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Variance decomposition of predictions of stem biomass increment for European beech: contribution of selected sources of uncertainty

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Abstract

The contribution of selected sources of uncertainty to the total variance of model simulation results of stem biomass increment - calculated from annual stem biomass predictions - of European beech \textit{(Fagus sylvatica L.)} was quantified. Sources of uncertainty were defined as the selected variables that influence the total variance of the model results. Simulations were made: (i) for ten regional climate models (RCMs) based on the IPCC scenario A1B and providing an ensemble of climate projections up to 2100; (ii) with two forest model types (FMTYPEs); (iii) for four forest management intensities (MANFORs); and (iv) for three time windows (TIMEWINDs), each spanning 15 years, starting in 2019, in 2049 and in 2079. Both models, the empirical SYBILA model and the process-based ANAFORE model, were calibrated using experimental tree growth data from four plots in central Slovakia between 1989 to 2003. Three of these plots, representing the four MANFORs, were subject to different prior intensities of thinning while one was left untouched as a control. The FMTYPE explained most of the total variance in the simulation results (39.9\%), followed by MANFOR (i.e. thinning intensity; 22.2\%) and TIMEWIND (12.0\%), while the effect of RCMs on model uncertainty was limited (< 1\%). Stem biomass increment results obtained from the two FMTYPES were different in absolute terms, but the models agreed well in their relative response to RCM, to MANFOR and to TIMEWIND. The total variance of the predictions was 10 times higher for the process-based model (ANAFORE) than for the empirical model (SIBYLA). These observations are the reason for the large contribution of FMTYPE to the total variance of the simulated stem biomass increment results.

**Keywords:** empirical model, process-based model, climate scenario, forest management, \textit{Fagus sylvatica} L.
1. Introduction

As trees grow old, forests unavoidably face the impact of imminent climate change. Forest management measures can contribute significantly to mitigation of and adaptation to these environmental changes. Conventional statistical models implicitly based on the assumption of stationary conditions may not be applicable for forest management decisions, but novel and improved process-based models predict forest growth under changing conditions. Management plans developed using either type of model require appropriate risk assessments (Walker et al., 2003). Uncertainty analysis of forest model results is thus crucial to support management decisions. The model uncertainties partly originate from input variables, including data required for the model set-up and the calibration, as well as from climate and forest management predictions. Uncertainty is also associated with the model boundaries (i.e., the extent of the ecosystem complex covered by the model), with the model structure itself and with the model parameters (Jones, 2000; Reyer et al., 2013). Only a part of this model uncertainty, however, is reflected in the variance of the model results. Other sources of error may also contribute to model uncertainty, but may not be quantifiable: either because they are unknown or because they are not included in the model.

Forest models incorporate aspects of system complexity as well as the non-linear relations and the feedback mechanisms among the system drivers (Tian et al., 2012). Over the last three decades forest models have become more process-driven and they now incorporate a multitude of parameters (Landsberg, 2003; Matala et al., 2003). Process-based models (PBMs) integrate the mechanistic functioning of the ecosystem by reproducing the ecological and physiological processes that drive the system, as well as their responses to external factors (Landsberg, 2003; Kurbatova et al., 2008). PBMs are useful tools for understanding the dynamics of an ecosystem and they can provide answers to questions on how ecosystems should be managed under changing environmental conditions (Korzukhin et al., 1996; Matala et al., 2003; van Oijen et al., 2005). However, having a multitude of parameters does not necessarily guarantee that the model predictions will be reliable.
The complexity of PBMs can be a strength, but also a weakness, because they rarely provide a unique answer to a practical management question (Mohren and Burkhart, 1994; Sands et al., 2000; Matala et al., 2003; van Oijen et al., 2005). Model improvements can result from a better understanding of the internal processes of the system, e.g., carbon allocation processes, nutrient availability in soils, nutrient uptake by trees, and competitive interactions (Seidl et al., 2011b). A better knowledge of the external impacts and disturbances – often human-induced – as well as their dependence on site location is also required (Landsberg, 2003; Kearney and Porter, 2009; Seidl et al., 2011a). The feedbacks and compensating mechanisms between ecological drivers also create challenges in model development (Ceulemans et al., 1999; Matala et al., 2005; Penuelas et al., 2008).

In contrast, empirically-based models (EBMs) are built on statistical relationships between forest growth and environmental variables obtained from field measurements (Fabrika, 2007; Hlásky et al., 2014; Pan et al., 2014). The choice of the forest model best suited for a particular research or management question is of crucial importance. Efforts have been made to combine the advantages of PBMs (theoretical understanding, flexibility, predictive power under changing conditions) and EBMs (robustness, limited input demand, ease of interpretation) by using multi-model inference (Hlásky et al., 2014) or by developing hybrid models (Makela et al., 2000; Baldwin et al., 2001; Peng et al., 2002; Girardin et al., 2008; Taylor et al., 2009).

When climate predictions provide an input for forest models, uncertainty is transferred from the climate model to the forest growth simulation (Lindner et al., 2014; Keenan, 2015). The uncertainties in regional climate predictions are caused by three sources: (i) the climate model uncertainty, which is resulting from the model structure and the parameterization and causes different responses to the same radiative forcing, (ii) the scenario uncertainty, which arises from the uncertainty in future environmental changes, as e.g. greenhouse gas emissions, and (iii) the internal variability, which is
the inherent temporal randomness of climate in the absence of any radiative forcing (Hawkins and Sutton, 2009, 2010). The relative importance of these three sources of uncertainty changes with the spatial and temporal scale. The internal variability becomes more important with decreasing spatial scale and with an increased occurrence of extreme events (Lindner et al., 2014). Model uncertainty increases with longer prediction periods. Scenario uncertainty increases even more with lead time (Hawkins and Sutton, 2009). Uncertainties from regional climate models (RCMs) can be quantified by using an ensemble approach, combining the results of multiple models to give the statistical probability of possible future climates (Lindner et al., 2014). Beside the physiological aspects, the state of a forest – i.e., its extent, species composition and canopy structure – and its biogeographical location also affect its response to disturbance and vice versa (Allen et al., 2010; Seidl et al., 2011b; Jactel et al., 2012). The effects of forest state and forest history should be correctly understood and taken into account in forest simulation studies, especially for European forests that are generally intensively managed (Spiecker, 2003; Boisvenue and Running, 2006; De Vries et al., 2006; Solberg et al., 2009). It is important to correctly estimate the costs and the benefits of different forest management measures and to account for a wide range of forest situations and potential future climate conditions.

In this contribution we (i) quantified the variance coming from different sources of uncertainty on predictions of tree growth; (ii) tested the significance of these sources of uncertainty; and (iii) assessed the contribution of different RCMs to the total uncertainty in the climate predictions. So, this study only investigated the uncertainty of the model results and it did not consider the effects of the different sources of variance on the actual predictions. As a case study we have modelled the annual stem biomass increment (ASBI) of European beech \textit{(Fagus sylvatica} L.), a dominant tree species in European forests and the most common deciduous species in central Europe (Dittmar et al., 2003). Drought-induced growth reduction and/or a decline of the species have been reported in southern Europe (Ciais et al., 2005; Jump et al., 2006; Piovesan
et al., 2008; Bontemps et al., 2010; Charru et al., 2010; Kint et al., 2012; Zang et al., 2014), but for central Europe an accelerated growth has been reported (Pretzsch et al., 2014).

2. Materials and Methods

2.1. Site description and sampling design

The forest site was located in the Kremnické Vrchy Mountains of the Western Carpathians, Slovakia (48° 38' N, 19° 04' E). The altitude ranged from 470 m to 510 m, with a total area of 4.5 ha having a slope with a western aspect and an inclination of 13% to 20%. The soil substrate consisted of andesite-tuff agglomerates and the soil type was Andic Cambisol with a high skeleton content (10% - 60%). During the measurement period (i.e., the calibration period) of 1989-2003 the annual average temperature was 8.6 °C and the average annual precipitation was 677 mm.

At the start of the 1989-2003 calibration period, the forest was 100 years old. Before 1989, it was managed according to usual forestry practice of less intensive thinning interventions from below (mostly the removal of damaged and low-quality trees). In the 30 years preceding the calibration period, the stand was thinned three times. In the period 1963–1972, 54 m³ ha⁻¹ were harvested from the stand. In the following two periods (1973–1982 and 1983–1988) the harvested thinning was 54 and 40 m³ ha⁻¹, respectively. European beech (Fagus sylvatica L.) was the dominant species (65 - 90%) in the forest stand, but hornbeam (Carpinus betulus L.), oak (Quercus robur L.) and fir (Abies alba Mill.) were also present. In February 1989 three plots of 0.35 ha each were established. These plots were subjected to strip shelterwood cutting of different intensities. The remaining number of trees per ha was respectively 160 for the heavily thinned plot (H), 243 for the medium thinned plot (M) and 397 for the lightly thinned plot (L). A fourth plot of 0.15 ha was left uncut as a control (C) with 700 trees per hectare. The thinning primarily focused on removing the interbreed species, dying and damaged trees, and trees of very low stem quality. Branches were left on the site to decompose naturally. More detailed information about the forest site and the forest management has been
reported previously (Jamnická et al., 2007; Kellerova, 2009; Barna et al., 2010; Janik et al., 2011; Barna and Bosela, 2015).

During the calibration period stem diameter at breast height (DBH) was measured annually using a diameter tape with a precision of 1 mm. Individual trees and measurement positions were clearly marked to minimize measurement errors. Tree height (h) was measured three times over the calibration period (1998-2003) using a hypsometer (Silva, Clino Master, Sweden in 1989 and 1995; Vertex, Haglöf, Sweden in 2003). For all other years h was interpolated from these measurements. DBH and h were always measured for each individual tree. The volume (v) of stems and branches was estimated using national volume regression equations based on DBH and h. These equations were derived for 12 tree species from the large database assembled in the Czech and in the Slovak Republics (Petráš and Pajtík, 1991). Stem biomass was obtained from the calculated stem volume and the wood density of beech (Pajtík et al., 2009).

2.2. Climate data

For the 1989-2003 calibration period, daily temperature, precipitation and wind speed data were obtained from the meteorological station in the village of Sliač (5 km from the forest site). Nitrogen wet deposition was measured at the site by 10 funnel-shaped collectors established on the forest floor of each plot. NO_3 and NH_4 depositions were then obtained by spectrophotometry. For more details about the sampling method see Janík et al. (2014) and Dubová and Bublinec (2006). Past CO_2 concentrations were obtained from the global values published by Tans and Keeling (2014).

Incoming radiation for the site was estimated using NOAA’s JavaScript solar position calculator recoded for Microsoft Excel (Pelletier, 2014).

In view of the limited spatial extent of the forest site under study, we followed the recommendation of Lindner et al. (2014) and used a regional (RCM) rather than a general (GCM) circulation model for making climate predictions. Different RCMs were run using the initial and boundary conditions.
provided by GCMs (Giorgi, 2006) to generate higher resolution meteorological fields. Because of this higher resolution, RCMs can resolve smaller scale features, such as topography and physical weather processes (Wang et al., 2004). Ten high-resolution daily RCMs were used, all disseminated within the framework of the European ENSEMBLES project (Van der Linden and Mitchell, 2009) and based on the same A1B scenario of IPCC (Moss et al., 2008). The A1B greenhouse gas emission scenario provides a balanced emphasis on all energy sources responsible for greenhouse gas emissions. At the ENSEMBLES data portal 30 models were available driven by the A1B greenhouse gas scenario. A total of 23 model output sets fulfilled the criterion of a sufficiently high spatial resolution (25 km x 25 km), but only 14 output sets covered the entire 1951-2100 period. Two other output sets were removed because they used the same RCM-GCM combination as another one, but with high- and low-sensitivity RCM settings. From the remaining 12 models one was not available at the website and another one contained too many data gaps at the end of the simulation period. A list of the 10 remaining model combinations (RCM-GCM) is provided by Dobor et al. (2015). Note that although the Representative Concentration Pathways have already been adopted by the IPCC for its Fifth Assessment Report (AR5) in 2014, only GCM results were accessible at this time. Time series of maximum temperature (T max), minimum temperature (T min), precipitation and wind speed were selected for the closest grid point to the meteorological station from a 25 km x 25 km horizontal resolution grid. Statistical bias correction was applied to site measurements for the period 1961-2009 using the cumulative distribution function fitting technique (also known as the quantile mapping/fitting or histogram equalization), at monthly time intervals. For precipitation, both the amount and the frequency were corrected. Future atmospheric CO2 concentrations for the model simulations where also adopted from the A1B scenario of IPCC. Future global radiation was estimated with the MT-CLIM model (Mountain Microclimate Simulation Model (Hungerford et al., 1989; Thornton and Running, 1999), which adequately estimated the daytime temperature and global radiation. Details of the method and its limitations were described previously by Moss et al. (2008) and Dobor et al. (2015).

Nitrogen deposition was kept equal to the average monthly value over the period 1989-2003 for each plot (20-25 kg ha\(^{-1}\) yr\(^{-1}\)) over the whole prediction period (2003-2100). The level chosen was
slightly lower than, but close to, the optimal nitrogen deposition for beech, 28 kg N ha\(^{-1}\) yr\(^{-1}\) (Kint \textit{et al.} (2012). No nitrogen deposition trends were observed, neither over years nor over seasons during the calibration period. This was concluded from an automated time series forecasting software provided by SAS statistical program (version 9.1, SAS Institute Inc., Cary, NC, USA). Predictions of nitrogen emissions and depositions depend on decisions with regard to land use, to agriculture, to energy policy, etc., as well as on the only partly known feedbacks between changes in the carbon and nitrogen cycles (Lamarque \textit{et al.}, 2011; van Vuuren \textit{et al.}, 2011; Ciais \textit{et al.}, 2013).

### 2.3. Forest model types

#### 2.3.1. Empirically-based model SIBYLA

SIBYLA (acronym for Simulator of Forest Biodynamics) is an individual tree, distance-dependent and climate-sensitive growth model (Fabrika and Dursky, 2005, 2006). SIBYLA uses the coordinates, DBH and h of every single tree in a stand with the possibility of including different species with different growth rates. In this study the growth, the inter-tree and inter-specific competition and the mortality sub-models were used. The growth and competition sub-models were adopted from the SILVA growth simulator (Pretzsch and Kahn, 1998; Pretzsch \textit{et al.}, 2002) that worked as follows. Species-specific responses of tree increment to climatic and soil variables were based on dose-response functions (Fabrika and Pretzsch, 2013). This made the sub-model suitable for climate impact studies (Fabrika, 2007; Hlásny \textit{et al.}, 2011; Hlásny \textit{et al.}, 2014). Growth increment was then modified by competition pressure. Competitive interactions between trees and among species were described using a competition index based on positions and dimensions of surrounding trees and the light cone principle (Pretzsch, 1995; Bosela \textit{et al.}, 2013). The mortality was simulated via a sub-model of tree survival probability and using the threshold of stand density. The mortality sub-model has been described previously (Ďurský \textit{et al.}, 1996; Ďurský, 1997). To make the SIBYLA model representative of central Europe, it was calibrated using a large-scale database of forest monitoring and inventory data from Slovakia.
For the site-specific calibration of each of the four forest plots in this study, soil and climate variables measured at the site at the beginning of the calibration period were used to initialise the model. Simulations were then performed for the entire calibration period (1989-2003). The calibration was done for each year using a regression function of the residuals (differences between measured and simulated values) versus the simulated increments. The regression coefficients were then used to correct the simulated increments. The measured DBH and h values from the four plots were therefore used for the calibration period. After calibration, an ad hoc variance reproduction procedure was applied based on Gaussian probability functions, in which stochastic variance was artificially created to include possibly unknown or unconsidered factors in the simulation process (Fabrika and Pretzsch, 2013). This resulted each time in 11 prognoses for each of the plots. They represented the source of variance ‘STARTSET’ for SIBYLA.

2.3.2. Process-based model ANAFORE

ANAFORE (acronym for ANAlysing FORest Ecosystems) is a climate-sensitive, eco-physiological PBM that uses a bottom-up approach to simulate forest growth. Processes at the leaf, the tree and the stand scales are modelled in half-hourly (carbon and water fluxes), daily (all carbon pools) and yearly (wood quality, forest growth and management) time steps, respectively. The model contains among others: (i) a detailed tree carbon allocation mechanism differentiating between transport, structure and storage carbon pools; (ii) a refined stem structure; (iii) a sub-model of labile carbon in the tree; and (iv) a detailed soil sub-model. In ANAFORE tree mortality was defined by the percentage of trees dying when the carbon balance became negative. An extensive and detailed description of the model has been published previously (Deckmyn et al., 2008).

A total of 146 species-specific physiological parameters could be optimized in ANAFORE to calibrate the model for the specific conditions of the particular forest plots of this study. An initial attempt to
calibrate ANAFORE using a Bayesian optimization method (van Oijen et al., 2005) produced no reduction in parameter uncertainty. ANAFORE was therefore calibrated by selecting, independently for each plot, 11 parameter sets out of a minimum of 20,000 runs. This selection was made according to the accuracy of the simulated time series with respect to the measured DBH data over the calibration period.

All the required input variables for each of the two models as well as the possible output variables, with their respective spatial and temporal scales, are summarized in Table 1.

2.4. Simulation design

We considered the following variables influencing the total variance of the model results, always referred to as the sources of uncertainty:

i. FMTYPE (Forest model type): two forest model types were used, an EBM (SIBYLA) and a PBM (ANAFORE).

ii. MANFOR (management of the forest): four forest study plots were subjected to different thinning intensities in 1989: H, heavily cut; M, medium cut; L, lightly cut; and a control, C, i.e. no thinning.

iii. CLIMMOD (climate model): 10 RCM results were bias-corrected and used for the simulations up to 2100. All of the RCMs were run based on the A1B SRES scenario of IPCC.

iv. TIMEWIND (time window): three 15-year time windows were used for the simulations, i.e., 2019-2033, 2049-2063 and 2079-2093. The simulations for each TIMEWIND always started at the same developmental stage of the forest plots. TIMEWIND reflects the contribution of time (in a climate change context) to the total variance and the changes in the relative contributions of the other sources of variance over time. We preferred this splitting method as long term simulations
could lead to misinterpretations caused by the change in relative contributions of the sources of uncertainty over time and by the changing interactions among them.

v. STARTSET (starting set-up of the model): 11 model starting sets for each plot and for each model separately were used. In SIBYLA, stochastic variations per plot were taken from the variance reproduction method described earlier. These stochastic variations were used to mimic the biological variability. For each plot in ANAFORE, the 11 parameter sets were produced by the model calibration.

Both models were used to simulate stem dry mass (in kg per tree), always for a period of 15 years, and for each combination of the three TIMEWINDs, the two FMTYPEs, the 10 CLIMMODs, the four MANFORs and the 11 STARTSETs. All combinations of the different categories of each of these sources of uncertainty constituted a total of 2640 different model runs, each with a different simulation design.

The variance decomposition of the RCM results of climate predictions for $T_{\text{min}}$, $T_{\text{max}}$ and precipitation included two sources of uncertainty:

i. RCM: the same 10 RCMs were used in the quantification of uncertainty in the forest model results. In this case they were not used as a source of variance of growth rate predictions, but in the context of the climate predictions.

ii. INTVAR: internal variability of the climate variable.

2.5. Statistical analysis

Variance decomposition of the forest model results was realized by performing an analysis of variance (ANOVA) with the average annual stem biomass increment (ASBI; in dry mass of an average tree) over the 15 years of simulation as the response variable for each of the simulation designs. The analysis was first made for the dataset including results of both FMTYPEs together (complete dataset) and subsequently for ANAFORE and SIBYLA, individually. The studied sources of uncertainty
were FMTYPE, CLIMMOD, MANFOR, TIMEWIND and STARTSET. After the ANOVAs for the main effects of FMTYPE (complete dataset), CLIMMOD, MANFOR and TIMEWIND only, their interacting effects were also added as covariates. Two different approaches were thus used. In the first approach these interactions were ignored and their effect was entirely included in the residual error of the model. In the second approach significant two-way interactions were retained. STARTSET (nested in MANFOR) was only added as a covariate in an additional ANOVA analysis and was in all former analyses treated as a completely random source of variance, i.e. part of the residual error.

In all the analyses the fraction of the total variance explained by each source of uncertainty was calculated by dividing the Sum of Square Error (SSE) of the main effect as well as of the potential interactions by the total SSE of the response. The variance explained by the different sources of uncertainty plus the residual error made up 100% of the variance.

Afterwards, the dependence of the ASBI results on the simulation design was studied to obtain information about the differences in results between both FMTYPES in relation to changes in the simulation design (input). The average ASBI was calculated within each category of the sources of uncertainty CLIMMOD, MANFOR and TIMEWIND for both FMTYPES separately. The correlation coefficients for category averages of consecutively CLIMMOD, MANFOR and TIMEWIND between both FMTYPES were computed. All the above-mentioned statistical analyses were done in the statistical SAS/STAT® registered software (version 9.1, SAS Institute Inc., Cary, NC, USA).

An additional variance decomposition was performed on the RCM climate variable predictions. As all RCMs used the same scenario (A1B), only the model uncertainty and the internal variability were estimated for climate predictions from 2000 until 2100. The averaged climate model results, computed as the annual average of all RCMs were expressed as changes compared to the average of the reference period 1971-2000 and were fit with a fourth-order polynomial using ordinary least squares calculations. A reference period of 30 years was used in line with the definitions of climate by the World Meteorological Organization. The RCM predictions were compared to the polynomial
(fitted for the averaged climate model results) and the variance of the differences was calculated per decade; then these variances were averaged through the RCM models. The model uncertainty was defined as the variance of the different models in a given decade. The residual error of the analysis was attributed to the inherent randomness of climate (INTVAR). The fractions of the total variance explained by RCM and INTVAR were calculated and reported as percentages of the total variance.

3. Results

3.1. Quantification of uncertainty in biomass increment predictions

The total variance of ASBI in the complete dataset, i.e., the dataset including both FMTYPEs, was $382.4 \times 10^3$ (std. dev. 618). The main effect ANOVA and the two-way interaction ANOVA models explained 74.9% and 86.2% of the total variance, respectively. These ANOVA models provided the SSE values for the calculation of the fractions of the total variance explained by each of the sources of uncertainty, i.e., FMTYPE, CLIMMOD, MANFOR and TIMEWIND, their eventual interactions and the residual error.

The largest part (39.9%) of the total variance of ASBI in the complete dataset was explained by FMTYPE. This was followed by MANFOR (22.2%) and then by TIMEWIND (12.0%). The contribution of CLIMMOD in the explanation of the total variance was small (0.84%; Fig. 1a). There were significant interaction effects between FMTYPE and MANFOR, between FMTYPE and TIMEWIND, and between CLIMMOD and TIMEWIND (Fig. 1b). These interaction effects accounted for 6.4%, 2.7% and 0.35% of the total variance of ASBI, respectively. The residual error accounted for 25.1% of the total variance in the main effect model and for 13.8% of the total variance in the two-way interaction model.

For the ANOVA model including only ASBI data from ANAFORE, 72.0% of the variance was explained by the main effect model and slightly more (76.8%) by the two-way interaction model (Fig. 1). For SIBYLA the explained variance was higher, ranging from 89.0% for the main effect model to 95.6% for the two-way interaction model. The total variance of the responses of ANAFORE was 10 times larger
than the total variance of the responses in SIBYLA ($209.7 \times 10^3$ against $20.18 \times 10^3$). TIMEWIND was a more important source of variance for SIBYLA than for ANAFORE (36.3% against 23.3%). Nearly half of the variance was explained by MANFOR for both models (48.7% for SIBYLA against 47.4% for ANAFORE). The residual error, was smaller for SIBYLA (11.0%) than for ANAFORE (28.0%).

For the ANAFORE model there were statistically significant interactions between CLIMMOD and MANFOR (4.1%) and between CLIMMOD and TIMEWIND (0.74%). For SIBYLA these interactions were also significant and accounted for 4.4% and 2.3%, respectively. The residual errors of the ANOVA model were reduced to 23.2% for ANAFORE and to 4.4% for SIBYLA after inclusion of these linear two-way interactions.

The residual error included the variance coming from non-significant two-way interactions and by potentially higher order interactions. In the case of ANAFORE the variance also resulted from the deterministic uncertainty from the different STARTSETS. In the case of SYBILA there was a small stochastic part of the residual error caused by the stochastic processes by which mortality and biological variation of the growth increment (reflected in STARTSERT) were modelled in each run separately.

After inclusion of the main effect of STARTSET and its two-way interactions with TIMEWIND and MANFOR in the ANOVA model for ANAFORE, an additional 15.2% of the total variance of ASBI was explained. The ANOVA model explained 92.6% of the total variance. The high variability caused by STARTSET was expected since the individual parameters from the selected STARTSETS were spread over a large range of their prior distribution (before calibration). For SIBYLA the STARTSET effect, here reflecting the use of stochasticity in the tree growth predictions, was not significant.

### 3.2. Effect of simulation design

For both FMTYPES the effect of the simulation design on ASBI, in particular the effect of the interactions between FMTYPES and CLIMMOD, between FMTYPES and MANFOR, and between FMTYPES and TIMEWIND are shown in Fig. 2. In relative terms, the effect of the simulation design on
ASBI was similar for both growth models, as evidenced by the significant correlations between both FMTYPES with correlation coefficients of 0.978 (p<0.0001), 0.969 (p=0.0313) and 0.939 (p=0.2240), respectively, for the category averages of CLIMMOD, MANFOR and TIMEWIND. However, the interaction effects between two of these sources of uncertainty – MANFOR and TIMEWIND – with FMTYPE were significant sources of uncertainty in the ANOVA of the complete dataset (Fig. 1). This means that in absolute values, the effect of the simulation design was not the same for both FMTYPES.

3.3. Quantification of uncertainties for regional climate predictions

The decadal evolution of the predicted $T_{\text{max}}$, $T_{\text{min}}$ and precipitation, expressed as change compared to the average of the reference period 1971-2000, depended on the RCM used (Fig. 3). For $T_{\text{max}}$ and $T_{\text{min}}$ the percentage of the variance explained by the internal variability was small during the entire prediction period from 2000 to 2100. It decreased from 16.5% to 6.8% for $T_{\text{max}}$ and from 10.2% to 7.9% for $T_{\text{min}}$. The remaining variance was explained by the use of the 10 RCMs changing from 83.5% to 93.2% for $T_{\text{max}}$ and from 89.8% to 92.1% for $T_{\text{min}}$. In absolute values, the total variance of the $T_{\text{max}}$ predictions increased from 0.35°C to 0.85°C, and the total variance of $T_{\text{min}}$ increased from 0.40°C to 0.52°C.

For precipitation, the fraction of the total variance explained by the internal variability decreased from 32.5% to 16.0% over the prediction period. The fraction of the total variance explained by the use of different RCMs increased from 67.5% in the decade 2000-2010 to 84.0% in the decade 2090-2100. The total variance of the predicted change in precipitation over the different RCMs was 275.85 mm in the decade 2090-2100, compared with 119.19 mm in the decade 2000-2010.

4. Discussion

A major part of the variance of ASBI was explained by FMTYPE. This is explained by the large absolute differences in ASBI results between both FMTYPES and the large uncertainty in the ASBI results of the
process-based model ANAFORE. PBMs and EBMs significantly differ in the way that uncertainty is generated and they do this at each place in the model environment were uncertainty is generated (Walker et al., 2003). First, the ‘context uncertainty’ of the model has to be considered. Although PBMs and EBMs represent the forest system by the incorporation of external climatological variables, state variables (defining the initial forest situation) and eventually the consideration of forest management measures, the system boundaries of both model types are different. For example, ANAFORE defined the soil system in great detail, while SIBYLA didn’t. On the other hand, SIBYLA defined the forest structure by describing each individual tree, and thus by including inter-tree and inter-specific interactions.

Secondly, differences in uncertainty were generated by the discrepancy between the inherent structure of the models and reality. In EBMs such as SIBYLA the ‘structure uncertainty’ lies in the restrictions of the empirical relationships and their integration into the model. These empirical equations are based on data that are not necessarily representative of the entire population and/or of other local conditions (Korzukhin et al., 1996). For SIBYLA the regression functions for some of the sub-models were partly based on data from Germany (Pretzsch, 1995; Pretzsch et al., 2002). For PBMs, the structure uncertainty primarily results from the limits in representing physiological processes and the feedbacks between them (Girardin et al., 2008). They can be considered as simplifications of the real processes and thus imperfect representations of reality. Both model types contain several known, but also a lot of unknown, uncertainties in their structure.

Thirdly, uncertainty differences came with the input data (input uncertainty) and the way they were used in the models. Several of the climate variables were introduced into both models with the same uncertainty, generated by the climate predictions. Other climate variables differed between the models or were not introduced in the same way, thus creating different uncertainties. The differences in climate effects on model results were enhanced by the way in which they were used afterwards (the model structure uncertainty). State variables were imported differently in both models, leading to differences in their effect on the uncertainty. With poor information about the
state variables, there is a lot of unknown uncertainty, not reflected in the results. In the context of
comparing a PBM and an EBM the ‘parameter uncertainty’ is also a very important cause of
differences in model result uncertainty. In PBMs the parameter uncertainty is determined by the
multivariate distribution of the parameters (van Oijen et al., 2013). For ANAFORE the parameter
uncertainty was reflected in the post-calibration parameter space and could be described
statistically. On the other hand EBMs are deterministic in nature. Parameter uncertainty is often
represented by the confidence intervals for the input regression functions, which is not the true
uncertainty representative of the population. It was thus impossible to quantify the real parameter
uncertainty of the SIBYLA model. The parameter uncertainty becomes more important as the site
conditions deviate more strongly from the calibration conditions. All the aforementioned
uncertainties together are reflected in the final ‘model uncertainty’.

Another important source of uncertainty in the ASBI results was MANFOR, the management that
resulted in different forest densities prior to the forest growth simulations. Since the four forest plots
were exposed to nearly identical environmental conditions, it was possible to estimate the
importance of this source of uncertainty. The potential of a forest to withstand slowly changing
stresses and acute stress events depends on its natural and human-induced history as well as on its
actual density and composition (Lindner et al., 2014). Also, the way in which models cope with
mortality becomes more important when forests deviate from their actual equilibrium state (Hlásny
et al., 2014). Tree-specific models are very useful to take the exact forest structure into account.
PBMs have the advantage that the simulated forest responds much more realistically to climate
change. Small, but sometimes drastic interactions between forest structure and climate change
might not be captured by either or both models.

Notwithstanding the conclusion that input climate predictions are an important source of uncertainty
in ecological impact studies (Olesen et al., 2007; Ruffault et al., 2014), the use of different RCMs did
not introduce much variance in the forest model results. By deliberately limiting the climate
scenarios to local variants of scenario A1B, the uncertainty from climate scenarios was not fully reflected in this study. Additional sources of unknown uncertainty, not captured in the variance decomposition, could have changed the absolute and relative importance of the sources of uncertainty. Although tree growth varies as a function of nitrogen deposition in a non-linear way (Magnani et al., 2007), we did not include any nitrogen deposition scenario in the study. Further, no climate extremes were included in the predictions. The uncaptured and unknown uncertainties depend on the forest model used and on the choices of sources of uncertainty to be included in the variance decomposition.

The similar relative effect of the studied sources of uncertainty on ASBI results for the EBM and the PBM is encouraging, however, caution is needed. To make growth predictions that apply outside the range of the environmental conditions of calibration, the tree physiological processes must be modelled realistically. In all aspects of modelling, there are inherent risks in extrapolating empirical relationships outside the environmental conditions of the calibration data set. However, in the context of this study ANAFORE was too complex, in other words, over-parametrized for the data available. The significant interaction effects of STARTSET with both TIMEWIND and MANFOR in the ANOVA model confirmed this. Furthermore, ANAFORE has been developed for newly planted young forests; we observed an overestimation of the growth rate when simulating the adult forest plots of the present study. The accuracy, the context and the structure of the model have to be aligned with the management questions and the range of environmental conditions over which the model should be applied (Battaglia and Sands, 1998). This emphasizes the need for intensive collaboration between forest managers and modellers in defining the best model for answering specific questions. The model requirements for input and calibration data as well as their spatial and temporal scales have to be matched to the data available, with a focus on providing answers to the practical questions under specific environmental and management conditions. Purely PBMs or EBMs, or hybrid models could all be useful.
Future research on forest growth predictions should be designed to enable better risk evaluation by decision makers and forest managers. This research would benefit from: (i) open-access databases containing a large range of forest and environmental variables measured at different spatial and temporal scales to enable correct model calibration and validation. The concept of ‘supersites’ is useful for calibrating parameter-rich models; (ii) ongoing efforts at comparing model structures and their sensitivity to (interacting) external driving variables; (iii) proper communication about the sources of uncertainty, about the quantity of these uncertainties and about the place in the model where these uncertainties are generated.

5. Conclusions

A decomposition of the total variance in forest model results indicated that the type of model employed, i.e., empirical or process-based, makes the largest contribution to the uncertainty in the final model result. Although different simulation designs had similar relative effects on the estimated annual stem biomass increments for both the empirical and process-based models, the absolute differences in the estimates between model types were large. Further, the process-based model results were accompanied with an uncertainty that was 10 times larger than those from the empirical model. The initial values of input state variables made a large contribution to the uncertainty of forest model results. This highlights the risk in forest management when using forest models to guide decisions.

Acknowledgements

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Table 1: Synoptic description of the main characteristics of the empirically based SIBYLA and the process-based ANAFORE models. * climate data input in daily or monthly time steps are downscaled by the model to half hourly time steps. **depending on data availability the modeller can choose to use either stand-level or tree-level input data. If only stand-level data are available, the model generates tree-level data (coordinates, diameter at breast height and height distribution) to use in the simulations.
<table>
<thead>
<tr>
<th>Input</th>
<th>Spatial resolution</th>
<th>Temporal resolution</th>
<th>Contents, remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ANAFORE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stand</td>
<td>stand</td>
<td>initial</td>
<td>site information (long., lat., slope), cohort information</td>
</tr>
<tr>
<td>species</td>
<td>tree/cohort</td>
<td>initial</td>
<td>number of species (up to 10)</td>
</tr>
<tr>
<td>tree</td>
<td>tree/cohort</td>
<td>initial</td>
<td>dimensions, carbon content in pools</td>
</tr>
<tr>
<td>branch</td>
<td>tree/cohort</td>
<td>initial</td>
<td>separate information about branches for each whorl</td>
</tr>
<tr>
<td>soil biota</td>
<td>stand</td>
<td>initial</td>
<td>information about mycorrhizae, saprotrophic fungi and soil microbes</td>
</tr>
<tr>
<td>soil physics</td>
<td>stand</td>
<td>initial</td>
<td>maximum volumetric water content and water potential, pH, thickness, texture</td>
</tr>
<tr>
<td>soil organics</td>
<td>stand</td>
<td>initial</td>
<td>thickness according to litter biomass and a constant organic matter density</td>
</tr>
<tr>
<td>element concentration and fraction</td>
<td>stand</td>
<td>initial</td>
<td>carbon and nitrogen contents divided in fractions of size and availability in each layer</td>
</tr>
<tr>
<td>management</td>
<td>stand</td>
<td>year</td>
<td>thinning timing and rules, rotation cycle</td>
</tr>
<tr>
<td>climate</td>
<td>stand</td>
<td>half hour, day or month *</td>
<td>incoming solar radiation, temperature, humidity deficit, wind speed, precipitation, CO₂, nitrogen deposition</td>
</tr>
<tr>
<td>wood grading</td>
<td>tree/cohort</td>
<td>initial</td>
<td>classes of wood quality (European standards)</td>
</tr>
<tr>
<td>log quality assessment species</td>
<td>tree/cohort</td>
<td>initial</td>
<td>four categories for which maximum norms can be given for 10 parameters (European standards)</td>
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<tr>
<td><strong>SIBYLA</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stand**</td>
<td>tree</td>
<td>annual</td>
<td>depends on data available (species, vertical layer, density, age, site index, etc.)</td>
</tr>
<tr>
<td>tree</td>
<td>tree</td>
<td>annual</td>
<td>diameter at breast height, height, crown dimension, crown depth</td>
</tr>
<tr>
<td>soil</td>
<td>stand</td>
<td>annual</td>
<td>soil moisture and nutrient content in simple categories</td>
</tr>
<tr>
<td>climate</td>
<td>stand</td>
<td>annual</td>
<td>temperature, temperature amplitude, length of growing season, precipitation</td>
</tr>
<tr>
<td>management</td>
<td>stand/tree</td>
<td>annual</td>
<td>different management options</td>
</tr>
<tr>
<td>Output</td>
<td>Spatial resolution</td>
<td>Temporal resolution</td>
<td>Contents, remarks</td>
</tr>
<tr>
<td>-------------------</td>
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<td>----------------------------------------------------------------------------------</td>
</tr>
<tr>
<td><strong>ANAFORE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stand</td>
<td>stand</td>
<td>day</td>
<td>wood biomass, root biomass, height, maximum leaf area index, soil carbon</td>
</tr>
<tr>
<td>stand scale fluxes</td>
<td>stand</td>
<td>day</td>
<td>gross primary production, netto primary production, heterotrophic respiration, soil respiration, evaporation</td>
</tr>
<tr>
<td>tree output</td>
<td>tree cohort</td>
<td>day</td>
<td>number of trees, carbon allocation (day), carbon content per pool (year), height, basal area, dimensions</td>
</tr>
<tr>
<td>fluxes</td>
<td>tree cohort</td>
<td>half hour</td>
<td>water and carbon fluxes</td>
</tr>
<tr>
<td>Phosphorus (P)</td>
<td>stand</td>
<td>day</td>
<td>organic P, minimum P, P uptake by mycorizhae, P uptake by tree, P transfer by mycorizhae, total tree P, Carbon:P in organic layer</td>
</tr>
<tr>
<td>soil</td>
<td>stand</td>
<td>day</td>
<td>carbon, nitrogen, P, water, carbon:nitrogen ratio</td>
</tr>
<tr>
<td>nitrogen uptake</td>
<td>tree/cohort</td>
<td>day</td>
<td>available nitrate, nitrate transfer by mycorizhae, available ammonia</td>
</tr>
<tr>
<td>harvest</td>
<td>tree cohort</td>
<td>year</td>
<td>standing and transported carbon, nitrogen all pools, harvested number of trees</td>
</tr>
<tr>
<td>monetary</td>
<td>stand</td>
<td>year</td>
<td>yield, particulate matter, water, carbon, nitrogen, prices</td>
</tr>
<tr>
<td>particulate matter</td>
<td>tree cohort</td>
<td>day/year</td>
<td>deposited, re-suspended, removed, on leaf particulate matter concentration, precipitation, evaporation, throughfall, water on leaf, wind speed above trees, canopy LAI</td>
</tr>
<tr>
<td>wood</td>
<td>tree/cohort</td>
<td>day</td>
<td>stem sapwood, stem heartwood, branches sapwood, branch heartwood</td>
</tr>
<tr>
<td><strong>SYBILA</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stand</td>
<td>stand</td>
<td>annual</td>
<td>mean height, mean diameter, wood biomass, root biomass, foliage biomass, chemical content, biodiversity of tree species, forest density and other wood production characteristics</td>
</tr>
<tr>
<td>tree output</td>
<td>tree</td>
<td>annual</td>
<td>height, diameter, wood biomass, root biomass, foliage biomass, chemical content, timber type.</td>
</tr>
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FIGURE LEGENDS

Figure 1: Variance decomposition of average annual stem biomass increment results (ASBI; kg tree$^{-1}$ yr$^{-1}$) expressed as percentage (%) of the total variance explained per source of uncertainty, for: (a) only the main effects of each source; and (b) the main effects and the two-way interactions.

Figure 2: Boxplots of the predicted annual stem biomass increment (ASBI; kg tree$^{-1}$ yr$^{-1}$) for the combinations of forest model types, FMTYPES, with: (a) regional climate model (CLIMMOD); (b) forest management (MANFOR) and (c) time window of the predictions (TIMEWIND). The two forest models used were ANAFORE and SIBYLA.

Figure 3: Regional climate model predictions for minimum temperature, maximum temperature and precipitation, all expressed as changes according to the average of the reference period for climate predictions 1971-2000. The model uncertainty and the internal uncertainty are shown as insets in each plot.