0.69	0.69	0.32	0.18
Norway spruce	0.68	0.69	0.46	0.44	7.63	7.74	76.1	77.3	0.84	0.74	0.18	0.43
birch	0.62	0.63	0.38	0.38	5.23	5.24	90.4	90.4	0.70	0.70	-0.05	0.22
Stand (plot-level summaries)												
Tree species	R		R^2		RMSE, $cm^2 \cdot ha^{-1} \cdot yr^{-1}$		%RMSE		Ac_{sys}		Ac_{unc}	
	new	old	new	old	new	old	new	old	new	old	new	old
Scots pine	0.90	0.89	0.80	0.75	1129.20	1087.27	39.5	38.1	0.99	0.92	0.78	0.81
Norway spruce	0.90	0.90	0.80	0.76	1509.33	1640.00	50.0	54.3	0.99	0.92	0.78	0.82
birch	0.87	0.87	0.76	0.74	552.07	566.13	67.2	69.0	0.99	0.92	0.71	0.75

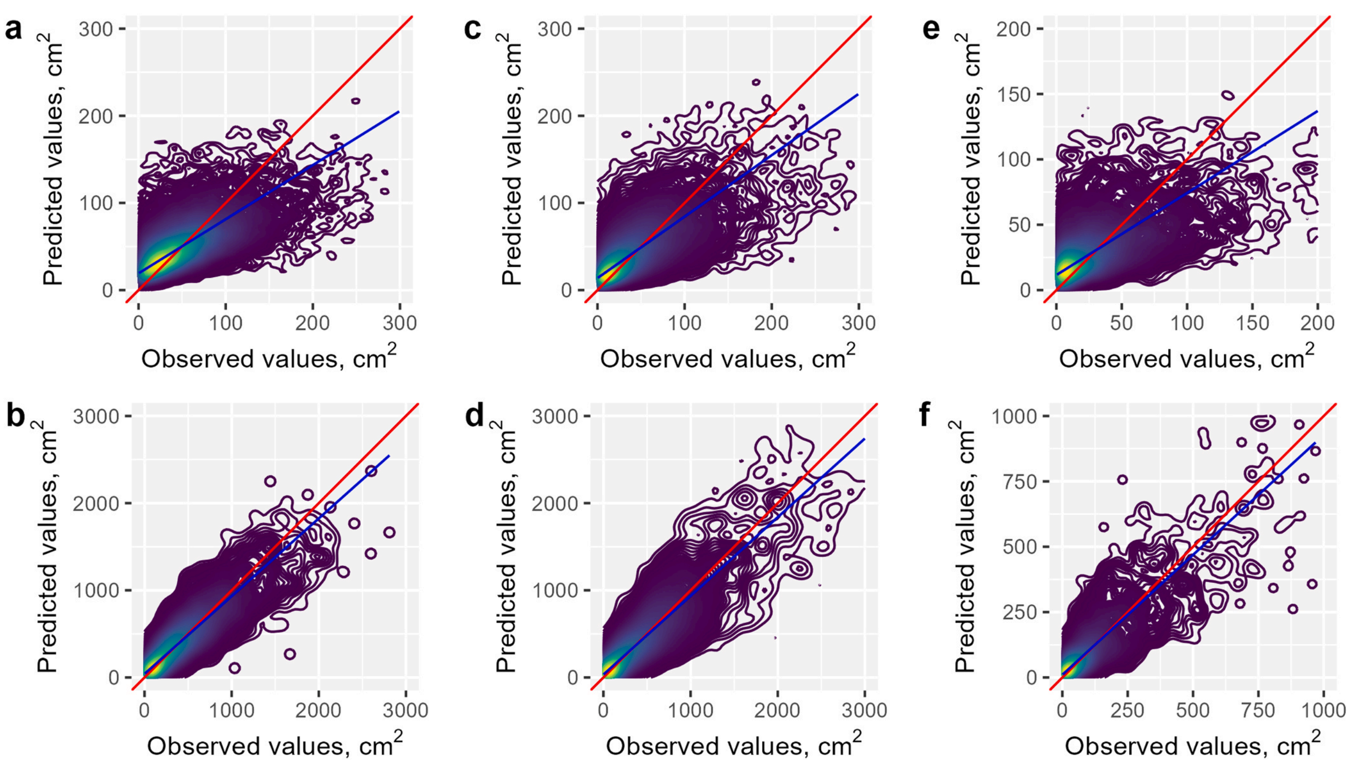

Fig. 3. Observed vs. predicted values, tree-level (top row) and plot-level (bottom row) estimates. Left column depicts Scots pine (a, b), middle column – Norway spruce (c, d), right column – birch (e, f). Contours represent density of points, red line shows 1:1 agreement, the GMFR line is blue.

competition index, effects of *BAL* were quite negligible and even not significant for Norway spruce. Effects of thinning and site index were similarly positive for all tree species, while for basal area-weighted quadratic mean diameter it was the opposite, with more negative values for the birch. According to our models, growth of all tree species benefited from a larger basal area of tree species different from the target tree on the plot. This effect was especially evident for Norway spruce (Fig. 4d). Diameter growth of Scots pine and birch seems to benefit from warmer conditions but not for Norway spruce (Fig. 4c).

The model calibrated on NFI data for Scots pine trees performed well on GG-experiment data (Table 4, Fig. 5). It achieved lower relative RMSE compared to the validation against NFI-data, especially at stand-level summaries, and higher R^2. The Scots pine function performed similar to independent NFI data subset in terms of systematic agreement coefficient, with almost no bias at stand-level summaries. Variance, as shown by unsystematic agreement coefficient, was far lower compared to the validation against NFI data (e.g., $AC_{uns} = 0.54$ for GG-data vs. 0.32 for NFI subset data).

3.2. *Temporal trends*

Regime shift analysis (RSA) did not reveal major changes in the last decade for Scots pine and the birch across the regions in Sweden, with exception for pines in Southern Sweden (Fig. 6) and birches in Northern Sweden (Fig. 7). Importantly, these new 'regimes' of tree growth patterns reflect only a few years before 2017, the beginning of the last available observation 5-year period in our NFI data set.

In contrast, we revealed more profound changes detected by RSA for Norway spruce (Fig. 8). While no significant changes occurred in the Northern Sweden, data from both middle part of the country (Svealand) and the south (Götaland, Fig. 9) exhibited a drop in residual value of fitted tree growth over the last five-seven years. This means that our model systematically overestimated the growth of spruce trees during this period, suggesting a possible decline of basal area increment.

Table 3
Model estimates.

Variable	Scots pine	Norway spruce	*Betula* spp.
	estimate	estimate	estimate
intercept	4.5881 ± 0.0192	4.8241 ± 0.0246	3.5790 ± 0.0490
tree DBH	1.5668 ± 0.0058	1.7971 ± 0.0044	1.8649 ± 0.0111
stand age	-0.7671 ± 0.0042	-0.9398 ± 0.0051	-0.8549 ± 0.0116
site index	0.2207 ± 0.0032	0.2878 ± 0.0040	0.2435 ± 0.0067
quadratic mean diameter	-0.0448 ± 0.0032	-0.0411 ± 0.0027	-0.1835 ± 0.0066
plot basal area	-0.3128 ± 0.0019	-0.3125 ± 0.0020	-0.2560 ± 0.0040
thinning indicator	0.1316 ± 0.0024	0.1240 ± 0.0025	0.1532 ± 0.0062
plot *BAL*	0.0006 ± 0.0002	NA	-0.0028 ± 0.0004
annual sum of temperatures	0.2044 ± 0.0051	-0.0740 ± 0.0083	0.1053 ± 0.0149
proportion of other tree species at the plot	0.0670 ± 0.0040	0.1956 ± 0.0041	0.1242 ± 0.0092

4. Discussion and conclusions

4.1. Model performance

We achieved moderate accuracies at tree level and high relative RMSE (reaching almost 80% of mean diameter increment), which were on similar level as reported by, e.g., the study based on Slovenian (Jevsenak and Skudnik, 2021), Swiss (Rohner et al., 2018), or pan-European (Schelhaas et al., 2018) NFI data. Our functions were only slightly better performing than classic functions (Elfving, 2010) implemented in Heureka system. Importantly, we used most of all available observations on permanent plots in Sweden since 1983 for calibration. The old functions were trained only on the initial subset of permanent NFI plots (measurements until 1997) but still showed a consistent and

Table 4
Performance of model for Scots pine on GG-experiment data.

Metric	Value	
	Tree level	Stand level (plot summary)
R	0.79	0.77
R^2	0.60	0.56
RMSE, $cm^2 \cdot yr^{-1}$	3.70	977
%RMSE	46.8	25.3
Ac_{sys}	0.78	0.99
Ac_{unc}	0.54	0.54

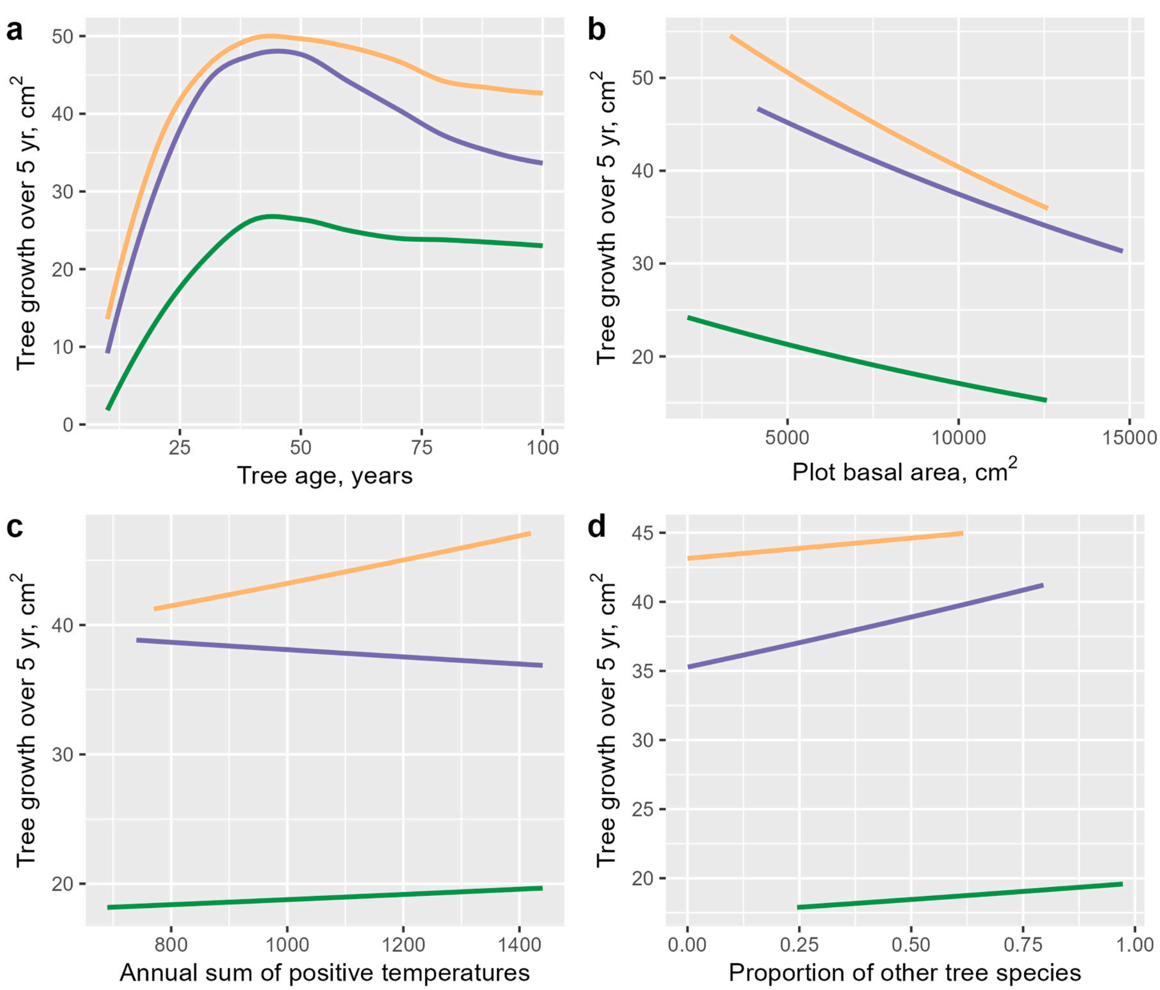

Fig. 4. Predictions for Scots pine (orange), Norway spruce (purple), and birch (green) vs. tree age (a), competition at plot level (b), local temperature regime (c), and proportion of other tree species (d). Tree sizes for age curves are calculated as averages for 10-years bins. All other model variables are used as their species-specific means in calibration data set.

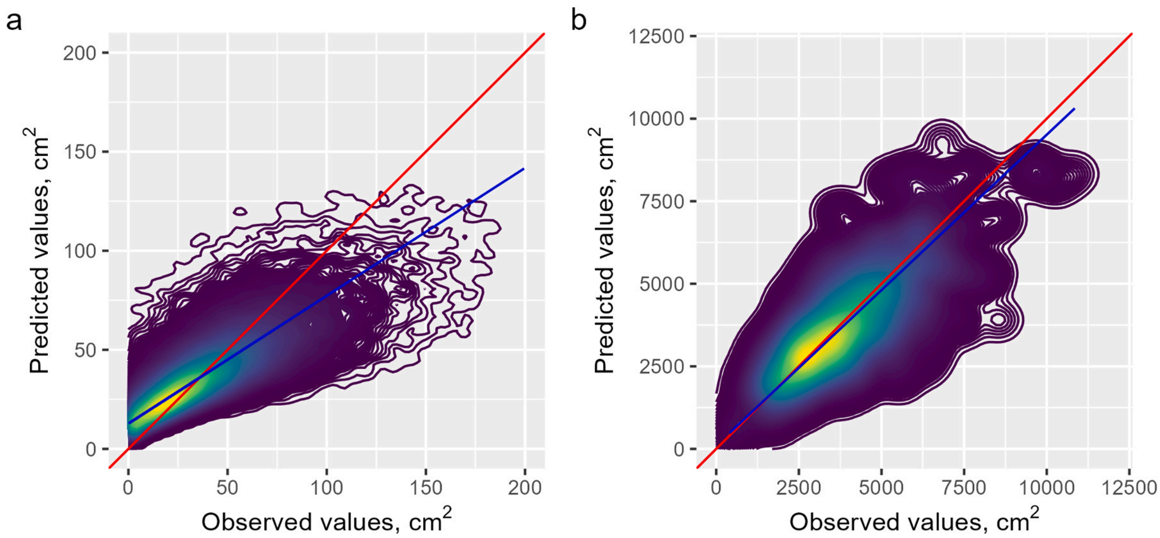

Fig. 5. Observed vs. predicted values (Scots pine), tree-level (a) and plot-level (b) estimates, GG-experiment data. Contours represent density of points, red line shows 1:1 agreement, blue line depicts GMFR agreement.

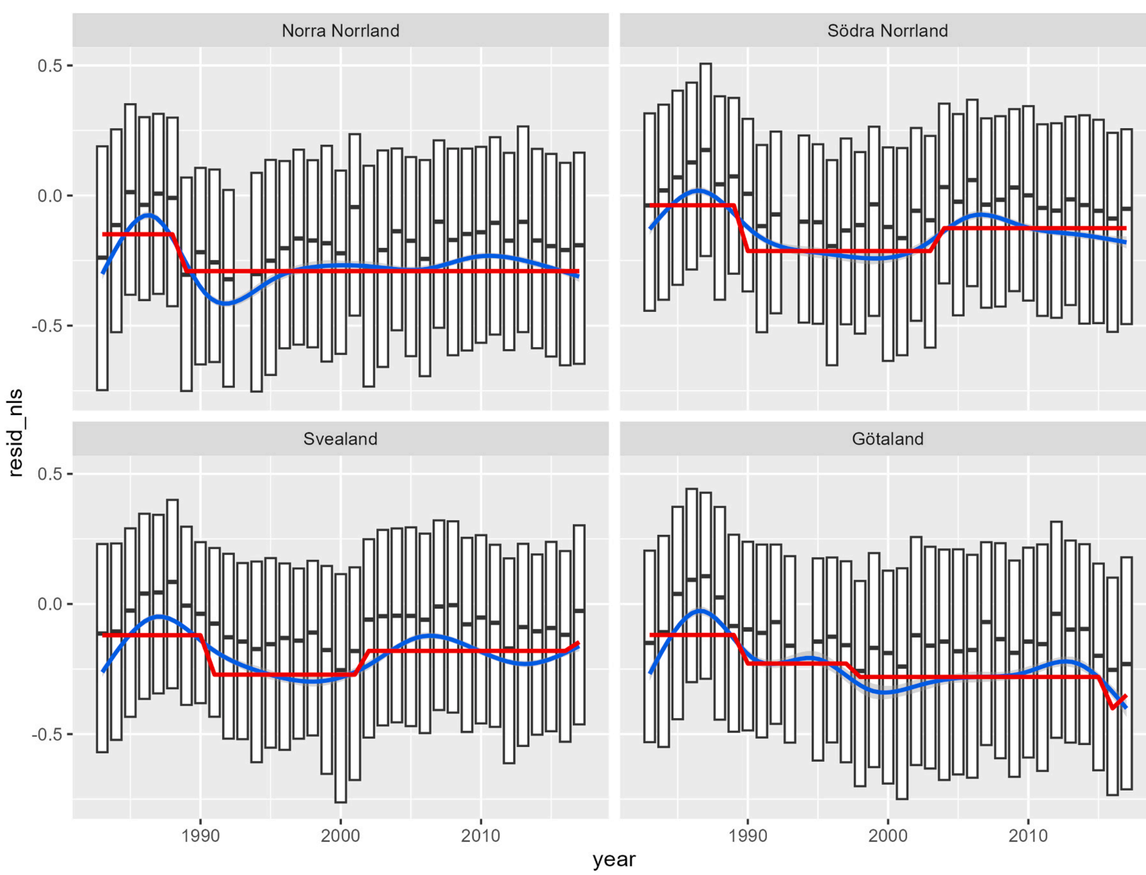

Fig. 6. Boxplots of residuals (Scots pine) across time. Only 25–75% of the range is illustrated. Blue lines depict smoothing by generalized additive model and red lines show mean residual values within temporal 'regimes' derived by RSA. Regions depict geographic differences in Sweden: Norrland – north, Svealand – middle part, Götaland – south of the country.

solid performance for the entire period (until 2022). Additionally, we did not try to correct measurement errors and discarded all observations with a 'negative' diameter growth. In this way we eliminated ~10% of observations from the training data set. Our model weights were simple and proportionally linked only to tree size, with a simple assumption that re-measurements of larger trees cause larger absolute errors. Model design was further simplified through selecting fewer and easier computable variables compared to the old functions. Our functions contained eight-nine predictors compared to 18–20 (for pine and spruce) in functions by Elfving (2010). Importantly, it allowed us to use NFI data also for validation, as we discarded several variables that were rather complicated to accurately attribute (e.g., fertilization

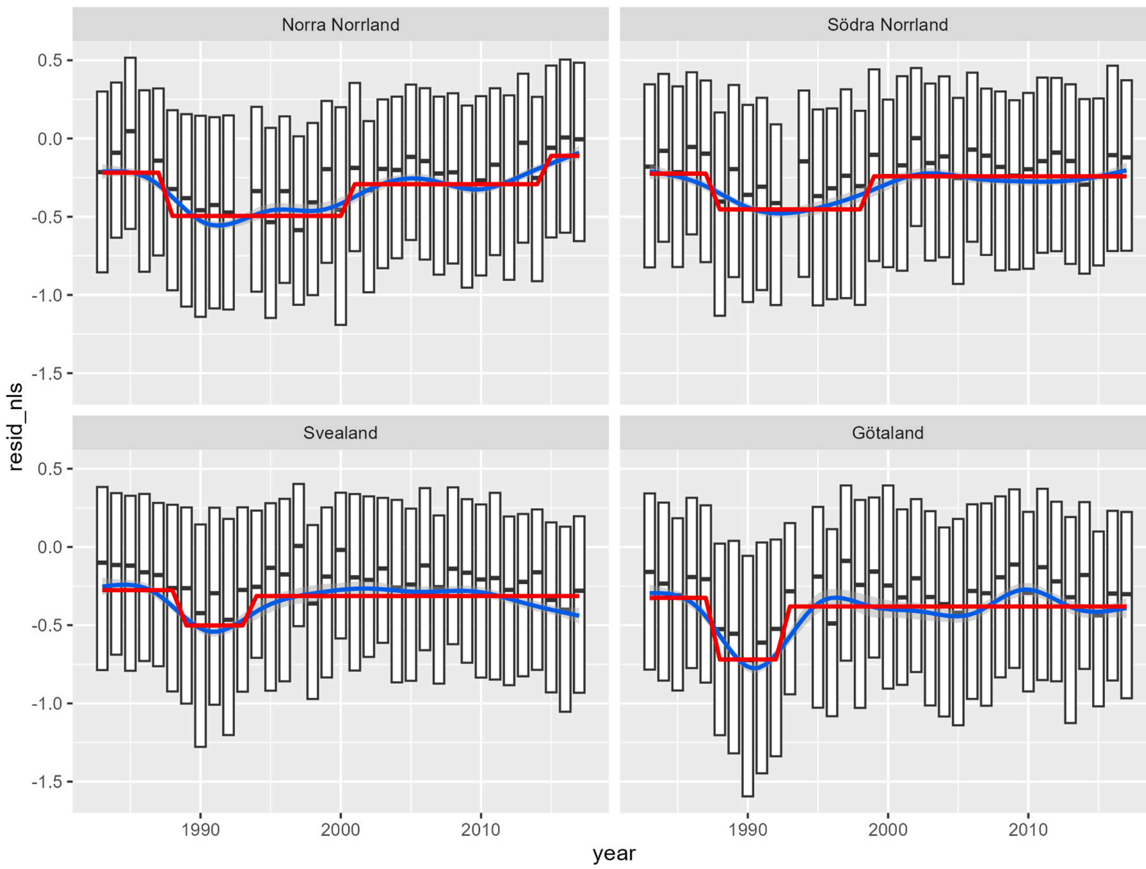

Fig. 7. Boxplots of residuals (*Betula* spp.) across time. Only 25–75% of the range is illustrated. Blue lines depict smoothing by generalized additive model and red lines show mean residual values within temporal 'regimes' derived by RSA. Regions depict geographic differences in Sweden: Norrland – north, Svealand – middle part, Götaland – south of the country.

treatments). On other hand, absence of this and other variables describing site conditions in detail has likely led to a higher variance in our models.

Our model for Scots pine performed far better on long-term experiment data from thinning GG-trials than on the validation NFI-data. These trials are classic in model validation both for tree- and stand-level functions in Sweden (Fahlvik et al., 2014; Goude et al., 2022; Grzeszkiewicz et al., 2025). Similar approach was used, for instance, by Bianchi et al. (2023), who used Finnish NFI data for calibrations and long-term experiment data for validation. We can outline several reasons why this difference in accuracy between independent NFI data subset and GG-data occurred in our case. First, breast height for diameter measurements was always marked on trees within GG trial plots. Unlike in NFI (McRoberts et al., 2010), it allows for consistent and objective DBH measurements. Second, GG-plots in Sweden represent even-aged pine monocultures, an object where tree growth can be predicted with higher accuracies compared to more heterogeneous stand settings and has good representation in the NFI data.

Our models reproduced well-known positive (site index; resource release after thinning) and negative (age, stand-level basal area as a competition factor; plot quadratic mean diameter) effects of stand and site variables. In addition, we identified notable effects of two other predictors: annual sum of positive temperatures and the proportion of plot basal area attributed to non-target species. The temperature variable showed a negative effect on spruce growth, while being positive for pine and birch (Fig. 5c). A similar negative temperature response for spruce was reported in earlier models by Elfving (2010), based on data largely collected before the mid-1990s. In contrast, a recent study of structurally heterogeneous stands in Finland (Bianchi et al., 2023) found a strong positive relationship between spruce growth and the same climatic variable. This discrepancy can be interpreted in a biogeographical context. Spruce growing near its colder climatic limits, either at high latitudes or high elevations, may benefit from warming through extended growing seasons and reduced temperature limitations (e.g., example in Norway, Andreassen et al., 2006; Merlin et al., 2024). Such growth acceleration under warming conditions has been both projected (Falk and Hempelmann, 2013) and observed (Lundgren et al., 2025). Consistent with this interpretation, Vospernik (2021) reported largely neutral spruce growth responses to warmer mean conditions in Austria, with a slightly negative slope when interannual temperature anomalies were considered. Models based on Swiss National Forest Inventory data (Rohner et al., 2018) similarly showed positive temperature effects for both Norway spruce and Scots pine. Together, these Central European alpine and northern boreal cases support the notion that spruce benefits from warming primarily where it currently grows under cool temperature constraints, whereas in warmer lowland regions increased temperatures may already exceed optimal growth conditions.

Regarding tree species mixtures, all target species (spruce, pine, and birch) in our analysis showed a positive growth response to increased proportion of other tree species (Fig. 5d). This finding is partly consistent with modeling results by Elfving (2010), who reported positive mixture effects for pine and spruce – but not for birch – based on data from the 1980s-1990s. Among the most common species mixtures in Sweden, pine-spruce combinations prevail (Lee et al., 2023). Recent studies have mainly focused on stand-level productivity and reported neutral-to-positive effects on Norway spruce growth when growing together with Scots pine (Sweden; Felton et al., 2016), or clearly positive outcomes of such mixtures (Norway; Kuehne et al., 2025). More generally, theory suggests complementary growth interactions when multiple tree species co-exist in European forests, often resulting in

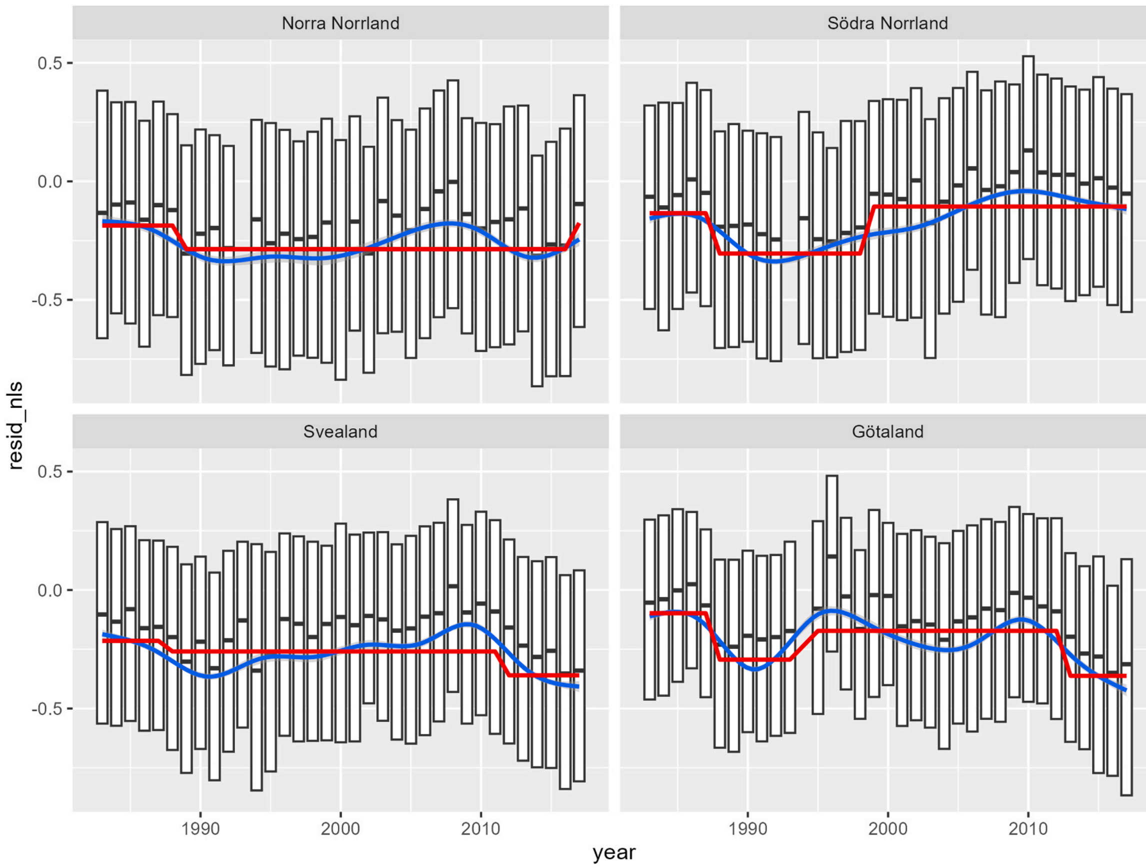

Fig. 8. Boxplots of residuals (Norway spruce) across time. Only 25–75% of the range is illustrated. Blue lines depict smoothing by generalized additive model and red lines show mean residual values within temporal 'regimes' derived by RSA. Regions depict geographic differences in Sweden: Norrland – north, Svealand – middle part, Götaland – south of the country.

over-yielding (Jactel et al., 2016; Forrester and Bauhus, 2016; Pretzsch, 2022). Species-specific interactions can be revealed using large data sets such as National Forest Inventories, and such effects do not necessarily imply positive complementarity for all species. For example, Vospernik (2021), using Austrian data, demonstrated strong species-specific mixture effects: European oak (*Quercus robur* L.) positively influenced spruce growth, whereas birch had no such effect. Conversely, only birch admixtures increased basal area increment of Scots pine, while all other species combinations had a negative effect on pine growth. In our modeling framework, we did not distinguish between light-demanding (pine, oak, birch) and shade-tolerant species (spruce, European beech *Fagus sylvatica* L.) when calculating the proportion of admixture. This choice was made to maintain a simple model structure and to emphasize the continued dominance of homogeneous stands in Swedish forestry (Lee et al., 2023).

4.2. Temporal trends

We followed approach used by Henttonen et al. (2024), with a modification by applying regime shift analysis (RSA) to the whole time series of model residuals instead of fitting separate functions for earlier and recent periods. We did not find any major changes in growth patterns for pine and birch, which did not surprise us. Scots pine stands dominate northern half of Sweden, where climatic projections do not forecast more drought-prone conditions up to the end of century (Eklund et al., 2015; MSB, 2017). Recent report on Swedish NFI (Skogsdata, 2025), which highlighted new data from 2020 to 2024 observations, reports again an increasing growth, though not for Norway spruce. Given that the rest of Swedish forests are comprised by Scots pine and broadleaves, we can attribute that total upward trend in volume growth is connected to favorable conditions for pine forests throughout the country. In Finland, Henttonen et al. (2024) have found similar long-term trend for Scots pine. The latest period (after 2000) showed the opposite trend for Southern Finland, while our findings suggest a very recent (since 2015) decrease for pine growth in Southern Sweden (Götaland).

Visual analysis of change in model residuals across the country (Fig. 9) and curves fitted by RSA illustrate opposite patterns for Norway spruce. Growth decline in the last decade was supplemented by thorough empirical analysis of NFI data (Mensah et al., 2023) and discussions attempting to attribute it with altering climate (Laudon et al., 2024). Our diameter increment function also overestimated growth of spruce trees mostly in southern and middle parts of Sweden. However, this phenomenon seems to be opposite in Finland, as Henttonen et al. (2024) detected consistently accelerating spruce volume growth at country level in general and in its southern part (in their paper referred as 'Region 2', same latitudes Central Sweden – Svealand) in particular. Their observations may not contradict our findings, as more continental Finnish climate can illustrate predictions on species range shift for Norway spruce towards higher latitudes (Falk and Hempelmann, 2013), while Southern Sweden is projected to exhibit future droughts (Eklund et al., 2015; MSB, 2017). In Swedish conditions, our models already demonstrate it through negative effect of annual sum of temperatures on diameter growth (Fig. 5), which is opposite for Scots pine and birch. Recent analysis of tree rings (Lundgren et al., 2025) additionally highlights how Norway spruce in Sweden exhibits negative effects of warming climate, but only in already warm (relative to cold northern part of the country) regions, i.e. south (Götaland).

Importantly, country-scale decline in spruce volume can hitherto be observed in the latest NFI measurements (Skogsdata, 2025). Laudon

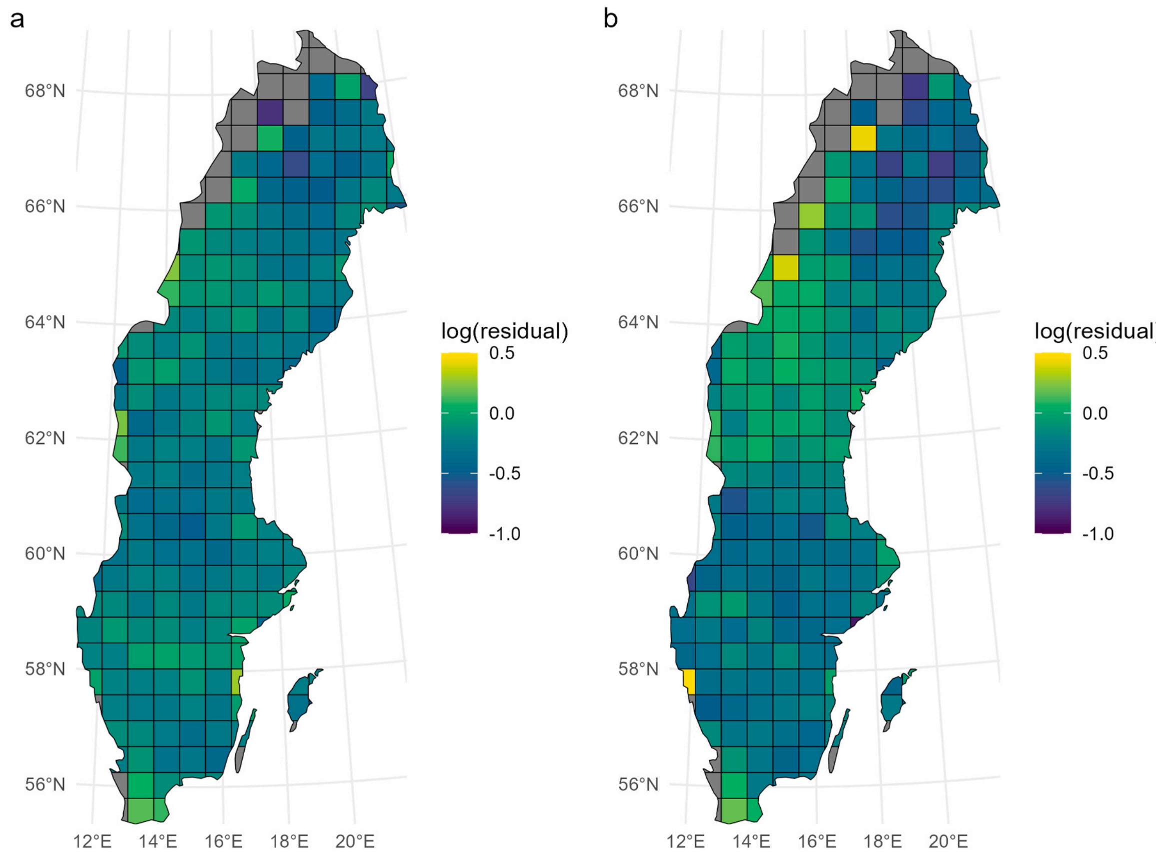

Fig. 9. Model residuals (Norway spruce, NLS function) across 50x50 km grid of Sweden. Left map (a) shows mean residuals on validation data set for observations 1983–2009 and right map (b) shows mean residuals for 2010–2022.

et al. (2024) bring examples on how this pattern can be linked to a decrease in water use efficiency, as decades of warming climate, coupled with an anthropogenic nitrogen fertilization, could cause less growth of fine roots (in favor of allocating to crown biomass) and thus smaller water uptake capacity. Mensah et al. (2023) highlighted the continuous growth of mean heights in Swedish forests at simultaneously no changing patterns of basal area increment (if ignoring the last decade), which can also be attributed to changing biomass allocation patterns under new climatic settings.

CRediT authorship contribution statement

Maksym Matsala: Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Mateusz Grzeszkiewicz:** Writing – review & editing, Validation, Software, Investigation. **Urban Nilsson:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Data curation, Conceptualization.

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.

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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.2026.123673.

Data availability

Data will be made available on request.

References

Andreassen, et al., 2006. Regional differences in climatic responses of Norway spruce (Picea abies L. Karst) growth in Norway. For. Ecol. Manag. 222 (1-3), 211–221. https://doi.org/10.1016/j.foreco.2005.10.029.

Bianchi, et al., 2023. Individual tree basal area increment models suitable for different stand structures in Finland. For. Ecol. Manag. 549, 121467. https://doi.org/10.1016/j.foreco.2023.121467.

Eklund et al. (2015): Sweden's future climate. Climate in Sweden 1860-2014. Swedish Meteorological and Hydrological Institute. ⟨https://www.smhi.se/en/publications-from-smhi/publications/2015-06-04⟩-swedens-future-climate (in Swedish).

Elfving, B. (2010): Growth modelling in the Heureka system. SLU – Faculty of Forestry.

Fahlvik, et al., 2014. Evaluation of growth functions used in the Swedish Forest Planning System Heureka. Silva Fenn. 48 (2), 1013. https://doi.org/10.14214/sf.1013.

Falk, W., Hempelmann, N., 2013. Species favourability shift in Europe due to climate change: a case study for Fagus sylvatica L. and Picea abies (L.) Karst. Based on an ensemble of climate models. J. Climatol., 787250 https://doi.org/10.1155/2013/787250.

Felton, et al., 2016. Replacing monocultures with mixed-species stands: ecosystem service implications of two production forest alternatives in Sweden. Ambio 45, 124–139. https://doi.org/10.1007/s13280-015-0749-2.

Forrester, D.I., Bauhus, J., 2016. A review of processes behind diversity—productivity relationships in forests. Curr. For. Rep. 2, 45–61. https://doi.org/10.1007/s40725-016-0031-2.

Fridman, J., Ståhl, G., 2001. A Three-step approach for modelling tree mortality in swedish forests. Scand. J. For. Res. 16 (5), 455–466. https://doi.org/10.1080/02827580152632856.

Gilson, et al., 2025. What makes a forest growth model climate-sensitive? An examination of statistical and silvicultural model needs under climate change. For. Int. J. For. Res. cpaf020. https://doi.org/10.1093/forestry/cpaf020.
Goude, et al., 2022. Comparing basal area growth models for Norway spruce and Scots pine dominated stands. Silva Fenn. 56 (2), 107107. https://doi.org/10.14214/sf.10707.
Grzeszkiewicz, et al., 2025. Evaluating the performance of mainstream Swedish growth models in uneven-aged forestry systems. For. Ecol. Manag. 582, 122560. https://doi.org/10.1016/j.foreco.2025.122560.
Henttonen, et al., 2024. Environment-induced growth changes in forests of Finland revisited – a follow-up using an extended data set from the 1960s to the 2020s. For. Ecol. Manag. 551, 121515. https://doi.org/10.1016/j.foreco.2023.121515.
Jactel, et al., 2016. Positive biodiversity –productivity relationships in forests: climate matters. Biol. Lett. 14, 20170747. https://doi.org/10.1098/rsbl.2017.0747.
Jevsenak, J., Skudnik, M., 2021. A random forest model for basal area increment predictions from national forest inventory data. For. Ecol. Manag. 479, 118601. https://doi.org/10.1016/j.foreco.2020.118601.
Ji, L., Gallo, K., 2006. An agreement coefficient for image comparison. Photogramm. Eng. & Remote Sens. (7), 823–833. https://doi.org/10.14358/PERS.72.7.823.
Kuehne, et al., 2019. Comparing performance of contrasting distance-independent and distance-dependent competition metrics in predicting individual tree diameter increment and survival within structurally-heterogeneous, mixed-species forests of Northeastern United States. For. Ecol. Manag. 403 205–216. https://doi.org/10.1016/j.foreco.2018.11.002.
Kuehne, et al., 2025. Interactive effects of species composition, site quality, and drought on growth dynamics of Norway spruce and Scots pine stands in Norway. For. Ecol. Manag. 590, 122804. https://doi.org/10.1016/j.foreco.2025.122804.
Lämås, et al., 2023. The multi-faceted Swedish Heureka forest decision support system: context, functionality, design, and 10 years experiences of its use. Front. For. Glob. Change 6. https://doi.org/10.3389/ffgc.2023.1163105.
Laudon, et al., 2024. Perspectives: swedish forest growth decline: a consequence of climate warming? For. Ecol. Manag. 565, 122052. https://doi.org/10.1016/j.foreco.2024.122052.
Lee, et al., 2023. Current state of mixed forests available for wood supply in Finland and Sweden. Scand. J. For. Res. 38, 442–452. https://doi.org/10.1080/02827581.2023.2259797.
Lessard et al. (2000): Diameter growth models using FIA data from the Northeastern, Southern, and North Central Research Stations. In: McRoberts, Ronald E.; Reams, Gregory A.; Van Deusen, Paul C., eds. Proceedings of the First Annual Forest Inventory and Analysis Symposium; Gen. Tech. Rep. NC-213. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station: 37–42.
Lundgren, et al., 2025. Unpacking climate effects on boreal tree growth: an analysis of tree-ring widths across temperature and soil moisture gradients. In: Biogeosciences, 22, pp. 6427–6443. https://doi.org/10.5194/bg-22-6427-2025.
Maleki, et al., 2022. Stand-level growth models for long-term projections of the main species groups in Norway. Scand. J. For. Res. 37 (2), 130–143. https://doi.org/10.1080/02827581.2022.2056632.
McRoberts, et al., 2010. Advances and emerging issues in national forest inventories. Scand. J. For. Res. 25, 368–381. https://doi.org/10.1080/02827581.2010.496739.
Mehtätalo, et al., 2025. A new growth curve and fit to the National Forest Inventory data of Finland. Ecol. Model. 501, 111006. https://doi.org/10.1016/j.ecolmodel.2024.111006.
Mensah, et al., 2023. Taller and slenderer trees in Swedish forests according to data from the National Forest Inventory. For. Ecol. Manag. 527, 120605. https://doi.org/10.1016/j.foreco.2022.120605.
Merlin, et al., 2024. Climate-growth relationships for Norway spruce and Scots pine remained relatively stable in Norway over the past 60 years despite significant warming trends. For. Ecol. Manag. 569, 122180. https://doi.org/10.1016/j.foreco.2024.122180.
MSB (2017): Droughts and wildfires in Sweden: past variation and future projection. ISBN 978-91-7383-757-6. 20 p.
Nilsson, et al., 2010. Thinning of Scots pine and Norway spruce monocultures in Sweden – effects of different thinning programmes on stand level gross- and net stem volume production. Stud. For. Suec. 219, 46.
Pretzsch, H., 2022. Facilitation and competition reduction in tree species mixtures in Central Europe: consequences for growth modeling and forest management. Ecol. Model. 464, 109812. https://doi.org/10.1016/j.ecolmodel.2021.109812.
Quiennec, et al., 2021. Developing a forest inventory approach using airborne single photon lidar data: from ground plot selection to forest attribute prediction. For. Int. J. For. Res. 95 (3), 347–362. https://doi.org/10.1093/forestry/cpab051.
Rohner, et al., 2018. Predicting individual-tree growth of central European tree species as a function of site, stand, management, nutrient, and climate effects. Eur. J. For. Res. 137, 29–44. https://doi.org/10.1007/s10342-017-1087-7.
Schelhaas, et al., 2018. Species-specific, pan-European diameter increment models based on data of 2.3 million trees. For. Ecosyst. 5, 21. https://doi.org/10.1186/s40663-018-0133-3.
Shao, et al., 2024. Large-scale inventory in natural forests with mobile LiDAR point clouds. Sci. Remote Sens. 10, 100168. https://doi.org/10.1016/j.srs.2024.100168.
Sharma, et al., 2011. Modelling dominant height growth from national forest inventory individual tree data with short time series and large age errors. For. Ecol. Manag. 262, 2162–2175. https://doi.org/10.1016/j.foreco.2011.07.037.
Skogsdata (2025): Aktuella uppgifter om de svenska skogarna från SLU Riksskogstaxeringen Tema: Tillväxt, avverkning och naturlig avgång. ⟨https://www.slu.se/globalassets/slu.se/om-slu/organisation/institutioner/skoglig-resurshushallning/riksskogstaxeringen/dokument/skogsdata/skogsdata_2025_web.pdf⟩.
Vospernik, 2021. Basal area increment models accounting for climate and mixture for Austrian tree species. For. Ecol. Manag. 480, 118725. https://doi.org/10.1016/j.foreco.2020.118725.
Wikström, P., et al., 2011. The Heureka forestry decision support system: an overview. MCFNS 3, 87–94.