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Testing the application of process-based forest growth model PREBAS to uneven-aged forests in Finland

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ABSTRACT

The challenges of applying process-based models to uneven-aged forests are the difficulties in simulating the interactions between trees and resource allocation between size classes. In this study, we focused on a process-based forest growth model PREBAS which is a mean tree model with Reineke self-thinning mortality and was originally developed for even-aged forests. The primary aim was to test the application of PREBAS model to uneven-aged forests by introducing different diameter at breast height (DBH) size classes to better represent the forest structure. Additionally, we introduced a new mortality model MOR_{new} to PREBAS which is developed for uneven-aged stands and compared with the current PREBAS version in which a modification Reineke rule is used. The tests were conducted in 26 old Norway spruce dominated stands in southern and central Finland with three consecutive measurements (on average a 25-year study period). To evaluate the model performance, we compared the estimations of stand averaged diameter at breast height (*D*), stand averaged tree height (*H*), stand averaged crown base height (*Hc*), stand basal area (*B*) and density (*N*) with measurements. Moreover, biomass estimations of each tree component (foliage, branch and stem) were compared to estimations from empirical models. Results showed that introducing size distributions can represent better stand structure and improve the model predictions compared with data. Moreover, the new mortality model MOR_{new} showed promise with qualitatively more realistic results especially among the largest tree size classes. However, model bias still existed in the simulation although the predictions were improved. It revealed that further calibration of the PREBAS model with size classes should be done to better extend the model applicability to uneven-aged forests.

1. Introduction

There is an increasing focus on forests that are uneven-aged and older than commercial rotation (Diaci et al., 2011; Fu et al., 2017) due to the growing interest in forest management strategies that are targeted to biodiversity conservation and carbon sequestration (Busing and Garman, 2002; Gustafson, 2007). To cope with the conversion of forest management, many of the forest growth models have been developed for converting the simulation of even-aged into uneven-aged forests in the past years. They vary in terms of spatial from tree level such as BALANCE (Grote and Pretzsch, 2002), Heureka (Drössler et al., 2014) and SILVA (Pretzsch et al., 2002; Hilmers et al., 2020) to cohort/stand level such as 3-PG_{mix} (Gupta and Sharma, 2019), and they are defined as empirical model which is based on statistical equations (Heureka, SILVA) or process-based models which is based on describing physiological processes (BALANCE, 3-PG_{mix}).

Despite the varied models developed for uneven-aged forest, very few of them are process-based on a stand level resolution. For uneven-aged forest, a key question in process-based models is how to allocate the incoming light between trees of different size and species. A common starting point is the Lambert-Beer model, originally developed for horizontally homogeneous stands (Mäkelä and Hari, 1984; Sitch et al., 2003; Härkönen et al., 2010; Forrester and Tang, 2016; Minunno et al., 2019). Some models have used approximations where each single tree is treated as a canopy (Sitch et al., 2003), others have derived simplified expressions using detailed light interception models (Duursma and

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Mäkelä, 2007; Forrester and Tang, 2016), and some approaches have used more heuristic rules for adding up canopies with different light absorption properties (Härkönen et al., 2010). The approach of the PREBAS model with the canopy including mean trees of each species is similar to that proposed by Forrester and Tang (2016) for the 3-PG model adapted to multi-layered mixed species stands, with each mean tree described in terms of its vertical distribution of foliage and species-specific light extinction coefficients. Modelling mortality from a process-based perspective has proven to be quite complicated, because so many parallel processes are at play. Some mortality models base on reducing carbon budgets (Sitch et al., 2003; Franklin et al., 2012), but the related equations are very model specific. Because of these difficulties, a conventional description in both empirical and process-based models has been to divide mortality into different components, including competition-induced mortality, age-related mortality and random mortality (MacFarlane et al., 2002; Sands, 2004). The most important component for managed forests is the competition-induced, or density-dependent mortality, which has often been described using the −3/2 self-thinning law (Landsberg and Waring, 1997) or the Reineke self-thinning rule (Reineke, 1933). While these have generally been found to represent adequately the density-dependent mortality in even-aged stands, the other components of mortality include a lot of uncertainty and have therefore been found to be extremely difficult to predict in mixed, uneven-aged stands (Bugmann et al., 1997). In this study, we focused on a process-based model PREBAS. The current version of the PREBAS model uses a modification of the Reineke rule, which defines the maximum number of trees for stand/cohort mean diameter (Minunno et al., 2019).

A recent study reported that the PREBAS model calibrated using a regional dataset can reliably predict stand variables of even-aged forests with main commercial species cross Finland (Minunno et al., 2019). A remaining challenge is, how to apply PREBAS to uneven-aged forest where size variation between trees is large. To model uneven-aged forest growth, the important factors to consider include diameter distribution, species mix, growth and mortality (Weiskittel et al., 2011). There are two issues remaining to be solved in the existing PREBAS version. Firstly, the forest growth calculation is based on canopy photosynthesis, and dividing this between trees of different size and position is not straight-forward. Therefore, the first research question is how to modify the model to be applicable to multiple size classes. Secondly, the Reineke self-thinning rule (Reineke, 1933) is essentially a mean-tree based mortality equation that is more suitable for even-aged stands as well. A previous study has reported more flexible mortality models that were developed empirically for uneven-aged stands (Peltoniemi and Mäkipää, 2011). Consequently, the second research question is whether the performance of PREBAS will be improved by using different mortality models.

The primary aim of this study was to test the PREBAS model in uneven-aged forest with different size classes and species. We utilised data from 26 old spruce dominated stands in southern and central Finland with three consecutive measurements (over an average 25-year study period). The specific objectives of this study were: 1) to introduce DBH size classes to PREBAS model to better represent the stand structure and test the PREBAS model performance of existing model and modified model in multi-cohorts stands against observed tree structural variables and empirical calculations; and 2) to test the model performance by replacing the Reineke mortality model with a new mortality model which is specially for forests with different size classes developed by Peltoniemi and Mäkipää (2011).

2. Materials and methods

2.1. Model description and modification

2.1.1. Model description

The process-based model PREBAS consists of two modules, CROBAS (Valentine and Mäkelä, 2005) and PRELES (Peltoniemi et al., 2015), through which tree structure and stand dynamics are interconnected in the framework of carbon balance at an annual time resolution. The CROBAS model is a tree growth model which describes stand and tree growth as a result of carbon acquisition and allocation, and the PRELES model is a canopy photosynthesis model for estimating Gross Primary Productivity (GPP) and a simplified water balance. The PREBAS model simulates variables such as: stand density, biomass of five functional components, tree structural variables. A detailed description of the PREBAS model can be found in Minunno et al. (2019).

2.1.2. Description of layer photosynthesis

When PREBAS is run with multiple species represented by the species mean, photosynthesis is calculated following a modified Lambert-Beer scheme (Mäkelä et al., 2000; Duursma and Mäkelä, 2007). The whole canopy is divided into different layers based on the crown geometry which describes tree height, crown base height, and the shape of the crown envelope (cones or ellipsoids). Therefore, each canopy layer contains at least one cohort (Fig. 1). This model has shown fair performance for even-aged forests (Minunno et al., 2019), however, when variability of size is large, such as in an uneven-aged stand, the mean-tree approach may no longer be appropriate. A straight-forward expansion of the canopy-layer model would be to divide each species cohort into different size classes, retaining the assumption of horizontal homogeneity of the canopy. It should be noticed that although the canopy layer classification is based on canopy height, we base the size classification on DBH size class. This is because DBH varies more than height, so DBH contains more information about the tree's position than height, especially in our study plots which are unmanaged and may contain very old trees.

Here we explain how the photosynthesis in each canopy layer is calculated in a multi-cohort stand. First, the stand is described as a composition of multiple cohorts, and each cohort is presented as a mean tree (Fig. 1), following the DBH-based classification. Then, the whole canopy of all the mean trees is further divided into different canopy layers based on the tree top and crown base heights of each mean tree, and the layers are sorted in descending order (Fig. 1). The photosynthesis of layer i is calculated using Light use efficiency approach:

$$P_i = (1 - s_1 L_{c,i}) P_{0,i} f_{APAR,i} \tag{1}$$

where $L_{c,i}$ is crown length of layer i, s_1 is a species-specific parameter which represents hydraulic limitation on the rate of photosynthesis in relation to crown length, $f_{APAR,i}$ is the proportion of incoming radiation absorbed by canopy layer i and $P_{0,i}$ is the potential photosynthetic production with $f_{APAR,i} = 1$. $f_{APAR,i}$ of layer i is calculated by two approaches: (Minunno et al., 2019):

$$f_{APAR,i,1} = 1 - e^{-k_{eff} L_i} \tag{2}$$

$$f_{APAR,i,2} = \left\{ 1 - \exp\left(- k_H \frac{L_i}{A_{tot,i}} \right) \right\} A_{tot,i} \tag{3}$$

where k_{eff} is a species-specific effective extinction coefficient proposed by Duursma and Mäkelä (2007), L_i is the leaf area index of layer i, k_H is a species-specific extinction coefficient (Minunno et al., 2019) and A_{tot} is the crown coverage of layer i. $f_{APAR,1}$ is calculated based on a modified Lambert-beer Law (Duursma and Mäkelä, 2007) and $f_{APAR,2}$ is adopted from the LPJ model (Sitch et al., 2003). When crown coverage is high, $f_{APAR,i,2} > f_{APAR,i,1}$, because Eq. (3) applies to the homogeneous canopy assumption, while Eq. (2) accounts for clumping in dense stands. Therefore, we choose to use the smaller of the two:

$$f_{APAR,i} = \min\{ f_{APAR,i,1}, f_{APAR,i,2} \} \tag{4}$$

The f_{APAR} for layer i is the remaining proportion of light from layer $i + 1$. For canopy layer i with mixed species, we calculate the effective leaf

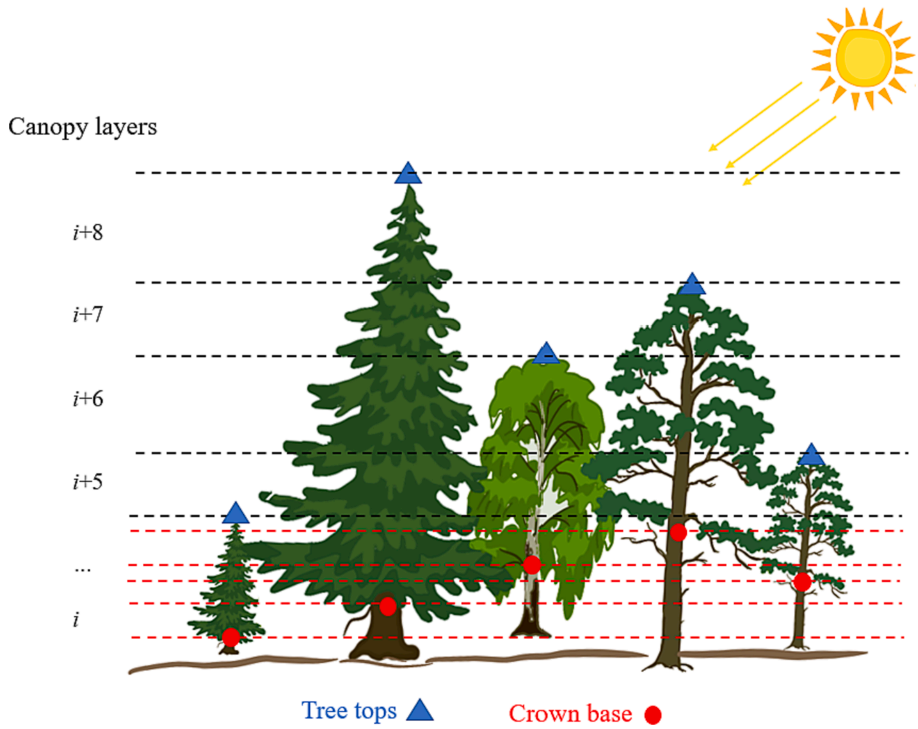

Fig. 1. Sketch map of the light interception of each canopy layer. Canopy layers are divided based on treetops and crown base. In this presented stand, 5 cohorts (species- and DBH size class-specific) are divided into 9 canopy layers in descending order.

area for each species using:

$$L_{eff,i} = \frac{k_{eff}}{K_H} \times L_i \tag{5}$$

L_i is calculated by multiplying W_f of each species and specific leaf area (SLA) which is a species-specific parameter. Then f_{APAR} for each species on layer i can be calculated, and the layer photosynthesis can be calculated using equation (1).

2.1.3. Description of mortality models

To estimate the tree mortality in multi-cohort stands, we test two distance-independent models. One is the Reineke mortality model which is used in the existing PREBAS version, and the other one is the mortality model introduced by Peltoniemi and Mäkipää (2011), we called it MOR_{new} in this study. The simulations of these two mortality models are compared against three consecutive observations.

- *Application of Reineke model to each DBH size class*

In the Reineke approach, the whole stand is divided into different cohorts; the cohorts are ordered according to the height, and the dominant canopy layer has the cohort with the maximum H index n. We denote N_i as the number of trees in size class i, then the total number of trees which can influence the mortality in size class i, N_{xi}, depends on the trees of the class i plus the trees of the cohorts that have taller trees. This is expressed as:

$$N_{xi} = \sum\nolimits_{j=i}^{n} N_j \tag{6}$$

The mean tree basal area of the trees including and above size class i, B_x, can be expressed as:

$$B_{xi} = \sum\nolimits_{j=i}^{n} (B_j \times N_j)/N_{xi} \tag{7}$$

where B_j is the basal area of average tree from size class j. Based on the Reineke rule (Reineke, 1933), the stand density index of size class i is calculated as:

$$LDI_i = N_{xi}\left(\frac{\sqrt{B_{xi} \times 4/\pi}}{25}\right)^E \tag{8}$$

where E is a constant specific to species and region (Skovsgaard and Vanclay, 2008). Here, we use $E = 1.66$ which is somewhat larger than the original Reineke exponent 1.605 but has been shown to work well in Finland for Scots pine, Norway spruce and Silver birch (Minunno et al., 2019). Further, LDI_i is compared to a species-specific parameter N_0 which indicates limiting number of trees the size class can carry when quadratic mean diameter at breast height is equal to 25 cm. Mortality occurs when $LDI_i > N_0$:

$$N_{mor} = \begin{cases} 0.02N_i \times LDI_i, LDI_i > N_0 \\ 0, LDI_i \leq N_0 \end{cases} \tag{9}$$

where N_{mor} is the number of dead trees and 0.02 is an empirical parameter suggesting the mortality of 2% of the size class density.

- *Application of MOR_{new} to each DBH class*

The MOR_{new} quantifies the competitive environment of all standing trees to predispose them to mortality suggested by Peltoniemi and Mäkipää (2011). For a subject tree i in a DBH size class, the competition index arising from competitor trees j is calculated using a variable Φ, which describes the shape of the competitor effect as a function of the size difference of a competitor j and the subject tree i (Eq.1a. Peltoniemi and Mäkipää, 2011):

$$CI_{\sqrt{D},i} = \sum_{j\neq i} \Phi_{i,j} \times N_i \times \sqrt{D_j} \tag{10}$$

where N_i is the number of trees in the size class where i is derived, D_j is the competitor tree size. The variable Φ is controlled by a step function:

$$\Phi_{i,j}(\alpha, dbh_T, \chi_{i,j}) = \begin{cases} \dfrac{e^{\alpha(\chi_{i,j}-D_T)}}{1+e^{\alpha(\chi_{i,j}-D_T)}}, if \chi_{i,j} - D_T < 1000/\alpha \\ 1, if \chi_{i,j} - D_T \geq 1000/\alpha \end{cases} \quad (11)$$

where α is a shape parameter to control the steepness of the logistic curve, $\chi_{i,j}$ the DBH difference between subject tree i and competitor tree j, the shape parameter D_T describes the sensitivity of subject trees to different sized competitors as a linear function of D_i (Peltoniemi and Mäkipää, 2011). It needs to be noticed that trees in the same size class do not have exactly the same DBH, and we assume there is a 5% standard deviation. Hence, $\chi_{i,j}$ in this situation is regarded to be $0.05D_i$. In the MOR_{new} model, competition-induced probability of mortality on each size class, M_p, is expressed as (Model 9. Peltoniemi and Mäkipää, 2011):

$$M_p = \exp(a_0 + a_1 \bullet CI_{\sqrt{D},i} + a_2 \bullet D_j + u) \quad (12)$$

where a_0 is an intercept, a_1 and a_2 are the parameters and u $N(0, \sigma_u^2)$ was determined as a random parameter caused by variability between plots (Peltoniemi and Mäkipää, 2011). In the estimates we replace u with $\sigma_u^2/2$ because the original model was developed from fitting a logarithmic equation to data (Baskerville, 1972). Consequently, the expected number of dead trees from size class i can be calculated by multiplying N_i and M_p.

2.2. Study site and field data description

In this study, we used a dataset that includes three consecutive measurements of 26 sites collected in southern and central Finland (LUMES dataset, Table 1) (Peltoniemi and Mäkipää, 2011). The study plots were established between 1990 and 1999 (first measurement, M1) on stands that were old-growth and had not been managed. The locations of individual trees were recorded so that they could be remeasured. The second (M2) and third measurements (M3) from the same trees were made in 2006–2007 and 2019, respectively.

Table 1
Details of sites information and sample collection in LUMES dataset. Ticks (√) denote the information was collected or measured, crosses (×) denote that no information was collected or measured.

Dataset	*LUMES*
Years	1990–1999; 2006–2007; 2019
Location	60°- 63°N, 23°- 30°E
Forest site type	herb-rich, mesic heath
Species	Scots pine, Norway spruce, Silver birch
Number of sample trees	3773
Individual tree age	×
Tree coordinates	√
DBH	√
Height	√
Crown length	√ (sample trees only)
Crown base height	√ (sample trees only)
Crown width	√ (sample trees only)
Foliage/ branch/ stem biomass	√ Scots pine and Norway spruce: Repola (2009) √ Silver birch: Repola (2008)

Among the 26 sites, most of the study plots are dominated by Norway spruce with varying mixtures of Scots pine, birch, aspen, and other broadleaf species. A total of 346 Scots pine, 3078 Norway spruce and 135 Silver birch, and 214 other broadleaved trees were traced over on average the 25-year study period (21–29 years). Stand density index (SDI) is calculated using number of trees and quadratic mean diameter for each site (Burkhart and Tomé, 2012). Detailed information for each plot can be found in Appendix 1. All the sample trees were divided into size classifications based on DBH of live and dead-standing trees in the M1: 5 cm - DBH_{max} with 5 cm interval.

2.3. Model evaluation

We simulated the development of each site for 30 years without thinning applied using different PREBAS approaches (Table 2), and all of them were initialised with the first measurement. In this study, regeneration and ingrowth were not considered because there was no complete record of this information: regeneration data were collected for M1 (three plots were missing) and M3, and ingrowth data was not recorded for many plots.

Model performance was evaluated by comparing the model simulation against reference data in M2 and M3. All the data were first normalized using mean observed data. Then the average model bias (AMB), model efficiency (EF) and mean square error (MSE) was calculated using the equations as follows (Pinjuv et al., 2006):

$$ABM = \frac{1}{n}\sum_{i=1}^{n}(y_i - x_i) \quad (13)$$

$$EF = 1 - \frac{\sum_{i=1}^{n}(y_i - x_i)^2}{\sum_{i=1}^{n}(y_i - \overline{y_i})^2} \quad (14)$$

$$MSE = \frac{1}{n}\sum_{i=1}^{n}(x_i - y_i)^2 \quad (15)$$

where x_i is the model predictions, y_i is the observations and $\overline{y}$ is the mean of observations. An AMB of 0 would indicate a model with no bias. EF value can range between -∞ to 1 and 1 indicates a perfect model.

As for biomasses and V which we did not measure, we compared the simulation results with the estimations using the empirical models by Repola (2008) and Repola (2009) (Appendix 3), and the reference V is determined by the stem biomass and wood density ($V_{ref} = W_s/\rho_s$).

3. Results

3.1. Stand level simulation accounting DBH size classes

One of the main modifications of PREBAS model was to introduce DBH size classes to better represent the structure of the uneven-aged forest. To start with, we calculated the layer-weighted stand level variables using approach I-III to compare with observed data. With all the approaches, the goodness of fit between simulated and observed data was better for structural variables: stand averaged diameter at breast height (D), stand averaged tree height (H), and stand averaged crown

Table 2
PREBAS model runs with different approach (I, II and III). Ticks (√) denote the approach was species or DBH size classes- specific and crosses (×) denote the approach was not species or DBH size classes- specific. *When we run the PREBAS model, the 214 other broadleaved trees were included in the runs. However, they were not included in the results presentation due to the small basal area proportion of these trees. Therefore, the cohort number takes account Scots pine, Norway spruce and Silver birch.

Approach	Species specific	DBH size classes-specific	Cohort number	Mortality
I	√	×	3	Reineke model
II	√	√	19*	Reineke model
III	√	√	19*	MOR_{new} model

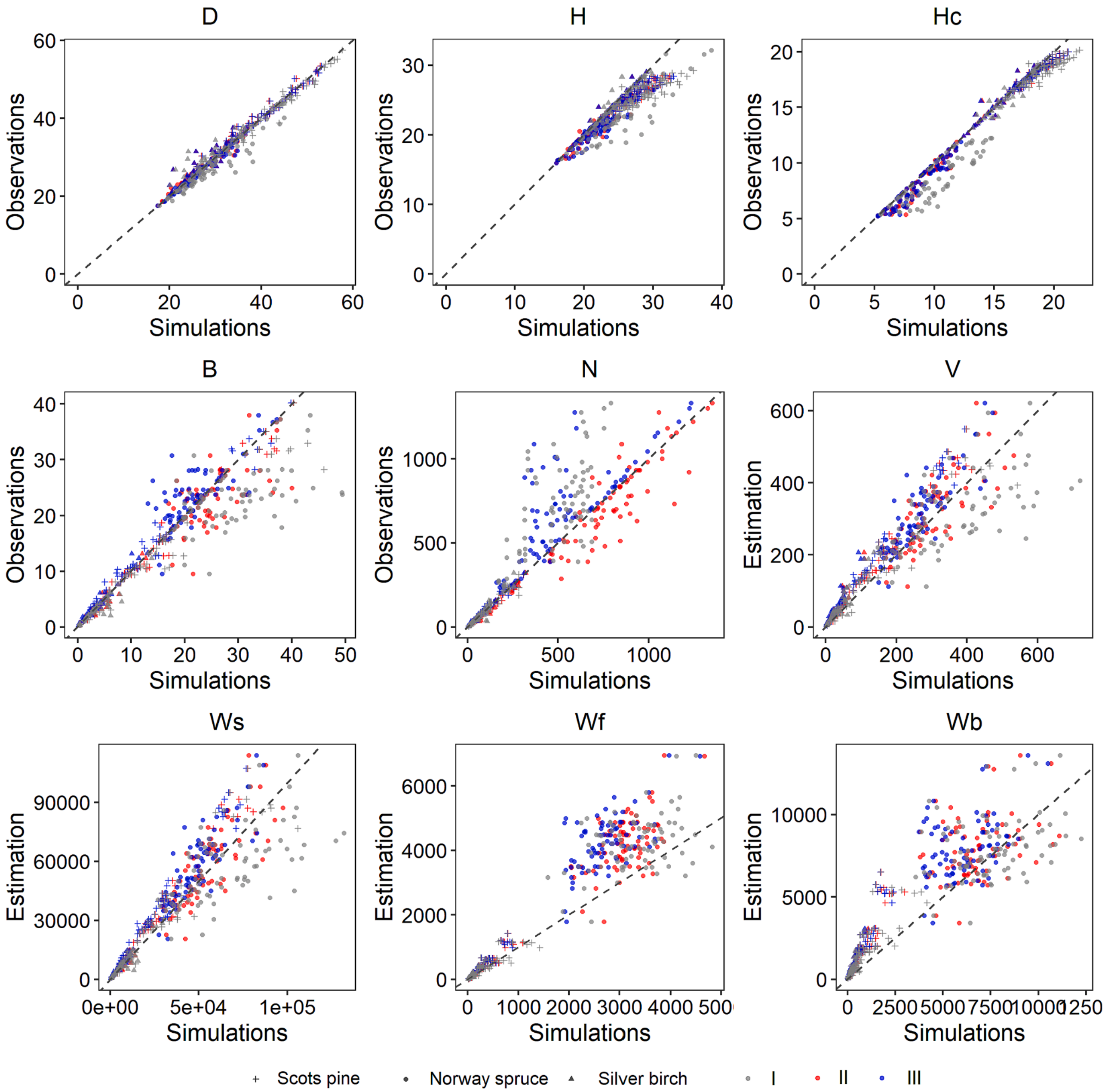

Fig. 2. Reference and simulated data from *LUMES* dataset on stand level. In each facet plot, grey colour refers to approach I (3 cohorts + Reineke), red colour refers to approach II (19 cohorts + Reineke) and blue colour refers to approach III (19 cohorts + MOR_{new}). D = Stand average diameter at breast height (cm), H = Stand average height (m), *Hc* = Stand average crown base height (m), *B* = Stand basal area (m^2 ha^{-1}), *N* = Number of trees (density), *V* = Volume (m^3 ha^{-1}), W_s= Stem biomass (kgC ha^{-1}), W_f= Foliage biomass (kgC ha^{-1}), W_b= Branch biomass (kgC ha^{-1}). Black dashed line indicates the 1:1 line. The number of the points for each approach are: $N_{Scots\ pine}$=78, $N_{Norway\ spruce}$= 78, $N_{Silver\ birch}$ = 39 (not all the sites have silver birch), the total number of the points in each facet plot is 585. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

base height (H_C) than those for stand variables: stand basal area (*B*), and density (*N*) (Fig. 2, Table 3). After introducing DBH size classes (approach II and III), model efficiency (EF) values of *D*, *H*, *Hc*, *N* and *B* were over 90% (except for *N* in Norway spruce and *V* in Silver birch), indicating higher overall accuracy than without DBH size classes (Table 3).

In addition, we compared biomass and volume estimations using approach I-III with calculations from empirical models (Appendix 3). Taking account of the DBH size classes showed better agreement with the estimations from empirical models in all the species by showing higher EF in approach II than in approach I (Table 3). After shifting the mortality models (approach III), the N was obviously improved compared with approach I while EF value indicated that only W_b in Norway spruce agreed more with empirical model estimation (Table 3). Additionally, volume (*V*) estimation showed the same pattern as W_s since it was calculated using W_s simulation and wood density.

Furthermore, we compared the annual volume increment against the estimations using empirical models. All approaches in PREBAS (I-III) showed larger annual volume increment in observation periods than estimations using empirical models (Appendix 3), and simulations with DBH size classes (approaches II and III) were closer to reference than without DBH size classes (approach I) (Fig. 3).

Table 3
Statistics of model fit for each variable and approach against reference dataset in terms of normalized mean squared error (NMSE), average model bias (AMB), and model efficiency factor (EF).*dH* = annual height growth, *dD*=annual diameter growth, *dB*=annual basal area growth. Data were normalized using the mean of the observations. Species: 1 = Scots pine, 2 = Norway spruce, 3 = Silver birch. For biomass and volume, the reference data was estimated from empirical models (Appendix 3). Additionally, statistics using un-normalized data is presented in Supplementary table.

Variables	Species	NMSE			AMB			EF		
		I	II	III	I	II	III	I	II	III
H	1	0.013	0.011	0.004	−0.083	−0.078	−0.044	0.986	0.988	0.996
	2	0.019	0.011	0.005	−0.102	−0.073	−0.039	0.979	0.988	0.995
	3	0.002	0.002	0.001	−0.012	−0.025	−0.010	0.998	0.998	0.999
D	1	0.001	0.001	0.001	−0.008	−0.004	0.011	0.999	0.999	0.999
	2	0.008	0.003	0.001	−0.056	−0.032	−0.005	0.992	0.997	0.999
	3	0.006	0.004	0.005	0.040	0.025	0.031	0.993	0.996	0.995
B	1	0.097	0.060	0.020	−0.127	−0.096	0.051	0.943	0.965	0.988
	2	0.140	0.095	0.038	−0.239	−0.210	0.090	0.854	0.901	0.960
	3	0.120	0.057	0.042	−0.161	−0.101	0.071	0.917	0.960	0.971
	1	0.003	0.002	0.001	−0.038	−0.036	−0.016	0.997	0.997	0.999
H_C	2	0.048	0.028	0.008	−0.169	−0.122	−0.058	0.943	0.966	0.991
	3	0.001	0.001	0.001	−0.011	−0.006	0.004	0.999	0.999	0.999
	1	0.036	0.033	0.016	0.008	−0.077	0.049	0.978	0.980	0.991
N	2	0.180	0.047	0.123	0.299	−0.120	0.230	0.845	0.960	0.895
	3	0.128	0.106	0.021	−0.043	−0.154	0.042	0.943	0.953	0.991
V	1	0.095	0.078	0.144	0.105	0.127	0.273	0.951	0.960	0.925
	2	0.138	0.082	0.065	−0.143	−0.102	0.188	0.874	0.925	0.941
	3	0.279	0.279	0.441	0.337	0.368	0.476	0.846	0.846	0.757
W_b	1	0.585	0.609	0.803	0.490	0.488	0.638	0.691	0.699	0.576
	2	0.084	0.075	0.124	0.054	0.058	0.261	0.921	0.929	0.882
	3	0.754	0.743	0.932	0.598	0.610	0.693	0.604	0.610	0.511
W_s	1	0.094	0.077	0.143	0.104	0.126	0.272	0.952	0.961	0.926
	2	0.139	0.082	0.065	−0.143	−0.102	0.188	0.874	0.925	0.941
	3	0.092	0.046	0.090	−0.042	0.006	0.177	0.951	0.976	0.952
W_f	1	0.207	0.173	0.239	0.148	0.171	0.340	0.885	0.904	0.868
	2	0.089	0.068	0.169	0.224	0.197	0.379	0.914	0.934	0.837
	3	0.365	0.319	0.493	0.334	0.343	0.473	0.820	0.842	0.757
dH	1	0.030	0.011	0.012	−0.163	−0.092	−0.100	0.967	0.988	0.987
	2	0.053	0.007	0.009	−0.197	−0.060	−0.085	0.943	0.993	0.990
	3	0.017	0.003	0.003	0.007	−0.007	−0.010	0.979	0.996	0.996
dD	1	0.014	0.007	0.006	0.014	0.040	0.035	0.981	0.991	0.991
	2	0.057	0.004	0.004	−0.150	0.005	−0.023	0.933	0.996	0.996
	3	0.057	0.023	0.023	0.152	0.100	0.098	0.914	0.965	0.965
	1	0.040	0.010	0.010	−0.098	−0.020	0.040	0.963	0.991	0.990
dB	2	0.351	0.135	0.086	−0.439	−0.129	0.080	0.698	0.884	0.926
	3	0.006	0.003	0.003	−0.044	−0.002	0.022	0.994	0.997	0.998

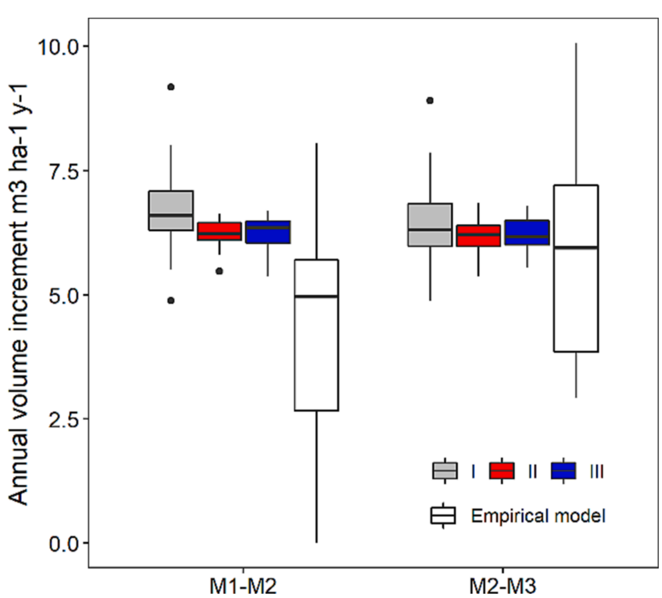

Fig. 3. Comparison of annual volume increment (volume increment + deadwood) on 26 sites in two observation periods using approach I-III and empirical model.

3.2. Tree growth and mortality simulation in different cohorts

On cohort level, normalized mean square error (NMSE) values of cohort level D, H, *Hc*, B and N were calculated respectively to explore the performance of different mortality models in different DBH size classes and species (Fig. 4). The NMSE in D, H and *Hc* was much smaller than B and N in all the species and Norway spruce showed more obvious difference between the two mortality models than the other two species (Fig. 4). Besides, the Norway spruce trees showed the largest error in the smallest DBH size class (DBH < 10 cm) for both mortality models, except for the *Hc* estimation of trees with diameter between 35 and 50 cm (Fig. 4).

On all the sites, annual DBH growth of Norway spruce trees was less than 0.4 cm and in most of the layers annual growth was 0.1–0.2 cm (Fig. 5, Supplementary figures, Fig.S1). MOR_{new} model clearly overestimated mortality in the smaller DBH size classes and had a larger error than the Reineke model (Fig. 4, Supplementary figures, Fig.S1). However, for spruce trees with diameter over 55 cm (DBH size layer > 10), the performance of the MOR_{new} model was superior to the Reineke model. For the other DBH size classes, the accuracy differences between the two approaches were generally negligible (Supplementary figures, Fig.S1).

3.3. Sample sites presentation

Here we take three sites to demonstrate the growth and mortality of Norway spruce simulated by two approaches in detail. The sites were

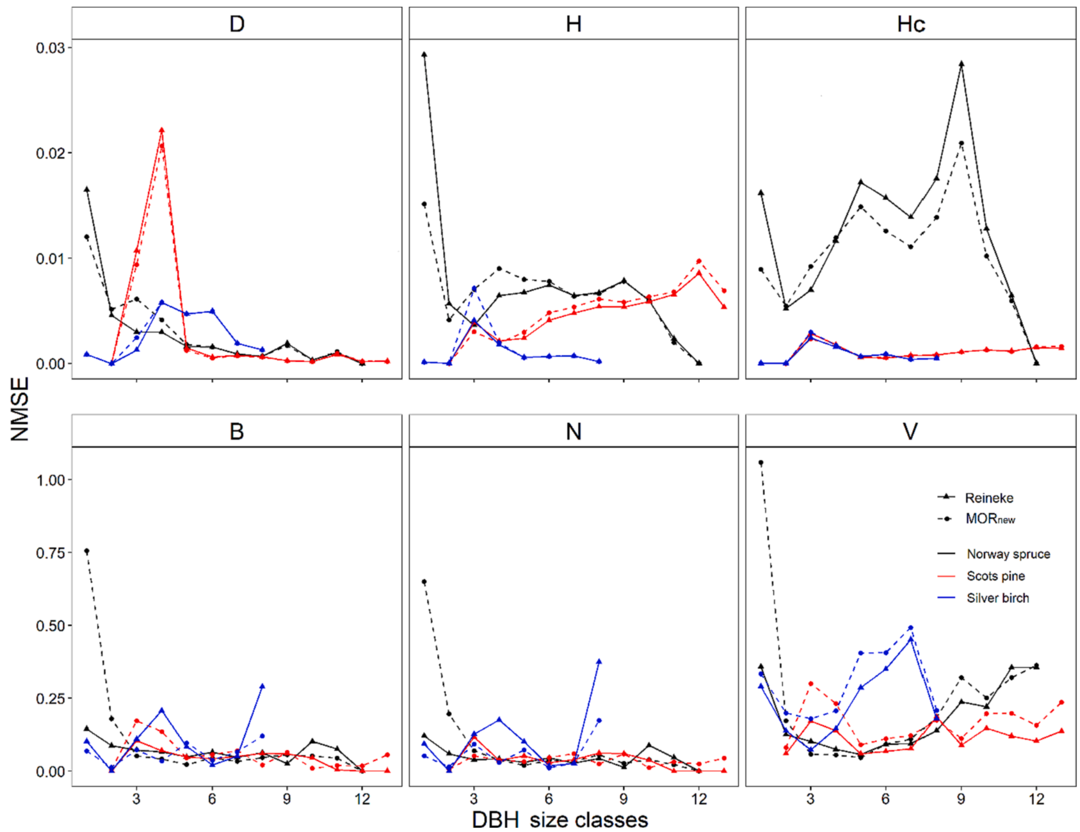

Fig. 4. Normalised mean squared error (NMSE) on each DBH size class for each variable and each species using approach II (Reineke model) and III (MOR_{new} model).

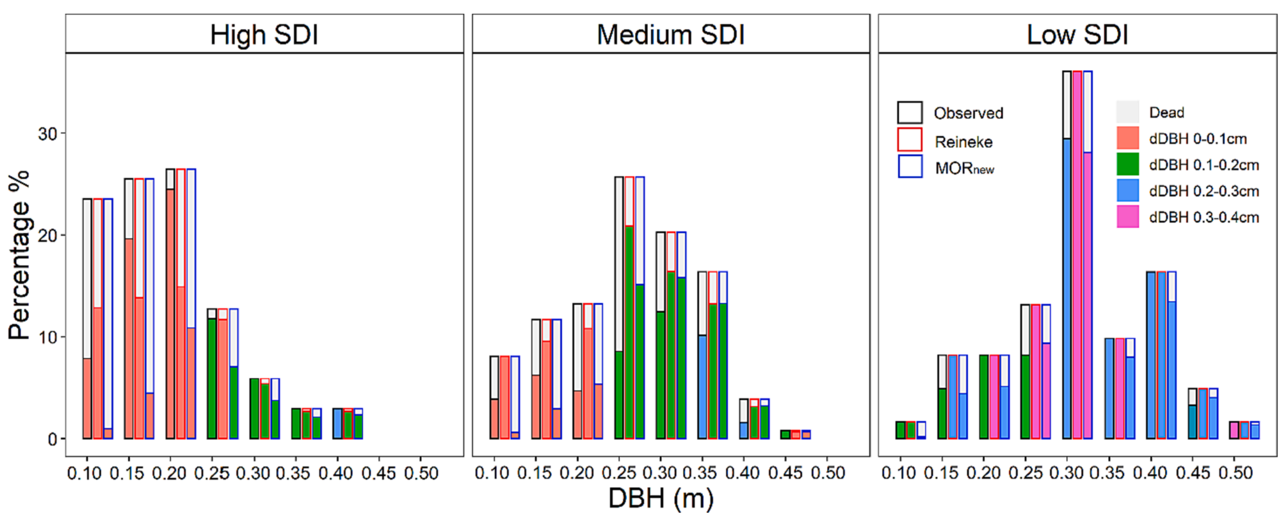

Fig. 5. Comparison of the proportion of living and dead trees at the last measurement (M3) using different mortality models with observation (Norway spruce). All these recorded trees were alive at the beginning of the period (M1). As for the living trees, different colour indicates the annual DBH growth of each DBH size class from M1-M3.

selected by ranking the stand density index (SDI) from the highest to the lowest: PA61(the highest SDI), PA06B (medium SDI) and VA207 (the lowest SDI) (Table A1). Generally, the MOR_{new} model showed a larger mortality proportion than the Reineke model regardless of DBH size class and SDI, and it seemed to overestimate mortality in the smaller size classes (Fig. 5, Supplementary figures, Fig.S1). When mortality was predicted by both approaches, smaller size classes tended to have a larger proportion of mortality (Fig. 6). On the site with low SDI, there was no mortality using the Reineke model while mortality occurred using the MOR_{new} model even though the number of trees was far from the maximum. On the site with high SDI, the MOR_{new} model overestimated mortality in all size classes and the performance of the Reineke model was superior to MOR_{new} (Fig. 5). On the site with medium SDI, the difference of the two mortality models was generally negligible for spruce trees with diameter over 30 cm while MOR_{new} performed better in the other size classes (Fig. 5). Furthermore, it is interesting to notice that MOR_{new} led to a larger DBH growth (Fig. 5) while the Reineke model implied a larger growth of height (Fig. 7).

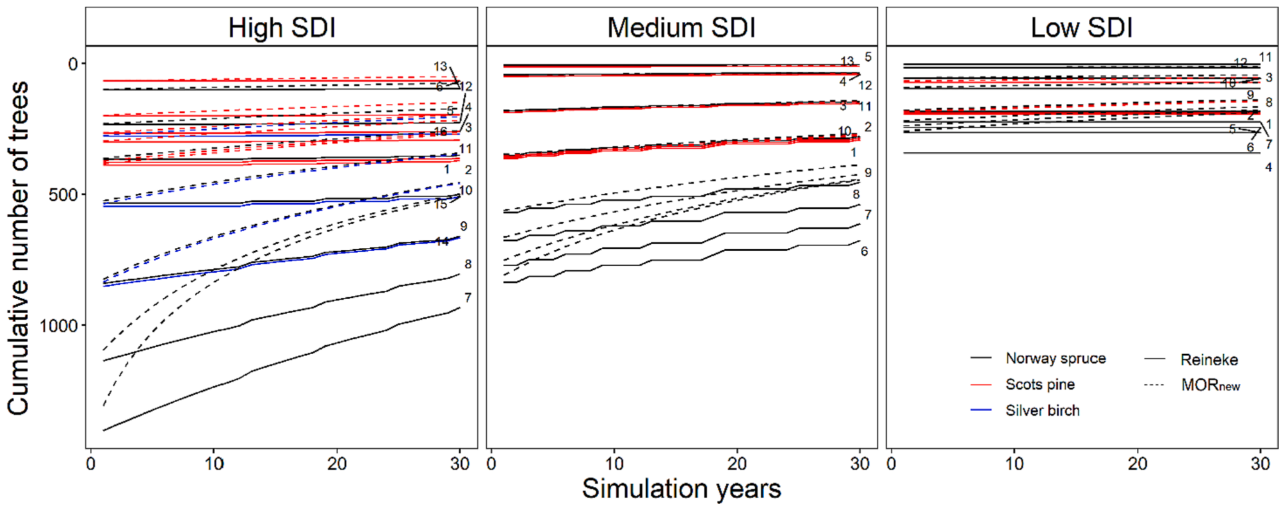

Fig. 6. The cumulative number of trees of representative sites from the top to the lowest canopy layer over the simulation year using different mortality models (all species included). Each line denotes the cumulative number of trees in the cohort itself and all trees in the cohorts above. The rank of the cohorts depends on the tree height of each cohort where the top line is the cohort with largest tree height. The lowest line denotes the cohort with lowest height and the number of values on this line equals the number of trees on the site. The corresponding species and DBH size class for each cohort can be found in Appendix 2.

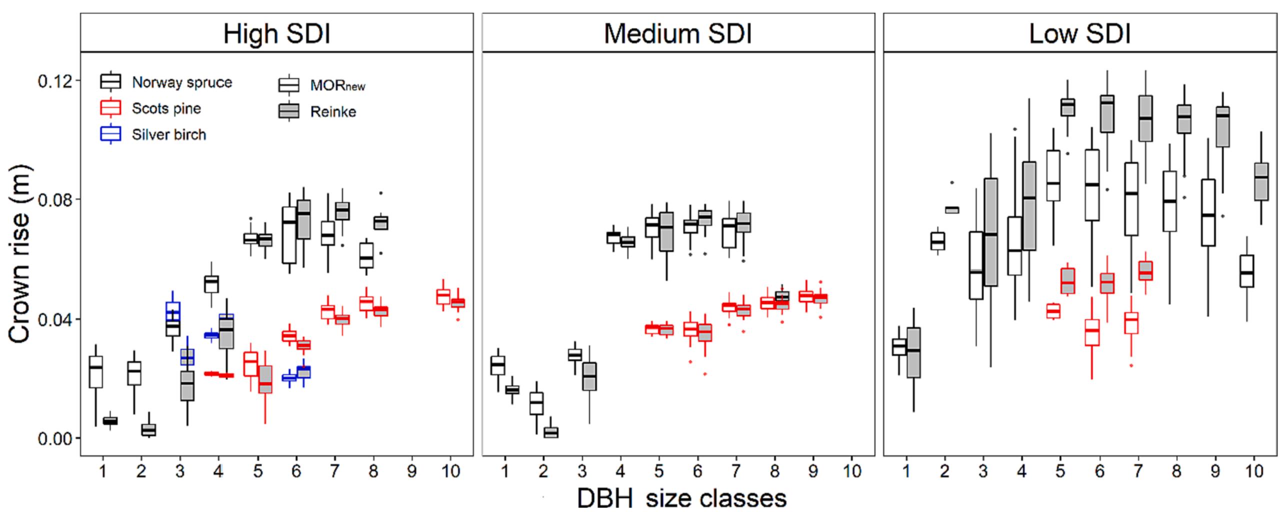

Fig. 7. Crown rise (increasing height of the crown base) on each DBH size class. Each box contains values in over the 30-year simulation period.

4. Discussion

In this study, our focus was on testing the applications of a new PREBAS model version in uneven-aged forest, where a mean-tree approach with self-thinning type mortality may no longer be appropriate. The results demonstrated that introducing size distributions generally improved the model predictions compared with data. Further, the alternative mortality model showed promise with qualitatively more realistic results especially among the largest tree size classes. However, the study also revealed some further needs of model calibration after the introduction of multiple size classes and a new mortality module in the model.

4.1. Data consideration and model bias

The PREBAS model was originally calibrated against time series data of standard forest mensuration variables (height, diameter and basal area) from forest management experiments, and the biomass equations used in the model were parameterised from independent, focused measurements of tree architecture and component biomass (Minunno et al., 2016). The parameters of these equations were further adjusted within plausible limits in the calibration process (Minunno et al., 2019). A focal variable in the model is the crown base height which has implications on all the biomass variables as well as stem form factor (Mäkelä, 1997), however, most datasets available for long-term model calibration do not include measurements of crown base height. The observations in the *LUMES* data sets used in this study can therefore provide some very useful information about further calibration needs of the model.

The negative bias of crown base height suggests that crown rise has been somewhat overestimated in the simulations (Table 3). The same is true of tree height, however, the mean error is larger for crown base height, indicating that the model is underestimating the lengthening of the crown. This is notable especially in Norway spruce. At the same time, foliage and branch biomasses have a positive bias, i.e., those variables were underestimated by PREBAS in comparison with the reference (Table 3). However, it should be noted that the reference estimates of W_s, W_f and W_b were modeled using multivariate equations (Repola, 2008, 2009). Tree height, stump diameter, crown length and crown ratio were the variables used to model the component biomass in our study

(Appendix 3). Additionally, Repola (2008, 2009) also provided models where crown height is not used as an additional predictor. It is noticeable that there is an obvious difference of the estimations using different models (Supplementary figures, Fig.S2). Therefore, we did not have exact data to justify if the biomass outputs from the equations were unbiased and evaluated the PREBAS model predictions.

Moreover, Hu et al. (2020) reported that some parameters in the PREBAS model are age-dependent. Application of age dependent parameters is problematic in a dynamic model, because it would require dynamically changing the parameter values on the basis of a very poorly known input variable. An alternative method of model improvement would be to try to explain the age dependence by some more detailed mechanism. In PREBAS, one possible mechanistic explanation could be that older trees have a larger proportion of heartwood at the base of the crown than young trees, due to the fact that both height growth and crown rise have slowed down and lower branches are losing parts of their foliage and producing disused pipes (Valentine et al., 2013). Their foliage mass per cross-sectional area at crown base could therefore be smaller than in younger trees, even if it was similar when compared with sapwood area (Berninger et al., 2005). Allowing for disused pipes at the crown base, as suggested by Valentine et al. (2013), could therefore be a necessary modification of the model for accounting for aging trees and / or multi-cohort stands.

4.2. Mortality patterns of the two mortality models

The existing PREBAS is a mean tree model with Reineke self-thinning mortality model which was originally applied to even-aged forests (Reineke, 1933; Drew and Flewelling, 1977) and has been used in forest models to predict mortality previously (Härkönen et al., 2019; Minunno et al., 2019). It assumes that there is a boundary line between the number of trees and the quadratic mean DBH, the mortality starts once the boundary line is reached (Burkhart and Tomé, 2012). With this approach in multi-cohort stands, mortality can occur in different size classes while it would be more likely in the smaller size classes (Eq. (6–9)) (Fig. 6). However, a U-shaped mortality pattern with respect to tree size has been observed in many studies (Goff and West, 1975; Harcombe, 1987; Hurst et al., 2011). This is because small trees have high mortality rates because of asymmetric competition for resources (Weiner, 1990). As the tree grows old, the mortality rate is high due to senescence, loss of physiological functions, higher vulnerability to extreme disturbance and so on (Mencuccini et al., 2005; Bennett et al., 2015). This explains the underestimation of mortality using Reineke model in the larger DBH size classes (>55 cm) (Supplementary figures, Fig.S1). Also, on the stand level, when stand density index is small, no mortality was modelled using the Reineke model during the whole 30-year simulation period (Fig. 6). This indicated the limitation of using Reineke self-thinning rules since mortality may happen before the stands hits the boundary line in a real forest.

In terms of the MOR_{new} model, it was initially developed for uneven-aged Norway spruce forests which takes different tree size classes into account to better represent structure in a stand. The MOR_{new} model calculates the mortality probability of the subject tree according to the competitors that are somewhat larger than the subject tree itself instead of the density (Peltoniemi and Mäkipää, 2011). This explains the better performance of MOR_{new} over the Reineke approach, especially in larger DBH size classes where Reineke fails to catch the U shape mortality pattern (Supplementary figure Fig.S1). However, the Reineke model was superior in smaller size classes which can be explained by previous studies showing that tree mortality in young forests is strongly density dependent and the density-dependent competitive mortality tends to decline as the dominant tree cohort reaches the full canopy (Getzin et al., 2006; Larson et al., 2015). In addition, both models showed higher mortality in small Norway spruce trees (DBH < 25 cm) than other size classes (Fig. 6). It is not surprising because studies showed that suppression deduced mortality is certainly a major part of the tree mortality regime in old-growth coniferous forest where small trees are abundant (Larson and Franklin, 2010; Holzwarth et al., 2013).

There is evidence from previous studies, that high stocking density reduces mean diameter and results in increasing stem slenderness and crown rise (Weiner and Thomas, 1992; Baldwin Jr et al., 2000). Also, it has been shown that the major effect of competition on tree structure is reflected on crown rise (Mäkelä and Vanninen, 1998; Ilomäki et al., 2003) which indicates that the mortality strategies can influence the growth of the remaining trees. Our results showed that trees tend to grow more in girth with the MOR_{new} model due to heavier mortality than predicted by the Reineke model (Fig. 5). On the contrary, trees grow more in the vertical dimension using the Reineke model (Fig. 7). This is consistent with the empirical observation that height growth is reduced less than diameter growth under strong competition (Weiner et al., 1990).

5. Conclusions

In this study, we tested the application of a process-based forest growth model PREBAS on uneven-aged mixed-species stands by introducing size classes and a new mortality model. The test was implemented on 26 spruce dominated forests over southern and central Finland. Our results demonstrate that the PREBAS version with DBH size classes can represent better stand structure and improve predictions, and it could also provide estimations for each DBH size class. Additionally, though predictions using the MOR_{new} mortality model showed bias in the density estimation of smaller DBH size classes, it still somehow shows the reality that mortality occurs even if the density is not large enough and it may also occur among the largest trees. For the operational application of PREBAS, we suggest using Reineke model for even-aged forests while MOR_{new} model is more appropriate for uneven-aged forests, especially in stands with low density and larger DBH size classes.

In conclusion, this study provides a sound basis for the further development of PREBAS to be applicable to uneven-aged and / or older stands. This should include further calibration of the model with size classes, to reduce the bias in some of the state variables found in this study. Furthermore, developing a submodel for natural regeneration or ingrowth will remain an important future task towards its applications in uneven-aged stands.

6. Contributions of the co-authors

All authors contributed to the study design. MH and FM contributed to the data analysis and interpretation of the results. MP contributed to the data preparation and results interpretation. AA contributed to data preparation and data analysis. AM contributed to the methodology development, discussion of the results and writing the manuscript outline. MH wrote the original draft and all authors contributed to the manuscript preparation and approved the final manuscript.

7. Funding Source Declarations

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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.

Data availability

Data will be made available on request.

Appendix 1

See Table A1.

Appendix 2

See Table A2.

Appendix 3

Determinations of observed value for each variable of each individual tree

Both tree height (H) and crown base height (H_C) of each individual tree was estimated using DBH and Hegyi's competition index (Hegyi, 1974; O'Neal et al., 1995) with a separate mix-effects model. Each individual tree was considered as the random part of each model. To calculate Hegyi's competition index, we applied the pairwise function in R from *spatstat* package. Additionally, we used the empirical models to estimate the biomass of foliage (W_f), branch (W_b) and stem biomass (W_s) (including stem wood and bark) (Repola, 2008, 2009). All the parameters of above models to estimate individual tree variables were species specific (Table A3).

Scots pine

$$\text{Stem wood}: \ln(y_i) = b_0 + b_1\frac{d_i}{(d_i+14)} + b_2\frac{h_i}{(h_i+12)} \tag{A1}$$

$$\text{Stem bark}: \ln(y_i) = b_0 + b_1\frac{d_i}{(d_i+12)} + b_2\ln(h_i) \tag{A2}$$

$$\text{Branch}: \ln(y_i) = b_0 + b_1\frac{d_i}{(d_i+12)} + b_2\frac{h_i}{(h_i+8)} + b_3\ln(cl_i) \tag{A3}$$

$$\text{Foliage}: \ln(y_i) = b_0 + b_1\frac{d_i}{(d_i+4)} + b_2\frac{h_i}{(h_i+1)} + b_3\ln(cl_i) \tag{A4}$$

Table A1
Site descriptions. BA is stand basal area in the first sampling. $\overline{dbh}$ = mean DBH in a stand. $CV_{\overline{dbh}}$ = coefficient of variation of the mean DBH in a stand. SDI is the site density index. M1, M2 and M3 is the year when the measurement implemented.

Site	Area (m^2)	BA (m^2ha^{-1})	BA_{spruce}/BA (%)	$\overline{dbh}$(cm)	$CV_{\overline{dbh}}$	SDI	M1	M2	M3
JO101	1600	40.3	62	17.7	0.489	914	1994	2007	2019
JO124	1600	41.9	63	19.5	0.494	902	1995	2007	2019
JO135	900	33.4	62	18.8	0.457	745	1996	2007	2019
JO144	900	36.7	61	17.2	0.398	842	1996	2007	2019
PA06B	1600	40.1	94	23.3	0.366	820	1995	2006	2019
PA121	2500	35.8	80	26.4	0.452	687	1999	2006	2019
PA123	2500	23.8	89	22.1	0.492	483	1999	2006	2019
PA131	2500	33.5	67	21.9	0.605	666	1999	2006	2019
PA132	2500	31.7	73	18.5	0.659	665	1999	2006	2019
PA6	1600	42.4	65	20.1	0.472	906	1993	2006	2019
PA61	900	65	63	20.4	0.604	1340	1995	2006	2019
PA62	900	64	57	19.4	0.656	1337	1995	2007	2019
PA63	900	55.6	63	16.9	0.720	1180	1995	2006	2019
PA67	1600	33.5	94	20.7	0.368	718	1995	2007	2019
PA7	1600	44.4	75	20.9	0.484	932	1993	2007	2019
PA8	1600	36.5	75	19.3	0.440	794	1993	2006	2019
VA101	2500	26.7	89	33.2	0.140	476	1990	2014	2019
VA109	1600	40.6	73	15.5	0.634	930	1992	2006	2019
VA112	900	23.5	80	11.4	0.802	591	1992	2006	2019
VA207	2500	18.3	84	23.6	0.480	365	1995	2006	2019
VA209	1600	40.7	66	21.2	0.358	864	1995	2006	2019
VA211	1600	38.7	98	22.3	0.473	785	1995	2006	2019
VA222	2500	29.1	68	24.8	0.661	553	1997	2006	2019
VA228	900	30.1	79	14.3	0.513	734	1999	2006	2019
VA401	1600	51.6	62	22.4	0.344	1073	1993	2006	2019
VA403	1600	45.6	74	23.9	0.522	897	1993	2006	2019

Table A2
Cohort in the simulation runs corresponding to the observation DBH classes and species on each site for Scots pine, Norway spruce and Silver birch.

Sim cohort	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Site
DBH	3	5	6	7	8	9	1	2	3	4	5	6	2	3	4	5	6	7	9	1	NA	JO101
Species	1	1	1	1	1	1	2	2	2	2	2	2	3	3	3	3	3	3	3	4	NA	
DBH	3	4	5	6	7	8	1	2	3	4	5	6	3	4	5	7	10	NA	NA	NA	NA	JO124
Species	1	1	1	1	1	1	2	2	2	2	2	2	3	3	3	3	4	NA	NA	NA	NA	
DBH	3	4	5	6	7	8	1	2	3	4	5	6	7	2	3	4	5	6	7	NA	NA	JO135
Species	1	1	1	1	1	1	2	2	2	2	2	2	2	3	3	3	3	4	4	NA	NA	
DBH	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	NA	NA	NA	NA	NA	JO144
Species	1	1	1	1	2	2	2	2	2	2	3	3	3	3	3	3	NA	NA	NA	NA	NA	
DBH	5	6	7	8	9	1	2	3	4	5	6	7	8	NA	NA	NA	NA	NA	NA	NA	NA	PA06B
Species	1	1	1	1	1	2	2	2	2	2	2	2	2	NA	NA	NA	NA	NA	NA	NA	NA	
DBH	4	5	6	7	8	9	11	1	2	3	4	5	6	7	8	9	10	1	NA	NA	NA	PA121
Species	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	4	NA	NA	NA	
DBH	4	5	7	8	1	2	3	4	5	6	7	8	10	6	1	4	NA	NA	NA	NA	NA	PA123
Species	1	1	1	1	2	2	2	2	2	2	2	2	2	3	4	4	NA	NA	NA	NA	NA	
DBH	6	7	8	9	1	2	3	4	5	6	7	8	9	10	14	3	4	NA	NA	NA	NA	PA131
Species	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	3	3	NA	NA	NA	NA	
DBH	6	7	8	9	10	11	1	2	3	4	5	6	7	8	9	10	5	6	7	1	NA	PA132
Species	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	4	NA	
DBH	3	5	6	7	8	10	1	2	3	4	5	6	7	2	3	4	5	6	7	8	9	PA6
Species	1	1	1	1	1	1	2	2	2	2	2	2	2	3	3	3	3	3	3	4	4	
DBH	4	5	6	7	8	10	1	2	3	4	5	6	7	3	4	6	1	NA	NA	NA	NA	PA61
Species	1	1	1	1	1	1	2	2	2	2	2	2	2	3	3	3	4	NA	NA	NA	NA	
DBH	2	5	6	7	8	9	10	1	2	3	4	5	7	1	3	NA	NA	NA	NA	NA	NA	PA62
Species	1	1	1	1	1	1	1	2	2	2	2	2	2	4	4	NA	NA	NA	NA	NA	NA	
DBH	5	6	7	8	9	10	11	1	2	3	4	5	1	NA	NA	NA	NA	NA	NA	NA	NA	PA63
Species	1	1	1	1	1	1	1	2	2	2	2	2	4	NA	NA	NA	NA	NA	NA	NA	NA	
DBH	5	6	1	2	3	4	5	6	7	1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	PA67
Species	1	1	2	2	2	2	2	2	2	4	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	
DBH	6	9	11	12	1	2	3	4	5	6	7	10	2	3	6	7	8	9	4	5	NA	PA7
Species	1	1	1	1	2	2	2	2	2	2	2	2	3	3	3	3	3	3	4	4	NA	
DBH	9	1	2	3	4	5	6	3	4	5	6	7	8	9	NA	NA	NA	NA	NA	NA	NA	PA8
Species	1	2	2	2	2	2	2	3	3	3	3	4	4	4	NA	NA	NA	NA	NA	NA	NA	
DBH	8	9	10	1	2	3	4	5	6	7	8	9	10	NA	NA	NA	NA	NA	NA	NA	NA	VA101
Species	1	1	1	2	2	2	2	2	2	2	2	2	2	NA	NA	NA	NA	NA	NA	NA	NA	
DBH	3	4	5	6	7	8	9	10	1	2	3	4	5	6	1	2	3	4	5	6	NA	VA109
Species	1	1	1	1	1	1	1	1	2	2	2	2	2	2	4	4	4	4	4	4	NA	
DBH	6	8	1	2	3	4	5	6	7	8	9	1	2	NA	NA	NA	NA	NA	NA	NA	NA	VA112
Species	1	1	2	2	2	2	2	2	2	2	2	4	4	NA	NA	NA	NA	NA	NA	NA	NA	
DBH	5	6	7	1	2	3	4	5	6	7	8	9	1	2	4	NA	NA	NA	NA	NA	NA	VA207
Species	1	1	1	2	2	2	2	2	2	2	2	2	4	4	4	NA	NA	NA	NA	NA	NA	
DBH	4	5	6	7	1	2	3	4	5	6	8	4	6	2	3	5	7	8	9	NA	NA	VA209
Species	1	1	1	1	2	2	2	2	2	2	2	3	3	4	4	4	4	4	4	NA	NA	
DBH	5	1	2	3	4	5	6	7	8	9	11	3	NA	NA	NA	NA	NA	NA	NA	NA	NA	VA210
Species	1	2	2	2	2	2	2	2	2	2	2	4	NA	NA	NA	NA	NA	NA	NA	NA	NA	
DBH	7	8	9	11	1	5	6	7	8	9	1	2	6	NA	NA	NA	NA	NA	NA	NA	NA	VA211
Species	1	1	1	1	2	2	2	2	2	2	4	4	4	NA	NA	NA	NA	NA	NA	NA	NA	
DBH	3	4	5	6	1	2	3	4	5	6	8	1	2	3	6	NA	NA	NA	NA	NA	NA	VA222
Species	1	1	1	1	2	2	2	2	2	2	2	4	4	3	4	NA	NA	NA	NA	NA	NA	
DBH	4	5	6	7	8	1	2	3	4	5	6	7	3	4	5	6	7	8	9	11	NA	VA228
Species	1	1	1	1	1	2	2	2	2	2	2	2	4	4	4	4	4	4	4	4	NA	
DBH	7	8	9	10	12	13	1	2	3	4	5	6	7	8	6	7	8	NA	NA	NA	NA	VA401
Species	1	1	1	1	1	1	2	2	2	2	2	2	2	2	4	4	4	NA	NA	NA	NA	
DBH	3	5	6	7	8	9	1	2	3	4	5	6	2	3	4	5	6	7	9	1	NA	VA403
Species	1	1	1	1	1	1	2	2	2	2	2	2	3	3	3	3	3	3	3	4	NA	

Table A3
Parameters of biomass estimation empirical models for each species.

Equations	Scots pine				Norway spruce				Silver birch			
Parameters	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11	A12
b_0	−3.72	−4.54	−5.16	−1.74	−3.55	−4.54	−3.02	−0.08	−4.87	−5.40	−4.15	−8.33
b_1	8.10	7.99	13.08	14.82	8.04	9.44	12.01	15.22	9.65	10.06	15.87	12.40
b_2	5.06	0.35	−5.18	−12.68	0.86	0.43	−5.72	−14.44	1.01	2.65	−4.40	–
b_3	–	–	1.11	1.21	0.02	–	1.03	1.27	–	–	–	–

Norway spruce

$$\text{Stem wood}: \ln(y_i) = b_0 + b_1\frac{d_i}{(d_i+14)} + b_2\ln(h_i) + b_3h_i \tag{A5}$$

$$\text{Stem bark}: \ln(y_i) = b_0 + b_1\frac{d_i}{(d_i+18)} + b_2\ln(h_i) \tag{A6}$$

$$\text{Branch}: \ln(y_i) = b_0 + b_1\frac{d_i}{(d_i+14)} + b_2\frac{h_i}{(h_i+5)} + b_3\ln(cl_i) \tag{A7}$$

$$\text{Foliage}: \ln(y_i) = b_0 + b_1\frac{d_i}{(d_i+4)} + b_2\frac{h_i}{(h_i+1)} + b_3\ln(cl_i) \tag{A8}$$

Silver birch

$$\text{Stem wood}: \ln(y_i) = b_0 + b_1\frac{d_i}{(d_i+12)} + b_2\ln(h_i) + b_3h_i \tag{A9}$$

$$\text{Stem bark}: \ln(y_i) = b_0 + b_1\frac{d_i}{(d_i+12)} + b_2\frac{h_i}{(h_i+20)} \quad \text{A10)}$$

$$\text{Branch}: \ln(y_i) = b_0 + b_1\frac{d_i}{(d_i+12)} + b_2\frac{h_i}{(h_i+12)} + b_3cl_i \quad \text{A11)}$$

$$\text{Foliage}: \ln(y_i) = b_0 + b_1\frac{d_i}{(d_i+2)} + b_2cr_i \quad \text{A12)}$$

where y_i is the biomass component tree i, d_i is tree diameter at stump height of tree i, $d_i = 2 + 1.25$d, and d is the tree diameter at breast height, h_i is tree height of tree i, cl_i is length of living crown of tree i, cr_i is crown ratio of tree i. b_0, b_1, b_2 and b_3 are fixed parameters.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120702.

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