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Individual tree basal area increment models suitable for different stand structures in Finland

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ABSTRACT

Forest growth models employed in Fennoscandia have been generally targeted at rotation forestry (RF) stands, relying on age as a key predictor. Uneven aged, irregular stands, such as the ones managed with continuous cover forestry, are becoming of increasingly common. New models suited for all kind of management approaches (i.e., age-independent) have been developed in Fennoscandia. Although the ongoing climate change is projected to strongly affect tree growth in boreal regions, climatic variables included in current models are usually restricted to temperature sum averages with simple links.

The objectives of our research were: 1) fitting a new age independent empirical tree basal area increment model (B2023) with inclusion of additional climatic variables for the main Nordic tree species (Norway spruce, Scots pine, and birches); 2) using independent data to validate both the new model and other two age-independent published empirical models (P2013, P2021); and 3) investigating the sensitivity of growth predictions of all the empirical models to climate change.

Our results showed that the new model B2023 was as accurate as P2013 when independently validated. Both models performed well in different forest structures and management alternatives (namely rotation forestry, continuous cover forestry, two-storied stands, and old-growth natural forests), although with few differences, and on average slightly better than P2021. At plot level, the new model B2023 showed slight underprediction for the overstorey pine layer in continuous cover forestry and two-storied stands. The predicted climate change scenarios increased simulated growth in all models, although P2021 showed very high values for spruce. We failed to include additional climatic variables than temperature sum in B2023, thus not improving much its accuracy under historical data, nor its sensitivity to future climate.

Concluding, the individual tree models here presented can be applied to a wide range of forest structures and managements in Fennoscandia. For long-term simulation scenarios, different approaches to improve the climate sensitivity of empirical, individual tree model should be explored.

1. Introduction

Forest management decision support systems have been widely used to simulate long-term forest growth, compare different scenarios, and predict future developments (Nobre et al., 2016). Many such studies were carried out in Finland to provide information to various stakeholders and decision-makers (e.g. Hynynen et al., 2014, 2015; Tahvonen and Rämö, 2016; Heinonen et al., 2017). Forest management decision support systems are also widely used by forest owners and other stakeholders for long-term planning in non-academic sectors.

Rotation forestry (RF) is currently the most common management regime in Finland. Many forest growth simulators employed in Finland to support decision-making have been calibrated on and targeted at RF stands. Examples are MOTTI (Hynynen et al., 2014), MELA (Hynynen et al., 2002) and SIMO (Härkönen et al., 2010). RF is carried out with final felling followed by artificial and/or natural regeneration that

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Received 1 June 2023; Received in revised form 25 September 2023; Accepted 27 September 2023 Available online 7 October 2023 0378-1127/© 2023 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/). develops at the same time, leading to even-aged stands where average stand conditions are highly correlated to age. Thus, those models are relying on age as one of the key predictors of stand growth (i.e., agedependent).

Uneven-aged and irregular stands, such as the ones resulting from continuous cover forestry (CCF) management, are becoming of increasing importance worldwide, including Fennoscandia (e.g. Kuuluvainen et al., 2012; Lundqvist, 2017). CCF is a silvicultural approach that avoids the use of large clear-felling and thus maintains a continuity of woodland conditions across the site (Mason, 2015). In CCF stands age either is not known or does not describe well the stand conditions, due to the more irregular pattern of regeneration. Thus, models suited for those conditions cannot rely on age (i.e., age-independent). Some age-independent models have been already developed in Finland and they could be applied to both RT and CCF (e.g. Pukkala et al., 2013, 2021).

All the models mentioned so far are empirical (i.e., fitted solely on direct observations with statistical methods), and may simulate regeneration, growth, and mortality of individual trees. The only climatic predictor used in all of them was the accumulated daily temperature above 5° , which always positively affected tree growth (albeit with

different links). The ongoing global climate change is predicted to strongly affect boreal regions. In Finland, mean annual temperature and precipitation are likely to increase by $2-6 \circ C$ and 6-18 %, respectively by 2100 (Kellomäki et al., 2018). These dramatic changes will strongly affect forest development, and they cannot be ignored in longterm simulations. However, if the new climate conditions will fall outside the range of calibration of the models currently employed, their results may not be accurate (Peng, 2000).

Efforts have been made in Finland to prepare forest growth simulators suited to changing climate conditions. PREBAS (Minunno et al., 2019) and FinnFor (Kellomäki and Väisänen, 1997) are process-based models, i.e. they use mathematical formulas representing the physiological response of trees to environmental inputs such as light, water and nutrients. Matala et al. (2005), Matala et al. (2006) integrated some of the physiological principles of FinnFor into MOTTI: first, the relative growth change under both increased temperature and CO₂ compared to the baseline levels was calculated through FinnFor, then the same relative growth change was applied to MOTTI simulations after a calibration based on the tree competition status. Other authors have developed climate responsive forest ecosystem models or gap models



Fig. 1. Location of plots used for modelling (graph a) and for validation (graph b). For the latter, 2S indicates two-storied stands, CCF is continuous cover forestry, NAT is natural, old-growth stands, and RF is rotation forestry.

(Kellomäki et al., 2008, 2018). Process-based models are considered more suitable to address variations in the bio-climatic conditions and for longterm research purposes, although they are less suitable for use in forest management. In this paper we will restrict our scope to the empirical individual tree modelling approach.

Our main aims were i) to prepare new tools for forest growth modelling in the changing forest conditions, namely irregular management approaches and the ongoing climate crisis; and ii) to investigate the responses of empirical forest growth models to climate change. Our specific research objectives were: 1) fitting a new age-independent, empirical, individual tree basal area increment model with inclusion of additional climatic variables; 2) using independent data to validate both the new model and other similar models available in literature; and 3) investigating the response of those models under different climate change scenarios.

2. Materials and methods

2.1. Fitting data

We used data covering the whole range of Finland (Fig. 1a). Although Finland can be considered lying fully within the boreal coniferous zone, four biogeographical or vegetation subzones can be individuated in the country: (from North to South) North-, Middle-, South-, and Hemi-boreal as defined by SYKE (2023). The two datasets used were:

The Finnish National Forest Inventory (NFI) 12 and NFI13 which covers without bias the present conditions of Finnish forests structures throughout the whole country. We retrieved 4.347 variable-radius plots with 71,252 trees. The NFI13 measurements were carried out in 2019 and 2020. We selected the same plots form the NFI12 data where the measurement year was in most cases 2014 or 2015, and in few cases 2016. Thus, typical time interval between the two measurements was 5 years. In NFI13, the plot radius is 4 m for trees with diameter at breast height (dbh) between 4.5 cm and 9.4 cm, and 9 m for trees larger than 9.4 cm in dbh. We selected only plots that were fully within one stand (to avoid as much as possible edge effects). The plots are placed according to a systematic clustered sampling design across the country: for more information, please refer to Korhonen et al. (2021).

The INKA dataset, a set of monitoring plots collected in a subsample of healthy and single-storied stands present in the NFI6 and NFI7. It covered the most common forest stands structure, fertility, and treatments for commercial RF present in the country. We retrieved 1,681 plots (circular with varying diameter, on average size 400 m²) with 62,053 trees. Measurements were carried out across 1976-1993 (2-3 times, on average every 5 years), resulting in 106,923 individual growth measurements. For more information, please refer to Hynynen and Ojansuu (2003).

In both cases, for each tree in the plot, dbh, species, and location were recorded. Total tree height was recorded only for a subsample of trees, and it was estimated for the remaining by calibrating speciesspecific Näslund height curves parameterized using the sub-sample trees (Näslund, 1936). We calculated the tree level growth as the basal area difference between the two measurements, scaled to 5-years. For this study we considered as target species Norway spruce (Picea abies Karst, henceforth spruce), Scots pine (Pinus sylvestris L., henceforth pine), and birch (Betula pendula Roth and Betula pubescens Ehrh.). All remaining species were grouped together and used only to calculate stand characteristics and predictors (see later). A summary of plot data is shown in Table 1.

2.2. Validation data

We used various Long-Term Experiments (LTEs) belonging to Natural Resource Institute Finland (Luonnonvarakeskus, or Luke) (Fig. 1b). In all cases, the same information as in the modelling datasets was

he Oxalis-	hows how	Natural		4,372			12,031				0		0		0		13,271	
includes t	Natural si		ct-	7,262			8,889				12,672		0		0		0	
s: omt +	onia type.		vt	18,820			43,686				78,968		12,762		910		0	
ı each clas	ss of Clado	type	mt	34,635			39,863				73,175		14,596		7,235		13, 271	
ws how many tree remeasurements fall within each class: om ct- the Calluna type and the lower fertility class of Cladonia t		Vegetation	omt+	10,514			12,851				67,980		6,090		7,149		0	
esent, they indicate the minimum, mean and maximum. Vegetation type shows how many tree remeasurements fall within e F Oxalis-Mianthemum type, mt the Myrtillus type, vt the Vaccinium type, and ct- the Calluna type and the lower fertility class imanaged forests (see Methods for more details).	Temp. sum	Degree days	586	1,166	1,546	521	982	1,357		567	1,221 $1,467$	$1,066\ 1,290$	1,514	1,232 $1,305$	1,473	810	1,202 $1,491$	
	Gini coeff.		0.01 0.16	0.44		0.06~0.24	0.48			0.00 0.12	0.33	0.09 0.38	0.70	0.06 0.35	0.57	0.20 0.28	0.47	
	Basal area of larger trees	(m ² /ha)	0.00 11.13	61.00		0.00 11.44	51.47			0.00 14.75	58.70	$0.00\ 13.66$	35.18	0.00 16.46	35.16	0.00 35.00	63.95	
	Basal area	(m ² /ha)	0.15 17.67	61.16		$0.16\ 16.85$	51.70			$0.37\ 24.57$	58.92	7.90 17.46	35.18	9.78 22.55	35.16	18.55 46.49	63.97	
	Mean stand height	(m)	4.13 14.50	29.21		1.85 13.38	28.21			7.14 16.59	30.81	8.32 16.98	27.45	9.56 14.13	20.04	$14.67\ 21.87$	27.98	
	Diameter	(cm)	4.50 15.82	58.60		0.20 13.15	48.50			0.90 16.16	46.80	0.10 10.84	47.75	0.20 10.89	30.40	3.10 18.61	58.70	
	Basal area increment	$(cm^2 5 * year^{-1})$	$-1.00\ 33.21$	333.33		$-1.00\ 28.04$	274.37			$-1.00\ 34.51$	307.03	$-1.00\ 21.13$	288.35	$-1.00\ 33.22$	175.76	$-1.00\ 12.02$	228.00	
alues are p	ility class o rowth or u	Birch trees		12,167			10,463				51,886		3,958		686		885	
sed. When multiple value pe and the higher fertility ents fall within old-grow	Spruce trees	tervals	19,809			34,684			ervals	82,536	82,536	18,270	6,323		11,163			
	vpe and the nents fall v	Pine trees	growing int	39,255			60, 142			of growing in	98,373		11,220		8,285		1,223	
f datasets ו	emeasurer	Plots	Number (4,341			3,081			Number (2,377		168		101		75	
Summary o.	Myrtillus ve many tree r	Dataset	Fitting	NFI			INKA			Validation	RF		CCF		2S		NAT	

collected (Table 1). We did not use these datasets for fitting the models since their coverage was limited regarding site fertility or bioclimatic conditions. However, each dataset was an extensive and detailed example of a specific forest structure or management. All experiments subjected to fertilization of any kind were excluded.

For the rotation forestry (RF) dataset we used three experimental series. HARKAS, including both pine- and spruce-dominated stands for a total of 291 plots (average size 1,000 m²), measured between 1960 s and 2010 s. The experiments were established to evaluate the effect of thinning of various intensities on mid-rotation stands. For more information, please refer to Mäkinen and Isomäki (2004a, 2004b). RKHARV, including birch-dominated stands for a total of 120 plots (average size 1,000 m²), measured between 1960s and 2010s. The experiments were established to investigate the effects of the time and intensity of thinning on the growth and technical quality of birch. For more information please refer to Niemistö (1997). VALJHAKK, including pine-dominated stands on mineral soils in Northern Finland for a total of 108 plots (size 900 m²), measured between 2000s and 2010s). The experiments were established to evaluate the effect of different thinning treatments on growth and regeneration. Some of the stands have been described in Kyrö et al. (2022).

For the continuous-cover forestry (CCF) datasets we used two experimental series. ERIKA, including spruce dominated stands in Central and Southern Finland, for a total of 21 plots (size $1,600 \text{ m}^2$), measured between 1990s and 2020s. The stands had been managed with single-tree selection since the 1980s, and then were selectively harvested 1–2 times during the experiment. They can be characterized as truly multiaged (with trees up to 170 years old) and full-storied (in the sense of Ahlström and Lundqvist, 2015). For more information, please refer to Valkonen et al. (2020). SUO_ERIKA, including pine dominated plots on drained peatlands in Central Finland, for a total of 10 plots (average size $2,100 \text{ m}^2$), measured between 1980s and 2020s. The stands have been managed with different treatments, such as selection cutting, strip cutting, small gap cutting, with different intensities including control plots. Some of the stands have been described in Leppä et al. (2020) and Shanin et al. (2021).

For the two-storied stands (2S) dataset, we used one experimental series: MAALIKU, for a total of 42 plots (average size 750 m^2), measured between 2003 and 2018. The stands are characterized by a dominant layer of either birch or pine, with a vigorous spruce understorey that could fully exploit the improved growing conditions after release from competition. For more information, please refer to Niemistö and Valkonen (2021).

For natural old-growth stands (NAT) dataset, we used one experimental series: LUMES, 53 plots of old-growth spruce dominated natural stands (size 750–3,150 m²), measured between 1991 and 2012. At the time of establishment, the plots had remained unmanaged for several decades and the age of dominant cohort were between 60 and 300 years. Thus, they were considered nearly natural forests. For more information, please refer to Isomäki et al. (1998) and Peltoniemi and Mäkipää (2011).

2.3. Climate data

Climatic data for all the locations were retrieved from ClimateDT (https://www.ibbr.cnr.it/climate-dt/), a web portal where scale-free climatic data are provided freely at global level using CRU-TS data (Harris et al., 2020) for the historical period (1901-current year) (Marchi et al., 2022). We used several climatic predictors: precipitation (based on monthly, seasonal, and annual intervals), mean temperature (based on monthly, seasonal, and annual intervals), temperature sum (annual growing degree-days above 5 °C), aridity indices (derived from both temperature and precipitation, based on seasonal and annual intervals), and continental indices (describing the annual temperature range). For each plot of both the fitting and validation datasets, we retrieved values for each year and then averaged them over every growing interval between remeasurements.

Furthermore, a sample of NFI locations in each bioclimatic regions (5%) were selected to estimate the same variables until year 2098. We used two Representative Concentration Pathway (RCP 2.6 and RCP 8.5, representing respectively a very low and very high greenhouse emission scenario) as defined by the Intergovernmental Panel on Climate Change (IPCC).

2.4. Available models

We searched internet repositories for published stem increment models according to the following criteria: i. individual tree as modelling unit; ii. age-independent; iii. distance-independent, or non-spatially explicit; iv. empirically fitted on data from Fennoscandia. The rationale was to find models suited for forest management planning in the region with relatively simple predictors that are easily available to most stakeholders. The only models fulfilling all criteria were the set of models prepared by Pukkala et al. (2013, 2021) with Finnish data. They both present species-specific, non-linear equations for spruce, pine, and broadleaves (the latter including dummy variables for different species), based on tree characteristics (diameter), competition indices (total stand basal area and species-specific basal area of larger trees, respectively symmetrical and asymmetrical competition), climate (temperature sum), and site fertility (vegetation type).

The set of models from Pukkala et al. (2013), henceforth P2013, was fitted on a dataset comprising two LTEs with multiple plot remeasurements, one experiment with past increment core measurements, and the Finnish NFI8 relascope plots. The data covers the period 1980s-2010s. The set of models from Pukkala et al. (2021), henceforth P2021, was fitted on the Finnish NFI10 and NFI11 relascope plots, covering the period 2005–2013. They were independently validated on a dataset comprising one LTE with multiple plot remeasurements, and one experiment with past increment core measurements (both previously used for modelling in Pukkala2013).

There were other regional individual tree models that did not fulfill all the selection criteria prepared in Norway (Andreassen and Øyen, 2002; Bollandsås and Næsset, 2009; Øyen et al., 2011). They were discarded because they included for site productivity either site index (i.e. dominant stand height at age 40 years, thus not real age-independent models) and/or a combination of latitude and altitude, which would have a very different empirical relationship with tree growth in different countries. Similarly, the age-independent, individual tree models presented in Sweden by Elfving and Nyström (2010) were discarded because they addressed site fertility using, amongst other predictors, soil related variables (such as texture and moisture) not present in our database.

2.5. Data analysis

2.5.1. Fitting of new model

We used the following non-linear mixed model form (Equation (1), fitted with the package *nlme* (Pinheiro et al., 2020) of R Statistical Software (R Core Team, 2022; R Core Team, 2022), to prepare species-specific individual tree basal area increment models:

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

where Δba was the individual tree basal area increment (cm² 5-year⁻¹); b_{pi} a random intercept for each plot *i* to account for the spatial correlation of trees in the same plots; $V_1 \cdots V_n$ the explanatory variables; $b_1 \cdots b_n$ coefficients to be determined during model fitting; and $\varepsilon_{pi,ml}$ the error for each measurement *l* in plot *i*. We used a variance power function to reduce heteroscedasticity (Dănescu et al., 2017; Wang et al., 2019). We fitted models separately for spruce, pine and birch using the same procedures.

We tested a wide range of candidate variables (Table 2), tested either as simple terms, interaction terms or after a transformation (such as

Table 2

List	of	candidate	predictors	for	the	basal	area	increment	model.
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Predictor	Acronym	Unit	Explanation
Tree diameter	dbh	cm	Tree size effect
Stand basal area	BAtot	$m^2 ha^{-1}$	Symmetric competition
Stand basal area,	BAtot.spruce, BAtot.	$m^2 ha^{-1}$	Symmetric competition
species-specific	pine, and BAtot.		for spruce, pine, and
	broadleaves		broadleaves
Basal area of larger trees	BAL	$m^2 ha^{-1}$	Symmetric competition
Basal area of	BALspruce, BALpine,	$m^2 ha^{-1}$	Symmetric competition
larger trees,	and BALbroadleaves		for spruce, pine, and
species-specific			broadleaves
Gini	gini	_	Stand diversity
Lorey's height	hg	m	Mean height, basal area weighted
Time after cutting	tc	_	Grouped by classes: tc1
0			0-5 years, tc2 $6-10$ years
			after, tc3 11-30 years, and
			tc4 > 30 years or never
Vegetation type	omt+, mt, vt, ct-	_	omt + for Oxalis-Myrtillus
			type or more fertile, mt for
			Myrtillus, vt for Vaccinium,
			and ct- for Calluna type or
			less fertile
Temperature sum	GDD5	Degree	Accumulated daily
-		days	temperature over 5 °C
Organic soil	peat	1/0	Organic (1) or mineral soil
-	-		(0)
Natural stands	natural	1/0	Older stands without
			recent management (1) or
			younger, managed stands
			(0)
Downy birch	Bpendula	1/0	Betula pendula (1) or
			Betula pubescens (0).

logarithmic). For the tree characteristics, we considered only tree diameter at breast height (dbh, cm), since it was the only variable measured directly in all calibration trees, both as original value and logor square-transformed terms. For competition we used: basal area sum of all trees (BAtot, m² ha⁻¹), calculated with all trees or only speciesspecific (i.e., only the trees of a certain species, BAtot.spruce, BAtot. pine, and BAtot.broadleaves); basal area sum of trees larger than the subject tree (BAL, m^2 ha⁻¹), calculated with all trees or only speciesspecific (i.e., only the larger trees of a certain species, BALspruce, BALpine, and BALbroadleaves). We also tested transformed terms and weighting the indices by the tree size. For stand diversity, we considered the Gini diversity index calculated with the diameter distribution (gini, dimensionless). For stand development, we considered Lorey's height, i. e., the mean tree height basal-area weighted (hg, m). For silvicultural interventions, we used the time after the last silvicultural intervention (any type of thinning or selective harvesting, without differentiating) using dummy variables as follow: time after cutting class 1 (tc1) if the growth period occurred 0-5 years after the intervention, tc2 if 6-10 years after, tc3 if 11-30 years, and tc4 if more than 30 years or never (used as baseline for the model). To describe the site fertility, we harmonized the NFI numerical classification indicating sites of progressively lower fertility, with the vegetation types according to Cajander (1949) and Tonteri et al. (1990) available for all the other datasets. The resulting classes of progressively lower fertility were: *omt*+ for Oxalis-Myrtillus vegetation type (including the few occurrences of the higher fertility class of Oxalis-Mianthemum type), mt for Myrtillus type, vt for Vaccinium type, and ct- for Calluna type (including the few occurrences of the lower fertility class of Cladonia type). These vegetation types are widely used in Finnish empirical modelling as descriptors for site quality (e.g., Motti, P2013, P2021). For the climate, we tested all the annual variables retrieved from climateDT, avoiding using at the same time more than one index describing the same process (such as temperature or precipitation). Eventually, the only climate variable entering the models (see following model fitting methods) were the temperature sum or growing degree-days above 5 °C (*GDD5*, °C). Additionally, we used some dummy variables to account for specific cases. We used *peat* to indicate peatlands (1) or mineral soils (0). We used *natural* to indicate older stands without recent management (1) or younger, managed stands (0). For the former, we assigned 1 to all fitting data fulfilling at least one of the following conditions: (i) stand age more than 100 and no thinning in the last 30 years, or (ii) forest management restricted by law, with no wood harvesting allowed. For validation data, we assigned 1 only to the NATURAL dataset. Exclusively in the birch model, we used *Bpendula* to differentiate between *Betula pendula* (1) or *Betula pubescens* (0). The range of most variables is shown in Table 1 (although for the competition indices we show only the total and not the species-specific values).

Before fitting the model, trees showing the largest and the smallest 0.1 % of basal area increment values within dbh classes 2 cm large, in both the modelling and validation data, were considered as outliers and removed (similar to Rohner et al., 2018), although they were used for calculating all predictors. We started fitting Equation (1) for each species as full model using all the predictors. Then we started removing predictors according to the following criteria: lower Akaike Information Criteria (AIC), better residual distribution in both the fitting and validation data, and sound biological validity. Eventually we reached a final model structure for each species. Henceforth, we refer to those models as B2023.

2.6. Independent validation

We used all the age-independent models to simulate the individual tree growth in each plot and measurement period of the independent validation dataset (i.e., each growing interval at a time). We considered only trees that were alive both at the beginning and the end of each period (i.e., excluding mortality and regeneration). For all models, we calculated both tree-level results and plot-level aggregates for each measurement period and compared them with the observations. We calculated Root Mean Square Error (RMSE) and Mean Absolute Error (MAE) and investigated trends in residuals both at tree-level and at plotlevel.

2.7. Sensitivity to climate change

We selected random plots from the fitting data in each bioclimatic zone (5% of the plots, around 40–70 per zone). We averaged the present and future GDD5 values for those plots, for 5-years intervals (16 growing periods from 2018 until 2098). We then simulated growth for each model as a function only of GDD5, 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. The rationale was not to get accurate predictions at tree level but only investigating the general climate-growth trend.

3. Results

3.1. Fitting of new model

We successfully fitted species-specific models for all the target species: pine, spruce, and birch (Table 3). For the latter, a dummy variable ensured higher growth for *B. pendula* compared to *B. pubescens*. Almost the same set of predictors were included in all models.

All models included tree size with two terms for diameter, one linear and one logarithmic, resulting in a quasi-sigmoid size-growth relationship that leveled off towards the largest size. On average such relationship fitted very well the observed one for most species and datasets combinations, except for underprediction of birch in 2S throughout the whole size range (less than 700 growth measurements in the whole dataset). Regarding climatic variables, only a positive log-transformed term for temperature sum was included in all models, and only for

Table 3

Summary of the new species-specific models (B2023). For the predictors: dbh is diameter at breast height (1.3 m from ground, in cm); GDD5 the accumulated temperature sum over 5 °C; omt, vt and ct, are respectively the vegetation types Oxalys-Mirtyllus, Vaccinium and Calluna; peat a dummy variable; BAtot the total basal area (m^2/ha) ; BAL the basal area of r trees larger than the subject tree (m^2/ha) , species-specific; tc1, tc2 and tc3 are classes of respectively 0–5, 6–10, and 11–30 years after last thinning; natural a dummy variable for old-growth, unmanaged forests and/or with restricted harvesting; natural and Bpendula dummy variables.

	PINE			SPRUCE			BIRCH		
Predictor	Value	St.error	p-value	Value	St.error	p-value	Value	St.error	p-value
intercept	-4.64676	0.21565	< 0.00001	-27.09344	7.78329	0.00040	-5.58173	0.40542	< 0.00001
log(dbh)	1.11369	0.00773	< 0.00001	0.94019	0.00732	< 0.00001	0.87250	0.01965	< 0.00001
dbh	-0.02383	0.00086	< 0.00001	-0.00569	0.00086	< 0.00001	-0.00550	0.00206	0.00764
GDD5	0.95146	0.03156	< 0.00001	6.85487	2.24376	0.00189	1.10755	0.05838	< 0.00001
GDD5 ²	NA	NA	NA	-0.38412	0.16163	0.01563	NA	NA	NA
omt+	0.11875	0.02746	0.00005	0.31115	0.01983	< 0.00001	0.25799	0.02737	< 0.00001
vt	-0.10105	0.01360	< 0.00001	-0.20045	0.02150	< 0.00001	(2)		
ct-	-0.33276	0.02155	< 0.00001	(1)			(2)		
peat	-0.50327	0.01677	< 0.00001	-0.12026	0.02211	< 0.00001	-0.19974	0.02726	< 0.00001
$\log(BAtot + 1)$	-0.31005	0.00916	< 0.00001	-0.15110	0.00129	< 0.00001	-0.25327	0.02136	< 0.00001
log(BAtot.spruce + 1)	NA	NA	NA	-0.13364	0.00127	< 0.00001	NA	NA	NA
BALpine/sqrt(dbh + 1)	-0.12883	0.00217	< 0.00001	-0.05693	0.00342	< 0.00001	-0.08504	0.00640	< 0.00001
BALspruce/sqrt(dbh + 1)	-0.10176	0.00603	< 0.00001	-0.13438	0.00245	< 0.00001	-0.12606	0.00690	< 0.00001
BALother/sqrt	-0.16954	0.01043	< 0.00001	-0.10034	0.00518	< 0.00001	-0.20389	0.00641	< 0.00001
(dbh + 1)									
tc1	0.11799	0.01020	< 0.00001	0.09863	0.01107	< 0.00001	0.15529	0.02368	< 0.00001
tc2	0.08046	0.01031	< 0.00001	0.14531	0.01277	< 0.00001	0.21034	0.02413	< 0.00001
tc3	0.02804	0.00793	0.00041	0.12821	0.01168	< 0.00001	NA	NA	NA
natural	-0.21470	0.02063	< 0.00001	-0.25715	0.02749	< 0.00001	-0.28851	0.04140	< 0.00001
Bpendula	NA	NA	NA	NA	NA	NA	-0.25282	0.01407	< 0.00001
Random effects	st.dev.			st.dev.			st.dev.		
Plot level	0.37221			0.38369			0.36892		

(1) Class ct- for spruce was considered as vt.

(2) Class ct- and vt for birch was considered as mt.

spruce there was an additional squared term for temperature sum that decreased growth at high temperature values.

The site fertility was addressed by dummy variables for the vegetation types that reflected their general trend of declining fertility from omt+ to vt and then ct-, and an additional negative term if the site was peatland instead of mineral soil. However, for spruce and birch there were not enough calibration data in ct- to determine a sound statistical effect, so that class was merged with vt during model fitting. For birch, then, unexpectedly also the class vt hence defined resulted not significant and merged with mt.

Competition amongst trees included both the symmetric and asymmetric aspects: for the former, a negative log-transformed term for total basal area; and only for spruce, a species-specific term for intraspecific competition. For the asymmetric competition, all species included negative terms for species-specific basal area of larger trees, weighted by the subject tree size.

The past silvicultural history of the plot was considered by dummy variables for the time passed after last thinning, showing a positive effect in the first (tc1) and second (tc2) 5-years period for all species. For spruce and birch, the second 5-years period had a stronger effect than the first, while for pine there was a declining trend with time. Then, only for the conifers there was still a positive effect possibly until 30 years from the intervention (tc3). Additionally, the indicator for old growth and/or unmanaged forests had a negative effect for all species.

3.2. Independent validation

All empirical models were fitting very closely the observed growth in the independent datasets (Fig. 2). Although there was a tendency of underprediction at the highest observed values, for most data (as represented by the ellipse including 95 % of the data points in Fig. 2) the simulated-observed regressions followed the identity line quite closely. More divergent results between models were shown for birch, and for P2013 for spruce.

For B2023, the residual distribution against the simulated values for all models was satisfactory and homogenous in most combinations of species and datasets, unless for few outliers outside the main bulk of data (Fig. 3). The major trends away from null residuals were seen in 2S, where it strongly underpredicted birch and spruce growth at the higher simulated values, and in CCF for birch, where it overpredicted growth for the highest the simulated values. For the other cases, there was a slight overestimation of the model for birch in RF and spruce in CCF, although for just a very small number of observations (<0.5 %).

When data were aggregated at plot level, the three models were even more similar in their predictions and accuracy, with the simulated values fitting quite closely the observations (Fig. 4). The main divergences from the identity line for all models were a slight growth underestimation of the pine component in 2S and of the birch component in RF for the higher values. For the pine component in CCF the B2023 was more accurate with an underestimation at the higher values (that are represented by the SUO_ERIKA dataset of pine dominated stands on drained peatlands), while P2013 and P2021 a strong overestimation. In general, P2023 tended to simulate slightly higher growth than the other two models.

Those above trends were confirmed by the calculation of root mean square errors (RMSE). Both at tree- and plot-level, in most datasets and species, the new model B2023 and P2013 had a similar accuracy, and both were slightly more accurate than P2021, although with few and small exceptions (Table 4).

For the B2023 model, the tree level residuals of the independent validation did not show any trend versus the model predictors for all species, including experimental design characteristics (namely length of the growing period, plot area, and revision year) (Supplementary information Fig. S1).

3.3. Sensitivity to climate change

According to the RCP 2.6 scenario, temperature sum would reach around 150 % of the present values in 2040, and then level off. For RCP 8.5 scenario, it would constantly increase and reach 200 % of the present values in 2100 with no sign of slowing down. No relative differences amongst bioclimatic regions were observed. All models fitted well the



Fig. 2. Simulated versus observed values for independent validation at tree level. Lines are GAM smoothing. Points are displayed only for the new model B2023, while P2013 is the model from Pukkala et al (2013) and P2021 from Pukkala et al. (2021). Diagonal continuous line is the identity line. The red ellipse includes 95% of the data.

temperature-growth relationship observed in the data (Fig. 5), an indication of how well the models behaved in the past and present climate. However, P2021 overpredicted spruce growth at higher temperature values. The sensitivity analysis in Fig. 5 shows the growth of a tree with medium dbh (15 cm), when all other predictors are kept at the medium observed values in the data but GDD5 is let to increase up to the values predicted in the RCP 8.5 scenario. For the future climate (i.e., GDD5 rising from 1,500 and above), tree growth in both birch and pine increased almost linearly with increase of GDD5 for all models, although P2021 showed the highest simulations for pine at all levels. For spruce, the differences were more marked: P2021 and P2013 had respectively a strong and medium exponential growth increase, while B2023 tended to increase more slowly (due to the second quadratic term for GDD5).

4. Discussion

This study expands on previous knowledge of individual tree ageindependent simulators in Fennoscandia, presenting a new set of basal area increment models suitable for all forest structures in Finland and highlighting the need of improved approaches for climate change scenarios.

According to the first research aim, we presented a new set of species-specific models that could be used in a wide range of forest conditions. Their performance was satisfactory in most of the forest structures, from rotation forestry to continuous cover forestry to natural old-growth stands. On average, the new set of models B2023 was as accurate as the previously published P2013, and slightly better than P2021, when independently validated on existing data, i.e., using the historical climate conditions. Overall, there were some biases only in some of the least represented cases, and less accuracy for birch than other species. At tree level, there were biases in the two-storied stands (underprediction for both birch and spruce at high growth) and in the continuous cover forestry (overprediction for birch and spruce growth only at the very highest values). When data were aggregated at stand level, only an underprediction for pine at high levels of growth in the overstorey layer of two-storied stands and in the drained peatlands continuous cover forestry stands was evident. We highlight that model P2021 includes a system for calibrating its simulations given existing growth observations for the units of interest, thus it has the possibility to improve its predictions. Regarding the focus on climate variables, the new model B2023 included only temperature sum as the existing ageindependent models in Finland (P2013, P2021), and only in spruce an additional quadratic term conferred a more curvilinear response to temperature. (Sánchez-Salguero et al., 2015) argued "that the past management of the forest overrides site conditions and climate effects through the legacies on stand structure and competition". That could be



model — B2023

Fig. 3. Raw residuals versus simulated values for independent validation at tree level. Lines are GAM smoothing. Points are displayed only for B2023. Horizontal continuous line is the identity line. The red dashed ellipse includes 95% of the data.

one of the reasons for the lower relative importance of climatic variables compared to other tree and stand predictors.

According to the second research aim, when the three set of models sere tested against future climate change scenarios (i.e., higher levels of temperature sum than the present times), there were more differences than when applied to historical climate data. P2021 showed a higher growth in pine than for the other two models (around 150 %) and a likely biologically unfeasible growth for spruce. P2013 showed higher growth than B2023 above GDD5 values of 2000 but not exceptionally different. The Swedish models from Elfving and Nyström (2010) showed similarities to P2021 for pine and spruce, but quite lower predictions for birch than all Finnish models (results not shown). Empirical models fitted on the past climatic conditions may not be suitable for extrapolation in the dramatically different future climate (Peng, 2000). It comes to no surprise that differences in the empirical model formulas gave small differences within the range of their modelling data but larger ones outside it. We highlight that the climate sensitivity analysis we carried out is not an accurate representation of the future tree growth rate in Finland. For example, Kellomäki et al. (2018) predicted a strong reduction in growth at the southern latitudes of Finland under the same RCP 8.5 scenario, contrary to what the models here tested would

simulate. We were mainly interested in the differences across the models and their general behaviour, which are proof that further research is needed to adapt empirical models to future climate scenarios.

Other individual tree, age-independent models retrieved for Fennoscandia did not use climate predictors but included site productivity only through geographical coordinates or the use of site index (Andreassen and Øyen, 2002; Øyen et al., 2011), or did not consider neither of them (Olsson and Fagerberg, 2019). Those approaches do not address the change in climate for the same location (due to the use of geographical coordinates) or may not be feasible in uneven-aged stands (due to the calculation of site index at a specific age). We are not aware of other empirical individual tree growth models in the Nordic countries addressing climate predictors in a more exhaustive way.

Other predictors behaved as expected: tree size had a positive effect on growth that levelled off for the largest trees, while symmetric competition decreased growth (e.g. Monserud and Sterba, 1996). The species-specific competition indices showed that intraspecific competition was stronger than inter-specific for spruce and birch, while from pine was the less important. For pine competition from broadleaves was the strongest, followed by spruce, and intraspecific the less important. Those results are in line with P2013 and partially with P2021, since in



Fig. 4. Results of independent validation at plot level. Lines are GAM smoothing of simulated values for different models versus observations. Points are displayed only for B2023. Diagonal continuous line is the identity line.

the latter there were not used all the species-specific indices. For Elfving and Nyström (2010), intraspecific competition was the only speciesspecific significant competition, with negative effect for all species although calculated differently (pine and spruce benefited by presence of other species, birch was impaired by other birch). However, in one case (spruce) the model ended up including five different competition indices. A more elegant approach for assessing species-specific competition effects may be the use of a numerical parameter such as wood density instead of several categorical variable (e.g. Kunstler et al., 2012). The dummy variables for site fertility also had effects in line with previous models in Finland, including P2013, P2021 and Motti. However, there were not enough modelling data in CT for spruce and birch. Tree level growth in both peat and old growth, unmanaged forests was lower than in younger, managed forests, in line with existing models (Aakala et al., 2013).

The thinning history of the plots had significant positive effects for all species, although with different temporal trends. Birch reacted more strongly immediately after thinning than both pine and spruce, and then the thinning response decreased with time, disappearing already after 10 years. Birch has been found to rapidly exploit growing space (Wang et al., 1995), sometimes more readily than pine and spruce (Juodvalkis et al., 2005). Spruce had a slow initial response, a peak response at 5years and then a decrease, although the positive effect was maintained until 30 years. Spruce trees usually needs a period of adjustment before being able to fully exploit the growing space (Metslaid et al., 2007; Bianchi et al., 2020), similar to other conifer species (Hann et al., 2003; Kuehne et al., 2016). Pine had its strongest response immediately after thinning, which decreased with time but was still maintained until 30 years. This was different from the above dynamic of slow start and later peak that was previously seen also for pine in Finland by Hynynen (1995), but similar to the results seen in Bianchi et al. (2022). The use of dummy variables indicating wider periods after thinning instead of a continuous annual response was due to the periodical growth measured, but they are still deemed reliable to account for the response after

Table 4

Root mean square errors (RMSE) and Pearson correlation coefficient (r) between simulated and observed values after independent validation for each model, dataset, and species, both at tree and plot level.

Dataset	species	B2023		P2013		P2021		
Tree level (cm ² $5*$ year ⁻¹)		RMSE	Pearson r	RMSE	Pearson r	RMSE	Pearson r	
2S	birch	18.2	0.93	19.9	0.92	19.3	0.86	
28	pine	23.0	0.58	21.1	0.62	21.7	0.60	
28	spruce	6.2	0.89	6.8	0.91	6.1	0.90	
CCF	birch	18.3	0.69	19.3	0.69	18.5	0.63	
CCF	pine	15.5	0.66	19.6	0.64	23.2	0.65	
CCF	spruce	17.6	0.84	16.6	0.84	22.3	0.83	
NAT	birch	15.6	0.60	21.3	0.58	18.4	0.49	
NAT	pine	20.5	0.51	21.2	0.51	29.4	0.52	
NAT	spruce	13.5	0.67	16.0	0.67	22.9	0.66	
RF	birch	19.3	0.66	19.8	0.62	22.5	0.45	
RF	pine	13.7	0.73	14.7	0.73	14.6	0.72	
RF	spruce	19.1	0.74	19.2	0.74	23.0	0.71	
Stand level (m^2 ha ⁻¹ year ⁻¹)		RMSE	Pearson r	RMSE	Pearson r	RMSE	Pearson r	
2S	birch	0.03	0.73	0.03	0.93	0.05	0.48	
2S	pine	0.26	0.68	0.21	0.74	0.21	0.72	
2S	spruce	0.08	0.91	0.07	0.93	0.10	0.92	
CCF	birch	0.04	0.90	0.04	0.92	0.04	0.92	
CCF	pine	0.12	0.95	0.18	0.95	0.24	0.95	
CCF	spruce	0.15	0.74	0.11	0.72	0.28	0.66	
NAT	birch	0.01	0.86	0.04	0.87	0.02	0.82	
NAT	pine	0.03	0.88	0.03	0.88	0.06	0.89	
NAT	spruce	0.10	0.25	0.17	0.22	0.30	0.25	
RF	birch	0.18	0.84	0.19	0.82	0.23	0.77	
RF	pine	0.12	0.92	0.14	0.92	0.15	0.91	
RF	spruce	0.20	0.86	0.21	0.86	0.28	0.83	

thinning (Kuehne et al., 2022). However, the calibration dataset did not record the type and intensity of the last silvicultural treatment. Interventions applied in the different forest silvicultural regimes may have different effect in terms of magnitude and timing of the responses (Hynynen et al., 2019), or even within the same kind of forest management if applied with different types and intensities (Mäkinen and Isomäki, 2004a, 2004b; Kuehne et al., 2016; Bianchi et al., 2020, 2022). That could be one of the reasons of the different results for pine than some previous literature. Still, there were no biases at tree-level for the different thinning classes in all species.

The trees' coordinates were recorded in most datasets, although with some gaps, but they were ignored during model fitting. In spatially explicit models, or distance-dependent, competition is usually function of the subject tree location regarding its competitors. However, they have been proved to provide small or negligible improvements over spatial-independent ones, even in spatially and structurally complex stands (Kuehne et al., 2019; Bianchi et al., 2020). Still, a proper investigation of the long-term consequences of using distance-independent models on irregular structures such as CCF should be carried out. Trees released by competition from selective harvesting or gap creation should have higher simulated growth, which is not possible in distanceindependent models.

To carry out a complete forest development simulation, tools to determine regeneration of new trees and mortality of existing trees are necessary. The ingrowth and mortality tools employed by P2013 and P2021, not tested in this study, do not use climatic predictors like in many other existing empirical models (e.g. Ferguson and Carlson, 1993; Eerikäinen et al., 2007). However, Klopcic and Boncina (2012) and Kolo et al. (2017) found some relationships between climate and regeneration in empirical models built on national forest inventory data. Climate change could have a direct impact on seed production and germination (Walck et al., 2011; Trifković et al., 2023), and tree survival both of at seedling and mature trees stage (e.g. Allen et al., 2010), due to changes in the average climatic pattern and the possible occurrence of more extreme events.

5. Conclusions

We presented new age-independent, distance-independent, empirical tree-level basal area increment models that can be used in the present climatic conditions in almost all forest structures and management regimes for the major tree species in Finland. When running long-term forest growth scenarios, response to the climate crisis should be considered, given the rapid and drastic change in climatic variables. The new models here presented seems to have more conservative results than the other available age-independent models in Finland. However, due to the varying results of the three models tested for the future climate scenarios and their comparison with existing studies, further research on how to improve the sensitivity of empirical models against climate change scenarios (such as hybrid models) is necessary.

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CRediT authorship contribution statement

S. Bianchi: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Writing – original draft. **J. Siipilehto:** Methodology, Writing – review & editing. **J. Repola:** Data curation, Writing – review & editing. **P. Niemisto:** Writing – review & editing. **K. Korhonen:** Data curation, Writing – review & editing. **M. Peltoniemi:** Data curation, Writing – review & editing. **H. Salminen:** Funding acquisition, Writing – review & editing. **J. Hynynen:** Supervision, Writing – review & editing.

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.



Fig. 5. Simulations of growth for all models according to increase of GDD5 (accumulated temperature sum above 5 °C). The continuous black line represents a GAM smoothing between growth and GDD5 observed in the data.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121467.

References

- Aakala, T., Fraver, S., D'Amato, A.W., Palik, B.J., 2013. Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA. Forest Ecology and Management 308, 128–135. https://doi.org/10.1016/j. foreco.2013.07.057.
- Ahlström, M.A., Lundqvist, L., 2015. Stand development during 16–57 years in partially harvested sub-alpine uneven-aged Norway spruce stands reconstructed from increment cores. Forest Ecology and Management 350, 81–86.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001.
- Andreassen, K., Øyen, B.-H., 2002. Economic consequences of three silvicultural methods in uneven-aged mature coastal spruce forests of central Norway. Forestry 75, 483–488. https://doi.org/10.1093/forestry/75.4.483.

- Bianchi, S., Myllymaki, M., Siipilehto, J., Salminen, H., Hynynen, J., Valkonen, S., 2020. Comparison of spatially and nonspatially explicit nonlinear mixed effects models for norway spruce individual tree growth under single-tree selection. Forests 11, 1338. https://doi.org/10.3390/f11121338.
- Bianchi, S., Huuskonen, S., Hynynen, J., Siipilehto, J., Niemistö, P., 2022. Tree-level differences in Norway spruce and Scots pine growth after extreme thinning treatments. Scandinavian Journal of Forest Research 37, 109–118. https://doi.org/ 10.1080/02827581.2022.2045348.
- Bollandsås, O.M., Næsset, E., 2009. Weibull models for single-tree increment of Norway spruce, Scots pine, birch and other broadleaves in Norway. Scandinavian Journal of Forest Research 24, 54–66. https://doi.org/10.1080/02827580802477875.
- Cajander, A.K., 1949. Forest types and their significance. Suomalaisen Kirjallisuuden Seuran Kirjapainon Oy, Helsinki, Finland.
- Dănescu, A., Albrecht, A.T., Bauhus, J., Kohnle, U., 2017. Geocentric alternatives to site index for modeling tree increment in uneven-aged mixed stands. Forest Ecology and Management 392, 1–12. https://doi.org/10.1016/j.foreco.2017.02.045.
- Eerikäinen, K., Miina, J., Valkonen, S., 2007. Models for the regeneration establishment and the development of established seedlings in uneven-aged, Norway spruce dominated forest stands of southern Finland. Forest Ecology and Management 242, 444–461. https://doi.org/10.1016/j.foreco.2007.01.078.
- Elfving, B., Nyström, K., 2010. Growth modelling in the Heureka system. Department of Forest Ecology and Management, Swedish University of Agricultural Sciences: Ume \aa, Sweden 97.
- Ferguson, D.E., Carlson, C.E., 1993. Predicting regeneration establishment with the Prognosis Model.pdf.
- Hann, D.W., Marshall, D.D., Hanus, M.L., Laboratory, O.S.U.F.R., 2003. Equations for predicting height-to-crown-base, 5-year diameter-growth rate, 5-year height-growth rate, 5-year mortality rate, and maximum size-density trajectory for Douglas-fir and western hemlock in the coastal region of the Pacific Northwest (No. 40), Research Contribution. Orgeon State University.

Härkönen, S., Mäkinen, A., Tokola, T., Rasinmäki, J., Kalliovirta, J., 2010. Evaluation of forest growth simulators with NFI permanent sample plot data from Finland. Forest Ecology and Management 259, 573–582. https://doi.org/10.1016/j. foreco.2009.11.015.

- Harris, I., Osborn, T.J., Jones, P., Lister, D., 2020. Version 4 of the CRU TS monthly highresolution gridded multivariate climate dataset. Scientific Data 7, 1–18.
- Heinonen, T., Pukkala, T., Mehtätalo, L., Asikainen, A., Kangas, J., Peltola, H., 2017. Scenario analyses for the effects of harvesting intensity on development of forest resources, timber supply, carbon balance and biodiversity of Finnish forestry. Forest Policy and Economics 80, 80–98. https://doi.org/10.1016/j.forpol.2017.03.011.
- Hynynen, J., 1995. Predicting the growth response to thinning for Scots pine stands using individual-tree growth models. Silva Fennica 29, 225–246.
 Hynynen, J., Eerikäinen, K., Mäkinen, H., Valkonen, S., 2019. Growth response to
- cuttings in Norway spruce stands under even-aged and uneven-aged management. Forest Ecology and Management 437, 314–323. https://doi.org/10.1016/j. foreco.2018.12.032.

Hynynen, J., Salminen, H., Ahtikoski, A., Huuskonen, S., Ojansuu, R., Siipilehto, J., Lehtonen, M., Rummukainen, A., Kojola, S., Eerikäinen, K., 2014. Scenario analysis for the biomass supply potential and the future development of Finnish forest resources (No. 302), Working Papers of the Finnish Forest Research Institute. Finnish Forest Research Institute, Vantaa, Finland.

Hynynen, J., Ojansuu, R., 2003. Impact of plot size on individual-tree competition measures for growth and yield simulators. Canadian Journal of Forest Research 33, 455–465. https://doi.org/10.1139/x02-173.

Hynynen, J., Ojansuu, R., Hökkä, H., Siipilehto, J., Salminen, H., Haapala, P., 2002. Models for predicting stand development in MELA System. Metsäntutkimuslaitos.

Hynynen, J., Salminen, H., Ahtikoski, A., Huuskonen, S., Ojansuu, R., Siipilehto, J., Lehtonen, M., Eerikäinen, K., 2015. Long-term impacts of forest management on biomass supply and forest resource development: a scenario analysis for Finland. European Journal of Forest Research 134, 415–431. https://doi.org/10.1007/ s10342-014-0860-0.

Isomäki, A., Niemistö, P., Varmola, M., 1998. Luonnontilaisten metsien rakenne seurantakoealoilla.

- Juodvalkis, A., Kairiukstis, L., Vasiliauskas, R., 2005. Effects of thinning on growth of six tree species in north-temperate forests of Lithuania. European Journal of Forest Research 124, 187–192. https://doi.org/10.1007/s10342-005-0070-x.
- Kellomäki, S., Strandman, H., Heinonen, T., Asikainen, A., Venäläinen, A., Peltola, H., 2018. Temporal and Spatial Change in Diameter Growth of Boreal Scots Pine, Norway Spruce, and Birch under Recent-Generation (CMIP5) Global Climate Model Projections for the 21st Century. Forests 9, 118. https://doi.org/10.3390/f9030118.
- Kellomäki, S., Väisänen, H., 1997. Modelling the dynamics of the forest ecosystem for climate change studies in the boreal conditions. Ecological Modelling 97, 121–140. https://doi.org/10.1016/S0304-3800(96)00081-6.
- Kellomäki, S., Peltola, H., Nuutinen, T., Korhonen, K.T., Strandman, H., 2008. Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. Philosophical Transactions of the Royal Society b: Biological Sciences 363, 2339–2349. https://doi.org/10.1098/rstb.2007.2204.
- Klopcic, M., Boncina, A., 2012. Recruitment of tree species in mixed selection and irregular shelterwood forest stands. Annals of Forest Science 69, 915–925. https:// doi.org/10.1007/s13595-012-0224-1.

Kolo, H., Ankerst, D., Knoke, T., 2017. Predicting natural forest regeneration: a statistical model based on inventory data. European Journal of Forest Research 136, 923–938. https://doi.org/10.1007/s10342-017-1080-1.

- Korhonen, K.T., Ahola, A., Heikkinen, J., Henttonen, H.M., Hotanen, J.-P., Ihalainen, A., Melin, M., Pitkänen, J., Räty, M., Sirviö, M., Strandström, M., 2021. Forests of Finland 2014–2018 and their development 1921–2018. Silva Fennica 55.
- Kuehne, C., Weiskittel, A.R., Wagner, R.G., Roth, B.E., 2016. Development and evaluation of individual tree- and stand-level approaches for predicting spruce-fir response to commercial thinning in Maine, USA. Forest Ecology and Management 376, 84–95. https://doi.org/10.1016/j.foreco.2016.06.013.
- Kuehne, C., Weiskittel, A.R., Waskiewicz, J., 2019. Comparing performance of contrasting distance-independent and distance-dependent competition metrics in predicting individual tree diameter increment and survival within structurallyheterogeneous, mixed-species forests of Northeastern United States. Forest Ecology and Management 433, 205–216. https://doi.org/10.1016/j.foreco.2018.11.002.

Kuehne, C., Weiskittel, A.R., Granhus, A., 2022. Examining approaches for modeling individual tree growth response to thinning in Norway spruce. Forest Ecosystems 9, 100060. https://doi.org/10.1016/j.fecs.2022.100060.

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N.E., Kattge, J., Coomes, D.A., 2012. Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. Ecology Letters 15, 831–840. https:// doi.org/10.1111/j.1461-0248.2012.01803.x.

Kuuluvainen, T., Tahvonen, O., Aakala, T., 2012. Even-aged and uneven-aged forest management in boreal fennoscandia: A review. Ambio 41, 720–737. https://doi.org/ 10.1007/s13280-012-0289-y.

- Kyrö, M.J., Hallikainen, V., Valkonen, S., Hyppönen, M., Puttonen, P., Bergsten, U., Winsa, H., Rautio, P., 2022. Effects of overstory tree density, site preparation, and ground vegetation on natural Scots pine seedling emergence and survival in northern boreal pine forests. Canadian Journal of Forest Research 52, 860–869. https://doi. org/10.1139/cjfr-2021-0101.
- Leppä, K., Hökkä, H., Laiho, R., Launiainen, S., Lehtonen, A., Mäkipää, R., Peltoniemi, M., Saarinen, M., Sarkkola, S., Nieminen, M., 2020. Selection cuttings as a tool to control water table level in boreal drained peatland forests. Frontiers in Earth Science 8, 576510. https://doi.org/10.3389/feart.2020.576510.

- Lundqvist, L., 2017. Tamm Review: Selection system reduces long-term volume growth in Fennoscandic uneven-aged Norway spruce forests. Forest Ecology and Management 391, 362–375. https://doi.org/10.1016/j.foreco.2017.02.011.
- Mäkinen, H., Isomäki, A., 2004a. Thinning intensity and growth of Norway spruce stands in Finland. Forestry 77, 349–364. https://doi.org/10.1093/forestry/77.4.349.
- Mäkinen, H., Isomäki, A., 2004b. Thinning intensity and growth of Scots pine stands in Finland. Forest Ecology and Management 201, 311–325. https://doi.org/10.1016/j. foreco.2004.07.016.

Marchi, M., Bergante, S., Ray, D., Barbetti, R., Facciotto, G., Chiarabaglio Pier, M., Hynynen, J., Nervo, G., 2022. Universal reaction norms for the sustainable cultivation of hybrid poplar clones under climate change in Italy. iForest 15, 47–55. https://doi.org/10.3832/ifor3989-015.

- Mason, W., 2015. Implementing continuous cover forestry in planted forests: experience with sitka spruce (Picea Sitchensis) in the British Isles. Forests 6, 879–902. https:// doi.org/10.3390/f6040879.
- Matala, J., Ojansuu, R., Peltola, H., Sievänen, R., Kellomäki, S., 2005. Introducing effects of temperature and CO2 elevation on tree growth into a statistical growth and yield model. Ecological Modelling 181, 173–190. https://doi.org/10.1016/j. ecolmodel 2004 06 030
- Matala, J., Ojansuu, R., Peltola, H., Raitio, H., Kellomäki, S., 2006. Modelling the response of tree growth to temperature and CO2 elevation as related to the fertility and current temperature sum of a site. Ecological Modelling 199, 39–52. https://doi. org/10.1016/j.ecolmodel.2006.06.009.
- Metslaid, M., Jögiste, K., Nikinmaa, E., Moser, W.K., Porcar-Castell, A., 2007. Tree variables related to growth response and acclimation of advance regeneration of Norway spruce and other coniferous species after release. Forest Ecology and Management 250, 56–63. https://doi.org/10.1016/j.foreco.2007.03.009.
- Minunno, F., Peltoniemi, M., Härkönen, S., Kalliokoski, T., Makinen, H., Mäkelä, A., 2019. Bayesian calibration of a carbon balance model PREBAS using data from permanent growth experiments and national forest inventory. Forest Ecology and Management 440, 208–257. https://doi.org/10.1016/j.foreco.2019.02.041.
- Monserud, R.A., Sterba, H., 1996. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. Forest Ecology and Management 80, 57–80. https://doi.org/10.1016/0378-1127(95)03638-5.
- Näslund, M., 1936. Skogsforsoksasstaltens gallringsforsokitallskong. Meddelanden fran Statens Skogsforsoksanstal 29, 1–169.
- Niemistö, P., Valkonen, S., 2021. Growth response to thinning in two-storied mixed stands of Scots pine and Norway spruce. Scandinavian Journal of Forest Research 36, 448–459. https://doi.org/10.1080/02827581.2021.1961017.
- Niemistö, P., 1997. Niemistö P. Ensiharvennuksen ajankohdan ja voimakkuuden vaikutus istutetun rauduskoivikon kasvuun ja tuotokseen 439-454. Metsätieteen aikakauskirja 439–454.
- Nobre, S., Eriksson, L.-O., Trubins, R., 2016. The use of decision support systems in forest management: analysis of FORSYS country reports. Forests 7, 72. https://doi.org/ 10.3390/f7030072.
- Olsson, J.-O., Fagerberg, N., 2019. En avståndsberoende tillväxtmodell på trädnivå för gran: en preliminär modell baserad på två skiktade bestånd i Götaland [A distancedependent growth model at tree level for spruce: -a preliminary model based on two uneven-sized stands in Götaland]. Linnaeus University, Department of Forestry and Wood Technology.
- Øyen, B.-H., Nilsen, P., Bøhler, F., Andreassen, K., 2011. Predicting individual tree and stand diameter increment responses of Norway spruce (Picea abies (L.) Karst.) after mountain forest selective cutting. Forestry Studies 55, 33–45. https://doi.org/ 10.2478/v10132-011-0100-z.
- Peltoniemi, M., Mäkipää, R., 2011. Quantifying distance-independent tree competition for predicting Norway spruce mortality in unmanaged forests. Forest Ecology and Management 261, 30–42. https://doi.org/10.1016/j.foreco.2010.09.019.
- Peng, C., 2000. Growth and yield models for uneven-aged stands: past, present and future. Forest Ecology and Management 132, 259–279. https://doi.org/10.1016/ S0378-1127(99)00229-7.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2020. nlme: Linear and Nonlinear Mixed Effects Models.
- Pukkala, T., L\u00e4hde, E., Laiho, O., 2013. Species interactions in the dynamics of even- and uneven-aged boreal forests. Journal of Sustainable Forestry 32, 371–403. https:// doi.org/10.1080/10549811.2013.770766.
- Pukkala, T., Vauhkonen, J., Korhonen, K.T., Packalen, T., 2021. Self-learning growth simulator for modelling forest stand dynamics in changing conditions. Forestry: an International Journal of Forest Research 94, 333–346. https://doi.org/10.1093/ forestry/cpab008.
- R Core Team, 2022. R: A Language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rohner, B., Waldner, P., Lischke, H., Ferretti, M., Thürig, E., 2018. Predicting individualtree growth of central European tree species as a function of site, stand, management, nutrient, and climate effects. European Journal of Forest Research 137, 29–44. https://doi.org/10.1007/s10342-017-1087-7.
- Sánchez-Salguero, R., Linares, J.C., Camarero, J.J., Madrigal-González, J., Hevia, A., Sánchez-Miranda, Á., Ballesteros-Cánovas, J.A., Alfaro-Sánchez, R., García-Cervigón, A.I., Bigler, C., Rigling, A., 2015. Disentangling the effects of competition and climate on individual tree growth: A retrospective and dynamic approach in Scots pine. Forest Ecology and Management 358, 12–25. https://doi.org/10.1016/j. foreco.2015.08.034.
- Shanin, V., Juutinen, A., Ahtikoski, A., Frolov, P., Chertov, O., Rämö, J., Lehtonen, A., Laiho, R., Mäkiranta, P., Nieminen, M., Laurén, A., Sarkkola, S., Penttilä, T., Ťupek, B., Mäkipää, R., 2021. Simulation modelling of greenhouse gas balance in continuous-cover forestry of Norway spruce stands on nutrient-rich drained

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peatlands. Forest Ecology and Management 496, 119479. https://doi.org/10.1016/j. foreco.2021.119479.

- SYKE, 2023. Metsäkasvillisuusvyöhykkeet [WWW Document]. URL https://ckan. ymparisto.fi/en/dataset/metsakasvillisuusvyohykkeet (accessed 1.10.23). Tahvonen, O., Rämö, J., 2016. Optimality of continuous cover vs. clear-cut regimes in
- managing forest resources. Canadian Journal of Forest Research 46, 891–901. Tonteri, T., Hotanen, J.-P., Kuusipalo, J., 1990. The Finnish forest site type approach:
- ordination and classification studies of mesic forest sites in southern Finland. Vegetatio 87, 85–98. https://doi.org/10.1007/BF00045658.
- Trifković, V., Bončina, A., Ficko, A., 2023. Recruitment of European beech, Norway spruce and silver fir in uneven-aged forests: optimal and critical stand, site and climatic conditions. Forest Ecology and Management 529, 120679. https://doi.org/ 10.1016/j.foreco.2022.120679.
- Valkonen, S., Aulus Giacosa, L., Heikkinen, J., 2020. Tree mortality in the dynamics and management of uneven-aged Norway spruce stands in southern Finland. European Journal of Forest Research 139, 989–998. https://doi.org/10.1007/s10342-020-01301-8.
- Walck, J.L., Hidayati, S.N., Dixon, K.W., Thompson, K., Poschlod, P., 2011. Climate
- change and plant regeneration from seed. Global Change Biology 17, 2145–2161.Wang, W., Chen, X., Zeng, W., Wang, J., Meng, J., 2019. Development of a mixed-effects individual-tree basal area increment model for oaks (Quercus spp.) considering
- forest structural diversity. Forests 10, 474. https://doi.org/10.3390/f10060474. Wang, J.R., Simard, S.W., (Hamish) Kimmins, J.P., 1995. Physiological responses of
- paper birch to thinning in British Columbia. Forest Ecology and Management 73, 177–184. https://doi.org/10.1016/0378-1127(94)03489-J.