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Fennoscandian individual tree basal area increment models for major forest tree species

Simone Bianchi [a], Cornelia Roberge [b], Johannes Schumacher [c], Johannes Breidenbach [c], Kari T. Korhonen [a] and Harri Mäkinen [a]

[a]Natural Resources Institute Finland (LUKE), Helsinki, Finland; [b]Swedish University of Agricultural Sciences (SLU), Umeå, Sweden; [c]Norwegian Institute of Bioeconomy Research (NIBIO), Ås, Norway

ABSTRACT

Sustainable forest management needs growth models. Few studies have explored regional models in Fennoscandia despite similar conditions and challenges. We examined the feasibility of regional models for basal area increment of Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), and birch (Betula pendula Roth. and *Betula pubescens* Ehrh.). We compiled over 880,000 growth observations and estimated competition indices, climate variables, and site fertility classes by integrating data from recent National Forest Inventories (2004–2023) in Finland, Norway, and Sweden. Using Random Forest models, we identified the main growth drivers across countries (tree size, accumulated temperature sum, latitude, competition, and site fertility), with minor differences in their responses across countries. However, periodic NFI measurements could not capture the effect of additional climate variables. Using species-specific nonlinear mixed models, we demonstrated that predictive regional models can be fitted using those main drivers. Although we achieved only moderate predictive performance (Weighted Absolute Percentage Error of 45–71%, depending on the species and country), there were no residual geographical biases. The results confirm the potential of Fennoscandian growth models to address shared challenges. Future work should better account for site fertility, integrate process-based approaches for climate responses, and carry out independent validation.

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Norway spruce; Scots pine; birch; growth models; non-linear modelling; random forest modelling; NFI

Introduction

Forest growth models typically describe the dynamics of regeneration, growth, and mortality at the level of individual trees or stands and many have been developed specifically for practical forest management applications. In Fennoscandia (Finland, Norway, and Sweden), such models are widely implemented within decision-support systems, including HEUREKA (Lämås et al. 2023), MELA (Nuutinen and Kellomäki 2001), MOTTI (Hynynen et al. 2014), SIMO (Rasinmäki et al. 2009), SITREE (Antón-Fernández and Astrup 2022) and others (Pukkala et al. 2013, 2021). Those models are generically empirical and mensurational, derived from inventory data using statistical methods. However, their validity is increasing challenged by intertwined climate change and biodiversity loss, as they are being used beyond the range of observations for which they were originally designed, thus possibly leading to inaccurate predictions (Peng 2000).

In Fennoscandia, ongoing climate change is predicted to increase temperatures and precipitation, although patterns may vary (e.g. increases in spring droughts) (Jacob et al. 2014; Ruosteenoja et al. 2018). Consequently, predicted forest dynamics will vary by species, geographical area, and climate scenario. Generally, tree growth could increase in the warming northern parts of Fennoscandia but decrease in the drying southern regions (Kellomäki et al. 2018; Goude et al. 2022). However, a recent growth decline has been observed throughout Fennoscandia (Mäkinen et al. 2022; Breidenbach et al. 2024; Laudon et al. 2024). The prevailing models designed for practical applications were developed under historical climate conditions. As such, they cannot be applied to new climate conditions (Bianchi et al. 2023).

There is increasing interest in enhancing forest growth models with better climate sensitivity (Metsaranta et al. 2024). For example, Heureka adjusts empirical growth functions using outputs from process-based models and climate scenarios (Lämås et al. 2023). Other recent efforts include the use of machine learning techniques to capture complex, non-linear relationships,

CONTACT Simone Bianchi simone.bianchi@luke.fi Natural Resources Institute Finland (LUKE), Latokartanonkaari 9, Helsinki 00790, Finland

as well as the incorporation of spatially explicit environmental variables such as climate gradients, soil properties, and competition indices (Boukhris et al. 2025). This challenge is widespread across Fennoscandia and demonstrate the need to continuously improve forest growth models. Furthermore, transnational datasets offer opportunities to improve model generality by expanding the range of observed conditions. However, despite similarities in environmental conditions and management, few efforts have been made to develop regional models (Siipilehto et al. 2020, 2021; Lee et al. 2023).

We propose developing a common Fennoscandian FGS based on transnational data, which would offer several benefits. The extended data range would increase the reliability of predictions in changing conditions. Specifically, the FSG would capture regional climate gradients and species responses more accurately than national models. Cross-border consistency would harmonize forest growth simulations across national borders. This would lead to increased regional collaboration in various applications, such as practical management, scientific research, and scenario analyses for policymaking.

This study is the first step towards achieving that goal. In this paper, we do not present a full simulator; rather, we develop and evaluate species-specific individual-tree basal area increment models as a first step towards a regional modelling framework. At the transnational level in Fennoscandia, we investigated individual-tree basal area increment of the most common Nordic forest tree species – Norway spruce (*Picea abies* (L.) Karst., henceforth spruce), Scots pine (*Pinus sylvestris* L., henceforth pine), and silver birch and pubescent birch (*Betula pendula* Roth. and *Betula pubescens* Ehrh., henceforth grouped as birch). We used a large database of over 880 000 individual tree growth (i.e. basal area increment) measurements from the recent National Forest Inventories (NFIs) in Finland, Norway and Sweden. Specifically, our research objectives were: (i) to understand the most important regional drivers of tree growth using machine learning methods; (ii) to verify if such drivers are consistent across countries; (iii) to prepare regional species-specific predictive Non-Linear Mixed Models (NLMMs), including cross-validation.

Material and methods

Study material

We used recent, repeated plot measurements from the NFI in Finland, Norway and Sweden to cover the current conditions of forests throughout the region (Table 1). Due to practical constraints, we only considered the most recent Finnish NFI data, which is based on fixed-radius plots. To avoid an imbalanced database, we only considered Norwegian and Swedish data from a similar period. We only studied sample plots on mineral soils for simplicity. The data were processed using R Statistical Software (R Core Team, 2025).

For Finland, we used 8 375 circular permanent plots from the Finnish NFI measured from 2014 to 2023, each revisited once after 5 years. The plot radius was 4 m for trees with a diameter at breast height (DBH, measured 1.3 m from the ground) between 4.5 and 9.4 cm, covering 50 m^2, and 9 m for trees with a DBH greater than 9.4 cm, covering 254 m^2. The plots were placed across the country according to a systematic clustered sampling design: further information in Korhonen et al. (2024). For Norway, we used 7 098 circular plots from the Norwegian NFI measured from 2004 to 2021, each revisited every 5 years. Each plot had a radius of 8.92 m and covered 250 m^2, measuring all trees with DBH greater than 4.9 cm. The plots were placed across the country according to a systematic clustered sampling design: further information in Breidenbach et al. (2020). For Sweden, we used 10 095 circular plots from the Swedish NFI from 2004 to 2022. Each plot had a radius of 3.5 m for trees with DBH between 4.0 and 9.9 cm and 10 m for trees with DBH greater than 9.9 cm. The plots were sampled in clusters in a systematic sample across the country: further information in Fridman et al. (2014). To harmonize the different inventories, we hereafter considered only trees with DBH above 5 cm.

To decrease edge effects, we removed plots that were not fully within one stand. The typical time interval between measurements was five years across all countries. Tree species and DBH were assessed for each stem in all plots (according to the previously described criterion for tree size). The dominant forest floor vegetation, an indicator of growth potential, was recorded according to different national classifications: Cajander (1949) in Finland, Larsson (2000) in Norway, and Hägglund and Lundmark (1977) in Sweden. We assigned each plot to a bioclimatic zone using the Environmental Stratification of Europe dataset (Metzger 2018), slightly modified due to its low resolution, especially along the Norwegian coast (Figure 1).

Data processing

The variable of interest was the growth of each tree alive both at the start and end of successive measurements, calculated as the difference in basal area (Δba, cm^2 $year^{-1}$). To convert the periodic growth measurements

Table 1. Summary of tree, stand, and site variables for each country and species.

Species	Individual tree measurements	Tree basal area growth (cm^2 $year^{-1}$)	DBH (cm)	Basal area, stand total (m^2 ha^{-1})	Basal area of larger trees (m^2 ha^{-1})	Ground vegetation class (VEG)	GDD5 (degree days)
Finland							
Spruce	42 851	−5.3 to 7.8 ± 7.5 to 84.0	5.0 to 16.1 ± 7.6 to 63.0	0.2 to 21.7 ± 10.3 to 63.1	0.0 to 14.4 ± 10.2 to 62.4	2.0 to 4.3 ± 0.6 to 6.0	577 to 1222 ± 207 to 1523
Pine	68 034	−5.2 to 6.3 ± 5.1 to 73.5	5.0 to 16.9 ± 6.8 to 62.3	0.2 to 17.5 ± 8.1 to 63.1	0.0 to 9.7 ± 7.2 to 55.3	2.0 to 3.6 ± 0.7 to 6.0	577 to 1143 ± 218 to 1516
Birch	22 044	−6.3 to 4.9 ± 5.4 to 78.6	5.0 to 13.2 ± 5.7 to 52.0	0.2 to 17.2 ± 8.9 to 62.7	0.0 to 10.2 ± 8.1 to 56.9	2.0 to 4.3 ± 0.7 to 6.0	591 to 1156 ± 235 to 1516
Norway							
Spruce	151 331	−6.0 to 5.7 ± 6.7 to 171.0	5.0 to 13.7 ± 7.6 to 66.2	0.1 to 25.3 ± 13.1 to 76.8	0.0 to 17.4 ± 12.3 to 76.7	3.0 to 4.4 ± 0.8 to 6.0	426 to 1033 ± 255 to 1696
Pine	53 678	−7.6 to 6.4 ± 6.2 to 96.2	5.0 to 18.9 ± 9.7 to 63.6	0.1 to 22.4 ± 11.2 to 75.6	0.0 to 12.9 ± 9.9 to 65.0	2.0 to 3.8 ± 0.9 to 6.0	446 to 1105 ± 273 to 1713
Birch	139 762	−5.2 to 1.7 ± 2.9 to 112.2	5.0 to 10.1 ± 4.8 to 57.3	0.1 to 17.4 ± 9.3 to 75.6	0.0 to 11.8 ± 8.7 to 75.3	2.0 to 4.5 ± 0.8 to 6.0	359 to 850 ± 265 to 1713
Sweden							
Spruce	195 862	−7.5 to 8.0 ± 8.0 to 178.2	5.0 to 16.8 ± 7.3 to 66.3	0.3 to 25.8 ± 10.5 to 71.7	0.0 to 15.8 ± 10.7 to 68.4	2.0 to 4.5 ± 0.8 to 6.0	511 to 1269 ± 316 to 1791
Pine	182 208	−7.3 to 7.9 ± 6.2 to 145.9	5.0 to 18.2 ± 7.5 to 64.0	0.3 to 21.3 ± 9.3 to 71.7	0.0 to 11.5 ± 8.1 to 66.5	2.0 to 3.9 ± 0.9 to 6.0	556 to 1207 ± 294 to 1808
Birch	10 271	−5.2 to 5.9 ± 8.1 to 105.8	5.0 to 16.2 ± 8.8 to 57.9	0.3 to 22.2 ± 10.7 to 66.3	0.0 to 13.4 ± 9.4 to 52.0	2.0 to 4.4 ± 0.9 to 6.0	511 to 1175 ± 333 to 1815

Ground vegetation classes (VEG) are described in Table 2. GDD5 is the temperature sum for the period 1990–2020. Values are shown as: minimum – mean ± standard deviation – maximum.

into annual growth rates, we calculated the length of the measurement interval based on the number of years between measurements and adjusted it according to the fraction of growth achieved at the time of measurement during the growing season. For this purpose, we defined annual growing seasons for each bioclimatic region (starting dates ranging from May to June and ending dates ranging from August to September) and assumed a sigmoidal growth pattern for DBH between these dates (with 50% growth at the midpoint). We then adjusted the growing interval accordingly (Söderberg et al. 1993; Mäkinen et al. 2008). We excluded extreme growth values considered as measurement errors. For positive outliers, we defined an upper threshold of Δba equal to the average growth plus three standard deviations. This threshold was estimated for each tree using a moving average (window size = 20) after sorting the data by DBH within each species group. We removed all measurements exceeding that threshold (1.03% of the dataset). For negative outliers, we removed measurements below DBH growth of −0.09 cm $year^{-1}$ (1.04% of the dataset), to remove a corresponding number of trees with negative growth and avoid a shift in mean growth.

The following plot-level variables were used as proxies for between-tree competition: basal area sum of all trees (BATOT, m^2 ha^{-1}), indication of two-sided or symmetric competition, where all trees compete for resources; and basal area sum of all trees larger than the target tree (BAL, m^2 ha^{-1}) (Wykoff 1990), indication of one-sided or asymmetric competition, where taller trees influence smaller ones, but not vice versa. We did not calculate separate species-specific competition variables (i.e. BATOT or BAL formed only by either spruce, pine, or birch) since our dataset included mostly pure species stands with relatively low presence of other tree species in the small plots used. We accounted for the different subplot sizes in the concentric plot designs when converting values to a per-hectare basis. We retrieved information on silvicultural interventions in terms of the number of years since the last thinning, selective harvesting, or similar partial removal of trees. We harmonized this information into a categorical variable ($THIN_{time}$), namely last removal conducted (i) less than five years ago; (ii) six to ten years ago; (iii) 11–15 years ago; and (iv) more than 15 years ago or never recorded, considered as unthinned and used as a reference.

We retrieved climate variables from ClimateDT (Marchi et al. 2024), a European downscaling tool that ensured data harmonization and avoided possible national biases. The following variables were tested: sum of growing degree-days above 5°C (GDD5, °C days); mean temperature of the coldest quarter (MTCQ, °C); temperature difference (TD, °C) which is the difference between the maximum and minimum temperature during the year and is interpreted as an index for the continentality/oceanity gradient; mean annual precipitation (MAP, mm); and annual heat moisture index (AHM, °C mm^{-1}), that is the mean annual temperature multiplied by 1,000 and divided by MAP. For each plot, we calculated the average values for the reference period (1990–2020) (suffix "_ref"), and the anomalies for each growing period (suffix "_anom"),

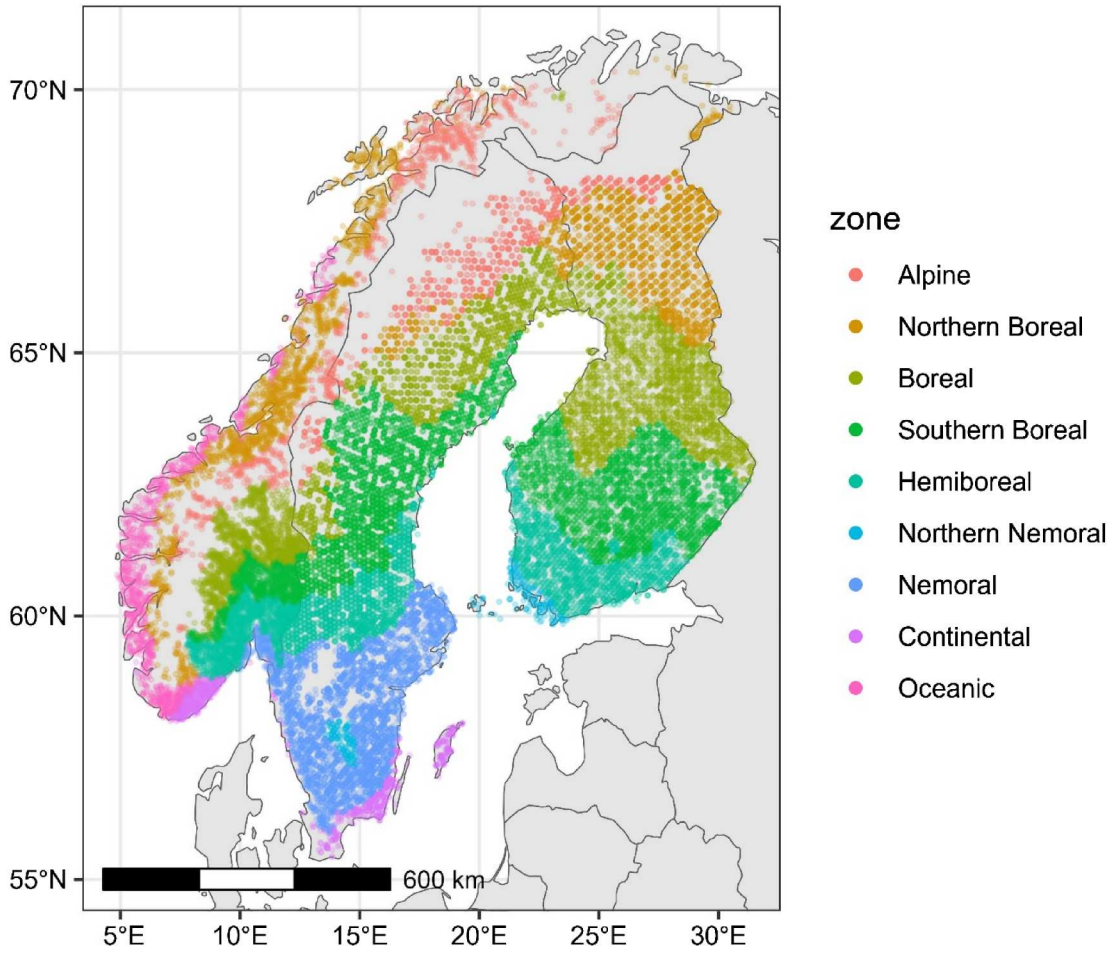

Figure 1. The locations of National Forest Inventory plots according to different climatic zones.

calculated as the difference from the reference period. Preliminary analyses shown high collinearity between MTCQ and TD: we kept TD_ref as indication of continentality, and MTCQ_anom as indication of warming winters (see Mäkinen et al. 2022).

We harmonized the ground vegetation classes (VEG) from the different national systems onto a common scale of increasing site fertility ranging from 1 to 6 (Table 2). Due to the low number of observations and low importance for practical forestry, plots in fertility class 1 were removed.

Modelling approach

The data were analyzed using R Statistical Software (R Core Team, 2025). First, we fitted species-specific Random Forest models (RF) for Δba using the package *ranger* (Wright and Ziegler 2017). Random forest is a machine learning method aggregating many decision trees built on bootstrapped samples of the data. Compared to other statistical models, it has advantages due to implicitly deal with correlation and high dimensional data, and avoiding the need of a priori functional form to be tested (Simon et al. 2023). We tested all the predictors described in the Data Processing subchapter, including the geographical classifications (country and bioclimatic zone). Before fitting the final models, we tested different values for some model hyperparameters (namely number of trees; number of predictor variables to consider at each split; and minimum node size) on a random subset of the data (20% of rows) for each species. We selected the combination of parameters which provided lower out-of-bag error and used them to fit the final models on the full data, ensuring model reliability without overfitting. For each fitted RF model, we subjectively selected the top predictors (around a third of the total variables tested) according to the permutation-based variable importance, i.e. how much the error increases when the values for that predictor are randomly permuted. For the top predictors, we investigated the effect curves by plotting the country-specific Accumulated Local Effect (ALE), i.e. the local prediction response to

Table 2. Ground vegetation classes for each national system and the relative site fertility scale.

VEG	Norwegian class	Swedish class	Finnish class
1	Alpine heath	Poor shrub	Barren heath forests
2	Coastal heath	Crowberry/Heather	Xeric heath forests
2		Sedge, high	
2		Sedge, low	
3	Berry–heather forest	Lingonberry	Sub-xeric heath forests
3	Calcicole herb forest		
4	Bilberry forest	Bilberry	Mesic heath forests
4	Small fern forest	Horsetail, Equisetum ssp.	
4	Floodplain forest		
4	Bilberry oak forest		
4	Bilberry beech forest		
5	Bilberry-rich forest	Broadleaved grass	Herb-rich heath forests
5	Low herb forest	Rich-herb with shrubs/ bilberry	
5	Pasture forest	Rich-herb with shrubs/ lingonberry	
5	Grey alder forest	Low-herb with shrubs/ bilberry	
5	Large fern forest	Low-herb with shrubs/ lingonberry	
5	Tall herb forest	Low-herb without shrubs	
5	Low herb oak forest	Thin leaved grass	
5	Elm-linden forest	No field layer	
5	Rich grass and sedge mire		
6	Low herb beech forest	Rich-herb without shrubs	Herb-rich forests
6	Alder-ash forest		

changes in those variables. We removed predictors showing unplausible biological effects, tune again the hyperparameters, and refit the models until we had a final robust model selection for each species.

Then, similar to the approach described by Bianchi et al. (2023) for a basal-area increment model based solely on Finnish NFI data, we fitted species-specific, nonlinear mixed models for Δba. We used the following nonlinear mixed form (Equation 1), fitted with the package *nlme* (Pinheiro et al. 2025):

$$\Delta ba = \exp\left(b_{pi} + b_1 * V_1 + \ldots + b_n * V_n\right) + \varepsilon_{pi.ml} \quad (1)$$

where Δba is the basal area increment for each individual tree (cm^2 $year^{-1}$); b_{pi} a random intercept for each plot i to account for spatial correlation between trees within the same plot; $V_1 \ldots V_n$ the explanatory variables; $b_1 \ldots b_n$ the coefficients to be determined during model fitting; and $\varepsilon_{pi.ml}$ the error for each measurement l in plot i. We tested the top predictors from the Random Forests models, in their original forms or after transformations (logarithmic, power function, and polynomial terms) as suggested by the results of the Random Forest models. When modelling birch, we included a dummy variable for *Betula pubescens*. However, here we did not use country and bioclimatic zone information to avoid overfitting, testing only climate and vegetation information as an indication of site potential. We later examined the distribution of residuals versus geographical categories to identify potential geographical biases. We began with the full set of predictors and iteratively removed variables to reduce the Akaike Information Criterion (AIC), or if their effects were biologically implausible, indicating potential overfitting. We considered models within a difference of two points in AIC comparable and selected the one with the fewest predictors. We investigated trends in residuals at the species and country levels for each predictor. We did not use any information about age because data were not available at tree level and stand age is not meaningful especially for trees growing in uneven-aged forests.

After finalizing the model structure for each species, we performed cross-validation by randomly partitioning each species-specific dataset into five folds, ensuring that data from the same stand were not split across folds. We refitted the final model structure without one fold and then used it to generate predictions for the omitted data. For those predictions, we calculated the Root Mean Square Error (RMSE, Equation 2); Weighted Absolute Percentage Error (WAPE, Equation 3), a more stringent and scale-independent metric quantifying total absolute prediction error as a percentage of the sum of the observed values, especially useful when there are zero growths in the database. For sensitivity analysis, the simulated growth for each model as a function only of one predictor, which we let to vary from the minimum observed in the modelling data to the maximum observed in the future scenarios. We kept all other model variables at the mean observed in the validation data.

$$RMSE = \sqrt{\frac{1}{2}\sum_{i=1}^{n}\left(y_i - \widehat{y_i}\right)^2} \quad (2)$$

$$WAPE = \frac{\sum_{i=1}^{n}\left|y_i - \widehat{y_i}\right|}{\sum_{i=1}^{n}\left|y_i\right|} \quad (3)$$

Results

The Random Forest models showed similar sets of most important variables across species (Figure 2), mostly with expected biological behaviour (Figures 3–5). Further, within species, there were only small differences across countries for the predictors' responses. Tree size (DBH) had the most importance in all species, with almost a linear positive effect. For pine and spruce there were none or negligible differences across countries for the most representative data. For birch, there was a small negative bias for Norway. Please

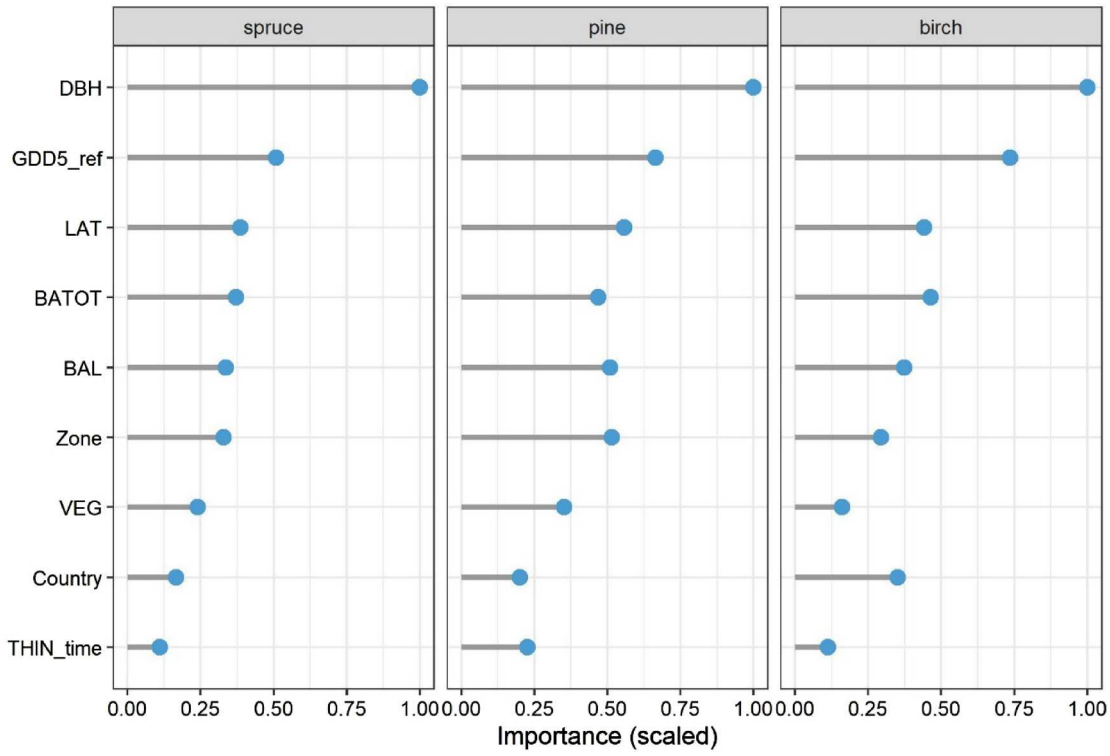

Figure 2. Permutation-based variable importance for each species-specific Random forest model. Values are scaled within each species by dividing by the most important variable value. DBH is diameter at breast height (cm); GDD5_ref is temperature sum for the reference period 1990–2020 (degree days); LAT is latitude (degrees); BATOT and BAL are basal area of all trees and of the trees taller than the target tree, respectively (m^2 ha^{-1}); Zone is bioclimatic zone; VEG is the site fertility classification described in Table 2; THIN_time is the time after the last thinning or partial cutting.

note that across the full DBH range the effect on predictions ranged around 25–35 cm^2 $year^{-1}$, while for the other variables was 2–5 cm^2 $year^{-1}$. Amongst climate variables, GDD5_ref was the second most important variable, and again with a strong positive effect. However, for pine, the effect of very few outliers at the lower end provided a concave response, but that could be easily dismissed as an artefact. For spruce and birch, there were some differences across countries for this species, especially a higher response for Sweden. All other climate variables had to be excluded for their unplausible biological effects, likely sign of overfitting. Then, a group of variables related to competition (BATOT and BAL), geographical location (Latitude and bioclimatic zone), and site fertility (VEG) shown a relatively medium importance. Latitude and bioclimatic were likely complementing photoperiod and additional climate information. Generally, they showed decreasing growth from southern and/or oceanic locations to northern and/or alpine locations. Again, there were influenced by some outliers at the lower latitudes and in fewer represented bioclimatic classes. Differences across countries were evident only in the less representative and harsher climates, Alpine and Northern Boreal. Pine and birch, as expected, showed less growth in Oceanic zone. Both competition variables, BAL and BATOT, showed strong growth reduction for the initial values (up to around 20 m^2 ha^{-1}) and then flattened. Again, some outliers caused unplausible positive behaviours at the very few extreme values. For pine, differences across countries were negligible. For spruce and BATOT, Norwegian trees seemed to suffer less competition at lower values

Table 3. Summary of the random effects models.

Species	Num.trees	mtry	min.node.size	Out-of-bag error	R2	RMSE	WAPE
Spruce	900	3	5	23.7	0.58	4.9	42.6
Pine	900	3	8	19.3	0.47	4.4	40.8
Birch	900	3	8	7.4	0.55	2.7	60.2

Num.trees is the total number of trees grown by the model, mtry is the number of variables randomly selected at every node, min.node.size is the minimum number of observations required in a terminal node, out-of-bag error is the prediction error for the samples not included in each training set, R2 is the variance explained, RMSE is root mean square error, and WAPE is weighted absolute percentage error.

and Finnish trees suffered less at higher values. For birch and both BATOT and BAL, Norwegian trees had a much flatter response to competition, almost negligible for BATOT. VEG showed increasing growth with increasing site fertility, but generally with a pronounced jump at the most fertile sites. The most notable differences across country were evident for spruce, which growth showed a lower response in the Norwegian data. Although $THIN_{time}$ had the least importance amongst the top variables, it showed higher growth for all species and countries in plots recently affected by partial removals of growing stock, which decreased with time and in unthinned plots. Diagnostic summaries for all Random Forest models are shown in Table 3. Although the species-specific Random Forest model incorporated nine predictors and a thorough multiparametric strategy, it captured only 47–58% of the observed variance, with a relatively high WAPE error (40–60%).

We successfully fitted nonlinear mixed models for all species (Table 4). Overall, the growth-relationship for the top predictors (DBH and GDD5_ref) were consistent to the ones indicated by the Random Forest models after log-transformation (Figure 6a and b). Only for pine and GDD5_ref, the relationship in the NLME model was flatter than for the Random Forest. Adding further climatic variables led to overfitting and unrealistic biological effects as in the Random Forest models. For competition, BATOT and BAL (divided by the square root of DBH) showed the same steep initial decrease followed by a lower response (Figure 6c and d) although not as sharp as in the Random Forest models. Latitude resulted significant only for the conifers, although with a relatively low effect (Figure 6e). For all species, VEG was significantly and positively correlated with growth, with a similar magnitude for all species, albeit with a lower effect compared to the other variables (Figure 6, plot f). Due to low number of observations at extreme values and difficult in converging, we simplified VEG with only three classes: VEGlow for the original 2 and 3, VEGhigh for the original 5 and 6, with the original class 4 (around medium fertility) as contrast. Time since the last thinning (TH_{time}) did not result in significant or biologically plausible responses, compared to the effect in the Random Forest models. Only for pine there was a plausible and significant small growth response to thinning in the first period (Table 4), while for the other species it had to be discarded.

The cross-validation showed acceptable levels of error in terms of RMSE, between 2.3 and 6.3 cm^2 $year^{-1}$ (Table 5). However, the results appeared worse when analyzed using WAPE, since the total absolute error was between 45% and 71% of the total observed values, slightly higher than for Random Forest models. WAPE was lower for the conifers and generally comparable between Finland and Sweden, but higher in Norway. However, no heteroscedasticity was observed when plotting the cross-validation residuals against either the geographical classifications (not used in modelling) or the model predictors (Figure 7).

Discussion

Our study is a step towards developing transnational forest growth models for Fennoscandia. Rather than presenting definitive models for operational use, we investigated and demonstrated the feasibility of harmonizing data and modelling approaches across Finland, Norway and Sweden, and revealed some challenges.

Across all species, the Random Forest (RF) models identified a similar set of commonly used biological and ecological drivers of basal area increment. Tree size (DBH) and cumulative temperature sum (GDD5_ref) were the most influential variables with almost linear positive effect in both modelling approaches. Especially, GDD5_ref had a strong positive influence and did not show signs of reaching an optimal plateau. This indicates that, generally in our sites, the 1990–2020 climate reference period still represented a range in which additional warmth generally enhanced tree growth. However, we excluded several climate variables from the RF models because they produced too complex and biologically implausible responses, likely a result of overfitting. Periodic NFI measurements cannot likely capture the short-term climate variability, particularly interannual drought stress, winter conditions, or heat anomalies. Furthermore, accumulated temperature sum alone cannot represent the full regional climate gradient. For that reason, latitude and bioclimatic zone were considered in the RF models, likely as proxies for photoperiod and additional climatic effects. Thus, our approach did not align with in-depth studies on the recent growth decline, which identified higher winter temperatures and greater water deficits as the most likely causes (Mäkinen et al. 2022; Breidenbach et al. 2024; Laudon et al. 2024). In a changing climate, integrating process-based approaches (e.g. soil moisture dynamics, evapotranspiration, and optimum temperature intervals) is necessary to improve predictions of physiological responses (Goude et al. 2022).

Country-level differences in predictor effects were generally small. The RF models revealed only minor deviations, usually in climatic extremes or in scarcely represented bioclimatic zones such as the Alpine and Northern Boreal regions. For birch, Norwegian trees showed slightly lower growth at a given DBH. For

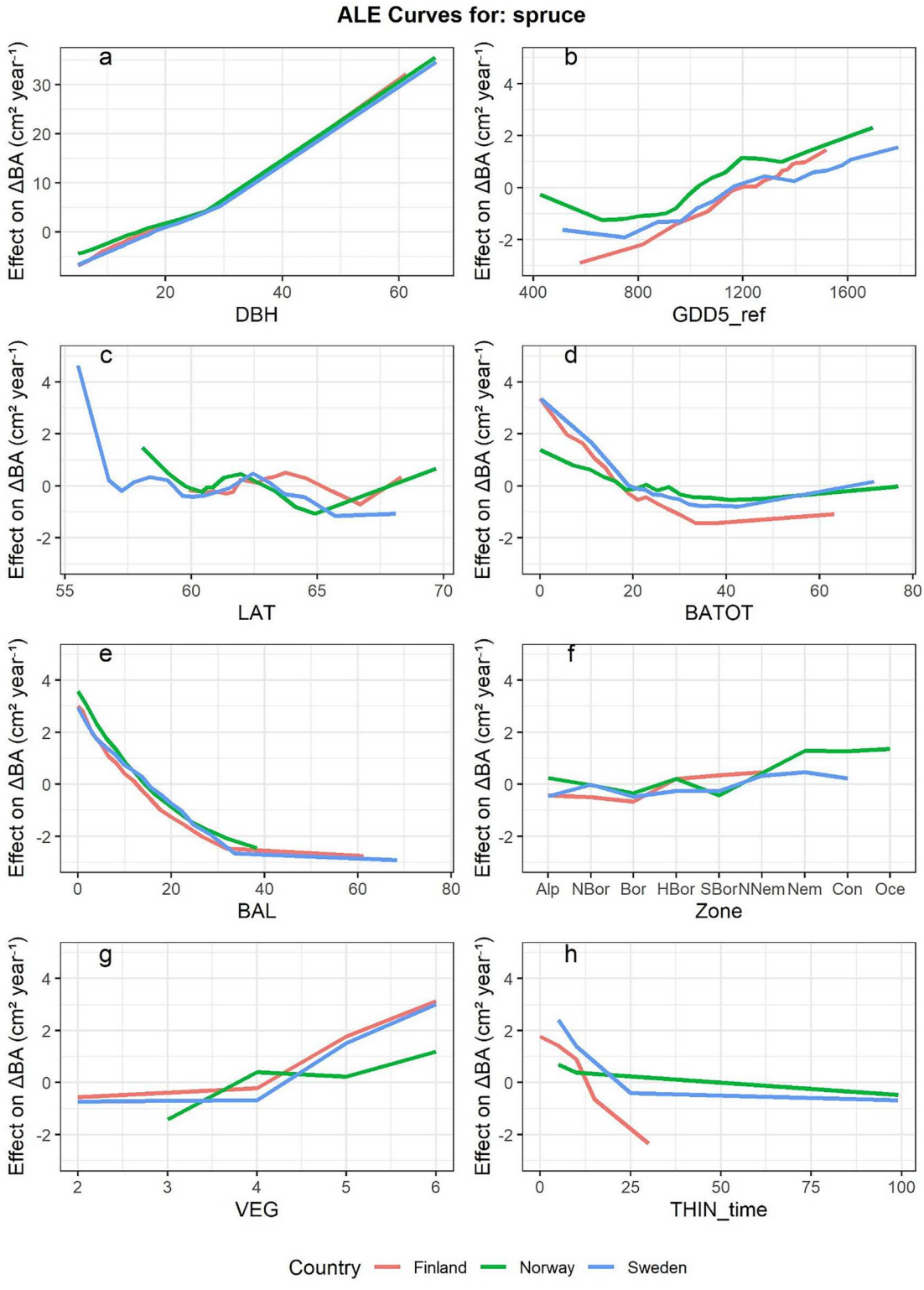

Figure 3. Accumulated Local Effect curves for spruce random forest model. The y-axis is the effect on tree growth (Δba, $cm^2\ year^{-1}$) by modifying each predictor. (a) DBH is diameter at breast height (cm); (b) GDD5_ref is temperature sum for the reference period 1990–2020 (degree days); (c) LAT is latitude (degrees); (d) BATOT and (e) BAL are basal area of all trees and of the trees taller than the target tree, respectively ($m^2\ ha^{-1}$); (f) Zone is bioclimatic zone; (g) VEG is the site fertility classification described in Table 2; (h) THIN_time is the time after the last thinning or partial cutting.

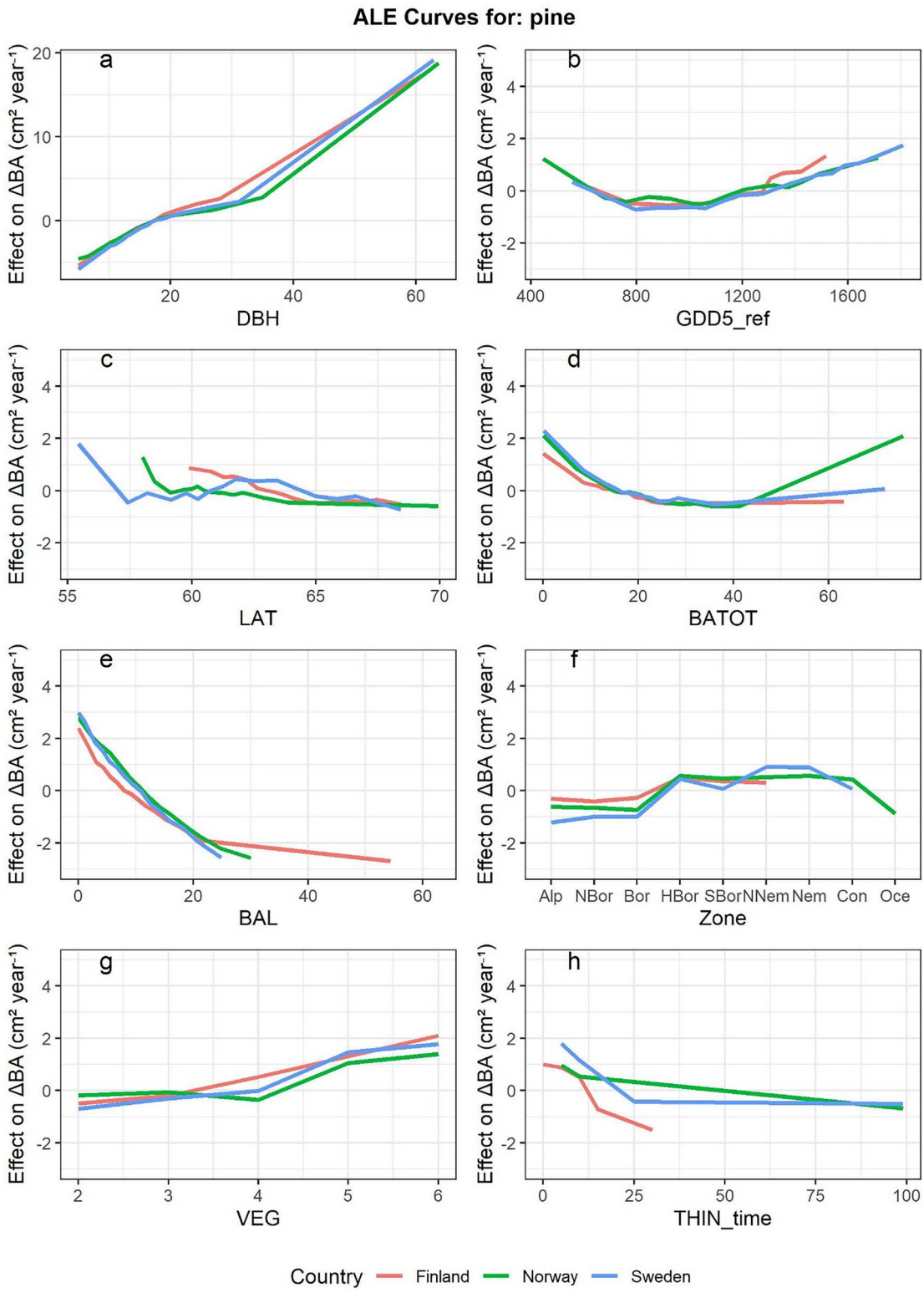

Figure 4. Accumulated Local Effect curves for pine random forest model. The y-axis is the effect on tree growth (Δba, $cm^2\ year^{-1}$) by modifying each predictor. (a) DBH is diameter at breast height (cm); (b) GDD5_ref is temperature sum for the reference period 1990–2020 (degree days); (c) LAT is latitude (degrees); (d) BATOT and (e) BAL are basal area of all trees and of the trees taller than the target tree, respectively ($m^2\ ha^{-1}$); (f) Zone is bioclimatic zone; (g) VEG is the site fertility classification described in Table 2; (h) THIN_time is the time after the last thinning or partial cutting.

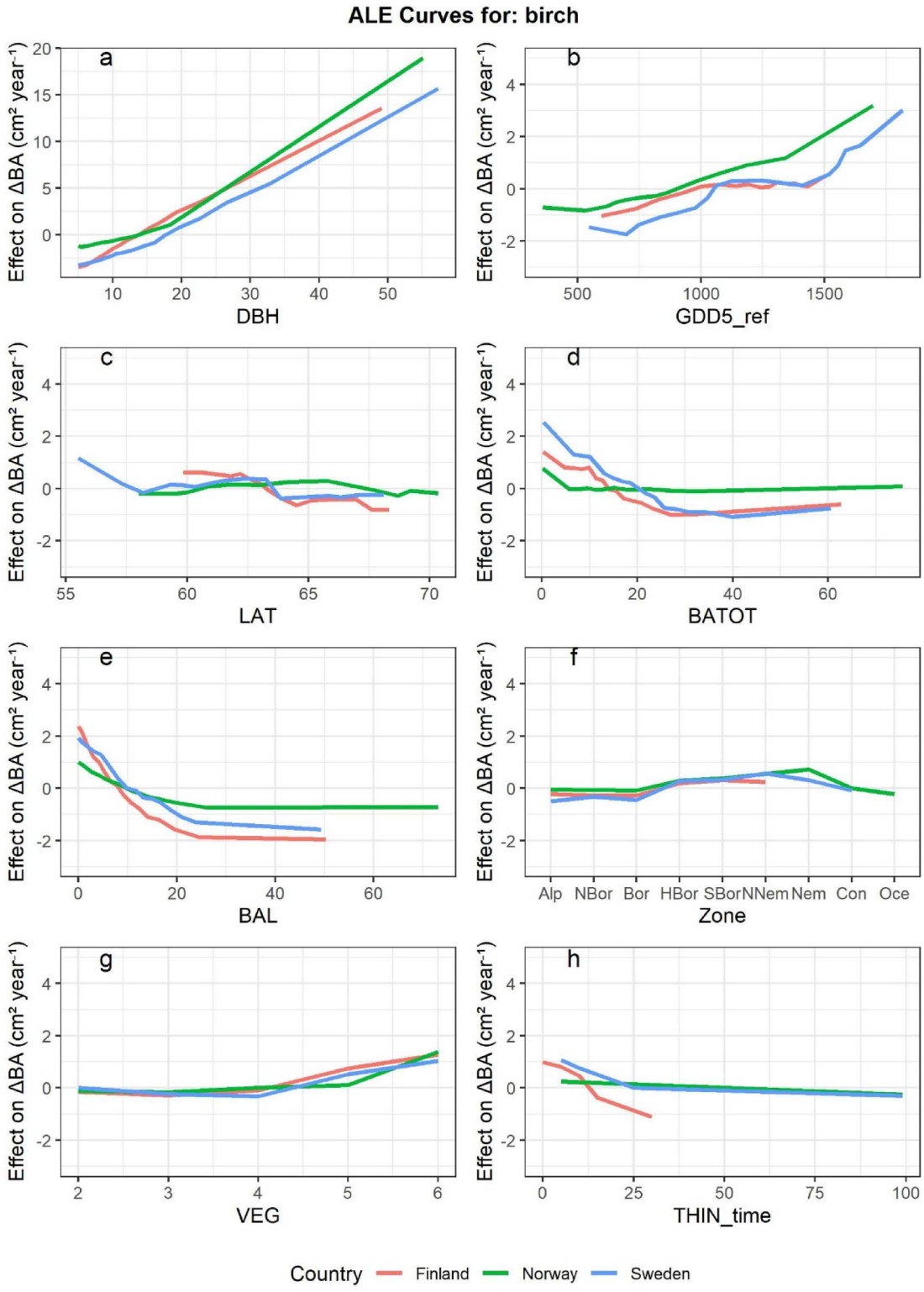

Figure 5. Accumulated Local Effect curves for birch random forest model. The y-axis is the effect on tree growth (Δba, $cm^2\ year^{-1}$) by modifying each predictor. (a) DBH is diameter at breast height (cm); (b) GDD5_ref is temperature sum for the reference period 1990–2020 (degree days); (c) LAT is latitude (degrees); (d) BATOT and (e) BAL are basal area of all trees and of the trees taller than the target tree, respectively ($m^2\ ha^{-1}$); (f) Zone is bioclimatic zone; (g) VEG is the site fertility classification described in Table 2; (h) THIN_time is the time after the last thinning or partial cutting.

Table 4. Summary of species-specific nonlinear mixed models for basal area growth of individual trees.

	Spruce			Pine			Birch		
Predictor	Estimate	SE	pValue	Estimate	SE	pValue	Estimate	SE	pValue
(Intercept)	−4.6188	0.2703	−4.6188	−1.4342	0.2440	<0.0001	−9.4835	0.1566	<0.0001
log(DBH)	1.0237	0.0045	1.0237	0.7084	0.0053	<0.0001	1.1493	0.0085	<0.0001
log(GDD5_ref)	0.9128	0.0219	0.9128	0.5471	0.0207	<0.0001	1.2372	0.0222	<0.0001
BATOT	−0.0256	0.0002	−0.0256	−0.0185	0.0003	<0.0001	−0.0197	0.0005	<0.0001
BAL/sqrt(DBH+1)	−0.0780	0.0007	−0.078	−0.1010	0.0009	<0.0001	−0.1125	0.0017	<0.0001
LAT	−0.0310	0.0022	−0.031	−0.0309	0.0018	<0.0001	NA	NA	NA
VEGlow	−0.1181	0.0080	−0.1181	−0.0365	0.0046	<0.0001	−0.1404	0.0149	<0.0001
VEGhigh	0.0895	0.0043	0.0895	0.0873	0.0042	<0.0001	0.0510	0.0095	<0.0001
THIN_time_05	NA	NA	NA	0.0377	0.0032	<0.0001	NA	NA	NA
Betula pubescens	NA	NA	NA	NA	NA	NA	−0.3694	0.0083	<0.0001
Random effect	**Variance**	**StdDev**		**Variance**	**StdDev**		**Variance**	**StdDev**	
(Intercept)	0.1630	0.4037		0.2599	0.5098		0.3448	0.5872	
residuals	15.842	3.9803		18.541	4.3059		4.9692	2.2291	

DBH is diameter at breast height (cm); GDD5_ref is the temperature sum for the reference period 1990–2020 (°C days); MTCQ_anom is the mean temperature of the coldest quarter, as an anomaly from the reference period 1990–2020 (°C); BATOT is symmetric competition ($m^2\ ha^{-1}$); BAL is asymmetric competition from larger trees ($m^2\ ha^{-1}$); VEG is a categorical classification of ground vegetation indicating increasing fertility, simplified from Table 2 (VEGlow is class 1 and 2, and VEGhigh is 5 and 6); Betula pubescens is a dummy variable for that species; SE is standard error.

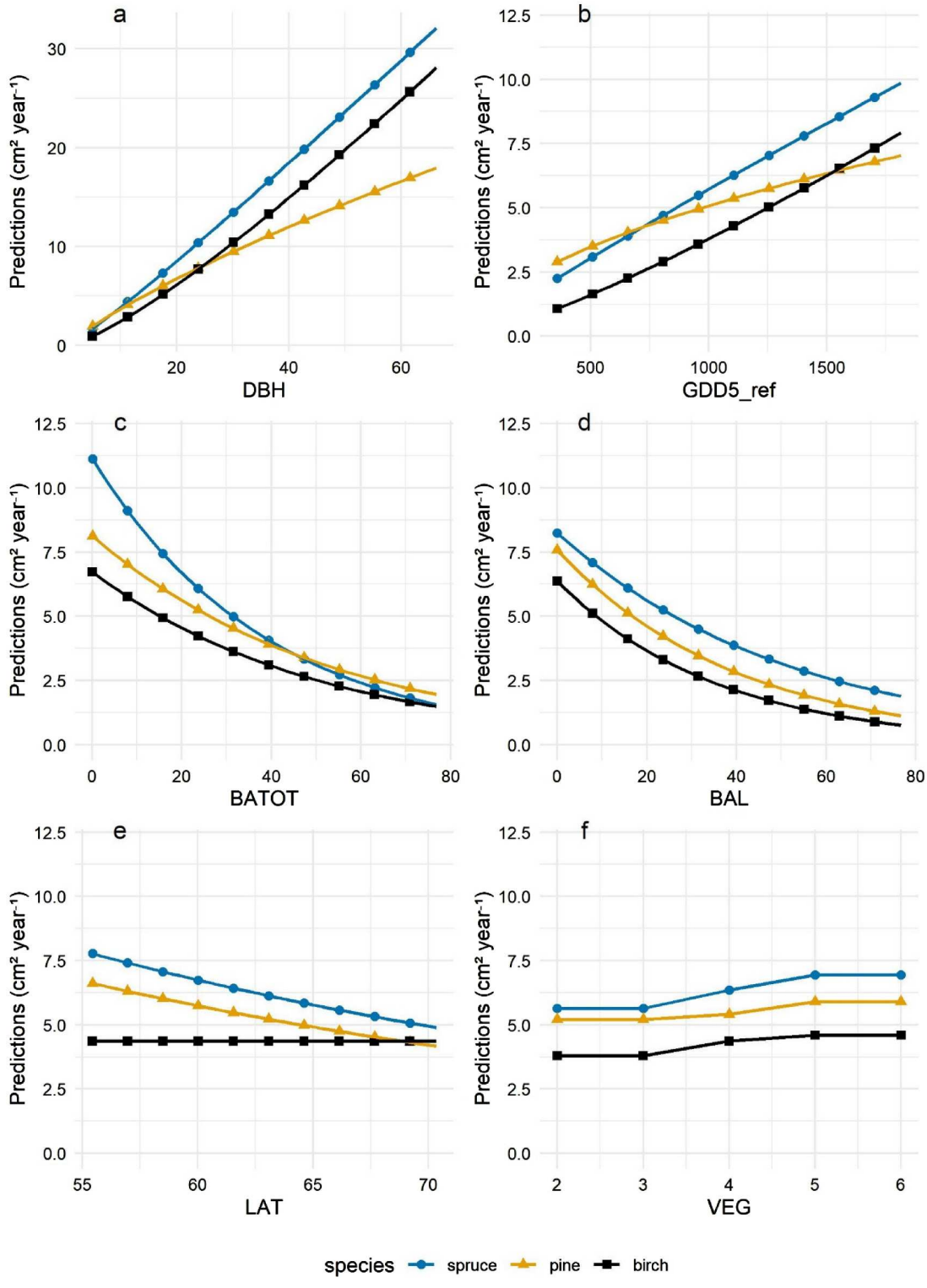

Figure 6. Predictions of the species-specific nonlinear models for the most important predictors across species. (a) DBH is diameter at breast height (cm); (b) GDD5_ref is temperature sum for the reference period 1990–2020 (degree days); (c) BATOT and (d) BAL are basal area of all trees and of the trees taller than the target trees, respectively (m^2 ha^{-1}); (e) LAT is latitude (degrees); (f) VEG is the site fertility classification described in Table 2.

Table 5. Prediction errors of species-specific nonlinear mixed models for basal area growth of individual tree, after cross-validation.

Country	Spruce RMSE	Spruce WAPE	Pine RMSE	Pine WAPE	Birch RMSE	Birch WAPE
Finland	5.63	46.3	4.19	45.1	3.92	47.2
Norway	5.46	57.2	5.27	54.7	2.29	71.2
Sweden	6.24	50.2	5.23	45.2	6.32	60.1

RMSE is root mean square error, and WAPE is weighted absolute percentage error.

spruce, temperature responses were somewhat higher in Sweden and competition effects differed slightly between Finland and Norway. Pine was the most consistent species, with negligible differences across countries.

We successfully developed species-specific nonlinear mixed-effects models (NLMM) based on the most important and biologically interpretable predictors identified from the RF analysis. Especially, we excluded geographic identifiers (country and bioclimatic zone) from the NLMMs to avoid overfitting. Thus, the lack of heteroscedasticity in the residuals across those geographical identifiers suggest that a regional modelling approach could be viable (e.g. Siipilehto et al. 2020, 2021; Lee et al. 2023). Results could be further improved by incorporating additional geomorphological features (e.g. slope and aspect), particularly in mountainous regions (Pretzsch et al. 2002). Soil characteristics (e.g. nutrient availability and soil depth) could complement or replace the coarse and heterogeneous ground vegetation classification employed here (Dănescu et al. 2017). Still, ground flora is often used as a proxy for nutrient availability, pH, and soil moisture to indicate site fertility (Lahti and Väisänen 1987; Pitkänen 1997). In our study, however, these classes did not have a strong effect in the nonlinear mixed models, and they showed some differences across countries in the generalized additive models. Nonetheless, future studies would benefit from a more consistent classification of ground vegetation across Fennoscandia.

We compared the prediction errors of our models with those of other age-independent, individual-tree basal area increment models in the region. The Finnish models, as presented in Bianchi et al. (2023) and Pukkala et al. (2013, 2021), exhibited comparable root mean square error (RMSE) accuracy when converted to one-year periods. However, the models in those previous studies underwent independent validation, mimicking a real-world application with likely higher potential of errors than our own. Similar RMSE values (4–5 cm^2 $year^{-1}$) were also observed for age-independent, individual-tree, basal area increment models from Sweden applied to CCF stands (Fagerberg et al. 2022a, 2022b). The former study involved a smaller dataset and cross-validation, while the latter involved wider independent validation of existing models (including HEUREKA). In Norway, the prediction errors from a similar model by Andreassen and Tomter (2003) cannot be directly compared due to the log-transformation of basal area increment. However, their residual distribution was similar. The comparable magnitude of errors of the present models with national cases provides further evidence of the viability of regional models. Unfortunately, Weighted Absolute Percentage Error (WAPE) remained relatively high (45–70%), likely reflecting the challenge of predicting a wide range of increments in heterogeneous NFI datasets. However, WAPE was not reported for those previous regional modelling studies, limiting direct comparison.

Competition amongst trees, as measured by total basal area or basal area of the larger trees only, had a comparable effect to that observed in other studies (Andreassen and Tomter 2003; Pukkala et al. 2013, 2021; Bianchi et al. 2023). However, we intentionally did not model species-specific competition due to the dominance of pure stands and small plot sizes. Recent tree removals were not significantly or plausibly correlated with tree growth in most cases. A plausible effect was shown only in the first years for pine, contrarily to other studies that observed a positive effect for longer time, albeit sometimes delayed (Hynynen 1995; Bianchi et al. 2023). Kuehne et al. (2022b) found multi-year periodic data, as used in our study, to be reliable enough for individual tree growth models to assess the delayed positive effect of thinning release. In our dataset tree removals were mostly assessed after the events, potentially leading to mistakes in the timing and typology estimations especially across the different datasets, and to unreliable modelling results. Due to the predominant low thinning in the region, it is also possible that higher values of basal area of larger trees is already describing stands without recent thinning interventions (i.e. poorly growing trees under many bigger competitors).

The aim of regional models is not to increase prediction accuracy within each country – local simulators are likely better adapted to local conditions – but rather to provide overall regional benefits, such as increased robustness to changing conditions and broader geographic applications. In any case, independent validation would be needed across the region. We also suggest expanding the scope of the study with more data from each country and by inter-annualizing the periodic growth to better understand the climate-growth relationships (Giebink et al. 2022; Kuehne et al. 2022a).

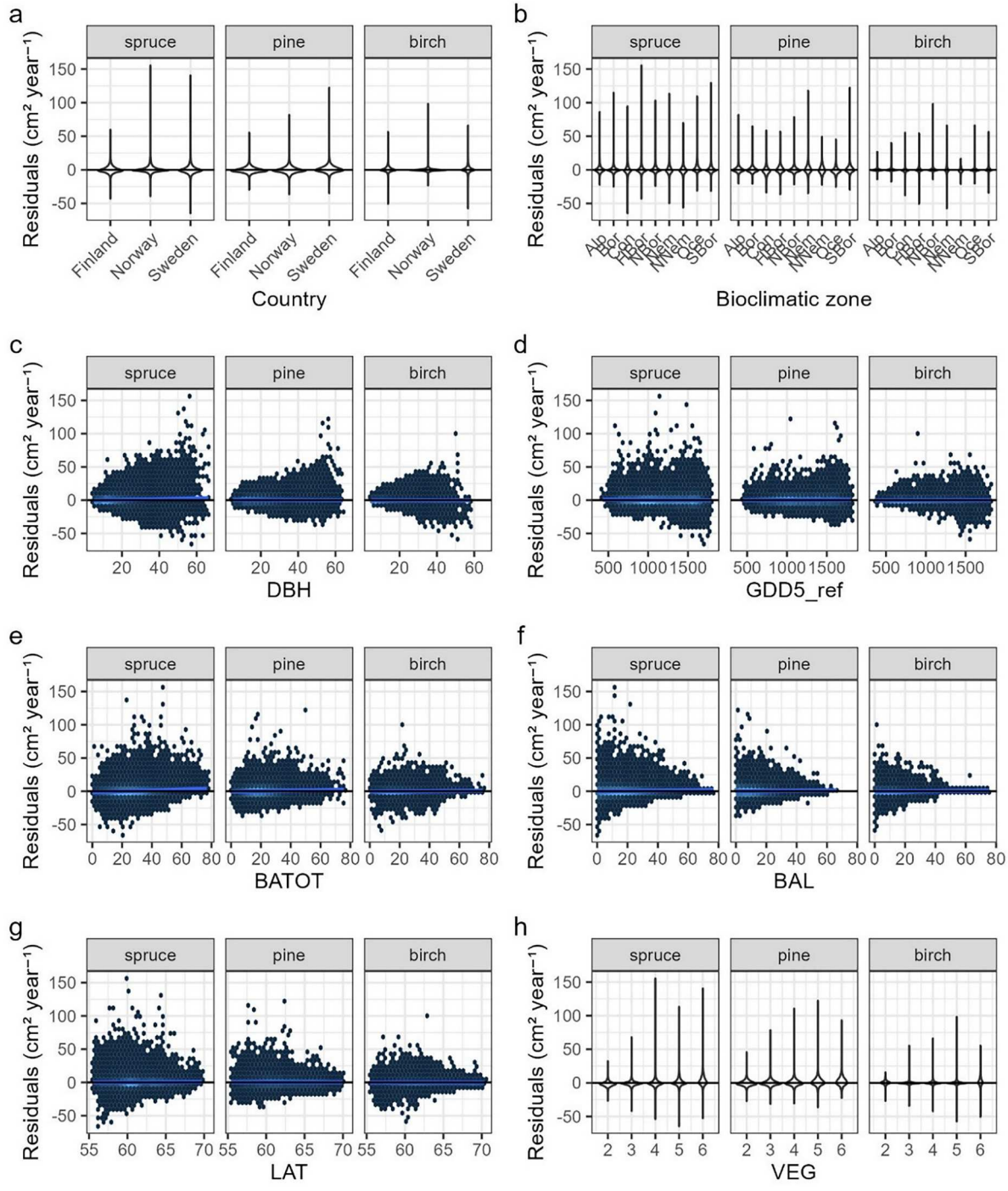

Figure 7. Residuals of the species-specific nonlinear models after cross-validation for the geographical classifications considered and the most important predictors across species. (a) country level; (b) bioclimatic level, where Alp is Alpine, NBor is Northern Boreal, Bor is Boreal, SBor is Southern Boreal, HBor is Hemiboreal, NNem is Northern Nemoral. Nem is Nemoral, Con is Continental, and Oce is Oceanic; (c) DBH is diameter at breast height (cm); (d) GDD5_ref is temperature sum for the reference period 1990–2020 (degree days); (e) BATOT and (f) BAL are basal area of all trees and of the trees taller than the target trees, respectively (m^2 ha^{-1}); (g) LAT is latitude (degrees); (h) VEG is the site fertility classification described in Table 2. The continuous blue line is a LOESS smoother between residuals and variables, practically overlapping the continuous horizontal line with y-intercept 0. Plots a, b & h are violin distribution plots, plots from c to i show higher density of data with brighter colours.

Conclusion

Our study identified the main regional drivers of basal area increment across Fennoscandia, finding that tree size, temperature sum, and competition consistently dominated growth responses as expected. Additional climate variables, including anomalies from the reference period 1990–2020, could not be reliably addressed with periodic NFI measurements. Then, we evaluated whether these drivers were consistent across countries and found only minor differences, mostly in extreme climatic zones and sparsely represented regions, indicating largely shared regional growth dynamics. Third, we developed species-specific nonlinear mixed-effects models that were able to predict basal area increment without systematic geographical bias, demonstrating the feasibility of a regional modelling framework despite only moderate predictive accuracy. Further models should improve on climate sensitivity by hybrid approaches and inter-annualizing tree growth.

Author contributions

CRediT: **Simone Bianchi:** Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft; **Cornelia Roberge:** Data curation, Resources, Writing – review & editing; **Johannes Schumacher:** Data curation, Resources, Writing – review & editing; **Johannes Breidenbach:** Data curation, Resources, Writing – review & editing; **Kari T. Korhonen:** Data curation, Resources, Writing – review & editing; **Harri Mäkinen:** Supervision, Writing – review & editing.

Disclosure statement

No potential conflict of interest was reported by the author(s).

ORCID

Simone Bianchi http://orcid.org/0000-0001-9544-7400
Cornelia Roberge http://orcid.org/0000-0002-0975-8323
Johannes Schumacher http://orcid.org/0000-0003-4592-9035
Johannes Breidenbach http://orcid.org/0000-0002-3137-7236
Kari T. Korhonen http://orcid.org/0000-0002-6198-853X
Harri Mäkinen http://orcid.org/0000-0002-1820-6264

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