

How random are predictions of forest growth? The importance of weather variability

Joanna Horemans, Olga Vindušková, and Gaby Deckmyn

Abstract: Quantifying the output uncertainty and tracking down its origins is key to interpreting the results of modelling studies. We performed such an uncertainty analysis on the predictions of forest growth and yield under climate change. We specifically focused on the effect of the interannual climate variability. For that, the climate years in the model input (daily resolution) were randomly shuffled within each 5-year period. In total, 540 simulations (10 parameter sets, nine climate shuffles, three global climate models, and two mitigation scenarios) were made for one growing cycle (80 years) of a Scots pine (*Pinus sylvestris* L.) forest growing in Peitz, Germany. Our results show that, besides the important effect of the parameter set, the random order of climate years can significantly change results such as basal area and produced volume, as well as the response of these to climate change. We stress that the effect of weather variability should be included in the design of impact model ensembles and in the accompanying uncertainty analysis. We further suggest presenting model results as likelihoods to allow risk assessment. For example, in our study, the likelihood of a decrease in basal area of >10% with no mitigation was 20.4%, whereas the likelihood of an increase >10% was 34.4%.

Key words: forest model, uncertainty, weather variability, basal area, production.

Résumé : Quantifier l'incertitude d'un résultat et en retrouver les origines est essentiel pour interpréter les résultats des études de modélisation. Nous avons effectué une telle analyse d'incertitude sur les prévisions de croissance et de rendement des forêts en tenant compte du changement climatique. Nous observons spécifiquement l'effet de la variabilité interannuelle du climat. Pour ce faire, nous avons mélangé aléatoirement les années climatiques, pour chaque période de 5 ans, dans les données de départ du modèle (résolution journalière). Au total, 540 simulations (10 jeux de paramètres, neuf mélanges climatiques, trois modèles climatiques globaux et deux scénarios d'atténuation) ont été réalisées pour un cycle de croissance (80 ans) d'une forêt de pin sylvestre (*Pinus sylvestris* L.) croissant à Peitz en Allemagne. Nos résultats montrent qu'en plus de l'effet important du jeu de paramètres, l'ordre aléatoire des années climatiques peut modifier considérablement les résultats de surface terrière et de production en volume, ainsi que la réponse de ceux-ci aux changements climatiques. Nous soulignons que l'effet de la variabilité météorologique doit être inclus dans la conception des ensembles de modèles d'impact et dans l'analyse de l'incertitude qui les accompagne. De plus, nous suggérons de présenter les résultats du modèle comme des probabilités, permettant ainsi une évaluation des risques. Dans notre étude par exemple, la probabilité d'une diminution de la surface terrière de plus de 10 % était de 20,4 % sans mesures d'atténuation, tandis que la probabilité d'une augmentation supérieure à 10 % était de 34,4 %. [Traduit par la Rédaction]

Mots-clés : modèle de croissance forestière, incertitude, variabilité météorologique, surface terrière, production.

Introduction

Impact and risk assessment in forestry is preferentially studied with the use of process-based models that, in contrast to empirical models, offer the possibility to mechanistically simulate forest functional changes and responses to changing environmental conditions (e.g., Korzukhin et al. 1996; Matala et al. 2003). Identifying the future consequences of global change and proposed management changes on the growth and functioning of forests is, however, inherently associated with high uncertainty (Tennoy et al. 2006). Uncertainty has multiple causes, but the overarching reasons are the ignorance about how greenhouse gas emissions will evolve as a function of energy production and consumption, and the incompleteness of the climatic and ecological model systems that predict how the climate changes in response to green-

house gas emissions, and how forests respond to these changes in climate (Pilkey and Pilkey-Jarvis 2007; Reyer et al. 2014). A conceptual basis for uncertainty management in model-based decision support brought some clarification in this domain (Walker et al. 2003), and more attention has since been given to the quantification of the main sources of uncertainty (Uusitalo et al. 2015). Bayesian calibration techniques, using Markov chain Monte Carlo (van Oijen et al. 2005) and other kinds of Bayesian or non-Bayesian algorithms (Gaucherel et al. 2008), shed light on parameter uncertainty and its implementation in model simulation and model outcome communication. Model ensembles further tackle the uncertainty arising from the forest models themselves by delivering information about variation in output caused by different model structures and assumptions (e.g., Friend et al. 2014). Although in such ensembles the correct weighting of

Received 29 October 2019. Accepted 27 July 2020.

J. Horemans. Université Catholique de Louvain (UCLouvain), Louvain-la-Neuve, Belgium; Plants and Ecosystems PLECO, Biology Department, University of Antwerp, Wilrijk, 2610, Belgium.

O. Vindušková and G. Deckmyn. Plants and Ecosystems PLECO, Biology Department, University of Antwerp, Wilrijk, 2610, Belgium.

Corresponding author: Gaby Deckmyn (email: gaby.deckmyn@uantwerpen.be).

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from copyright.com.

individual model output, related to the (in)dependency between model structures and parameter choices between different models, is still neglected, the use of model ensembles is a big step forward to the knowledge of realistic forest impact ranges. More uncertainty in forest model outcomes derives from the proposed storylines about future global societies. These future society scenarios are inserted in integrated assessment models of which the outputs are subsequently used in global climate models (GCMs) and regional climate models (Olesen et al. 2007). Multiple studies have been carried out to quantify the contributions of selected sources of uncertainty to the total variance of forest model outcomes, with widely varying results (Olesen et al. 2007; Nishina et al. 2015; Reyer et al. 2006). Such variance-based analyses not only allow us to interpret the model results in a stochastic way, but can also guide forest impact research towards tackling the domains that have the greatest impact on uncertainty. However, the results in each individual study are highly dependent on the simulation design and the incorporated sources of uncertainty and their levels.

Recently, several studies have emphasized the importance of extreme events such as long heat or drought periods in addition to the “average” changes in climate generally included in climate predictions (Seidl et al. 2011). Indeed, the occurrence of extreme events is predicted to increase as the climate changes. But even without an increase in extreme events (e.g., length of drought periods or heat waves), the day-to-day changes in weather affect the growth of plants (Razavi et al. 2016). For crop models, we know that between-year differences can be substantial, owing to the specific weather conditions (Powell and Reinhard 2016). It is unlikely that the yield of an annual crop in a very dry and a very wet year would equal the yield of two intermediate years. For trees, the sequence of climate years can have an even larger impact because their growth and reproduction depend on the weather in the previous year(s). Yet, in long-term forest studies, these effects are generally assumed to average out. Furthermore, for prediction lead time (the time between the issuance of a forecast and the occurrence of the phenomena that were predicted) within two decades, an important part of the total uncertainty in climate predictions could be ascribed to the internal variability of the climate system (Hawkins and Sutton 2009, 2011). This uncertainty attributed to variability in weather is mostly neglected in uncertainty analyses of forest model results or only incorporated indirectly by analyzing the climate predictions separately (Horemans et al. 2016). Also, in the communication of model results, this source of uncertainty is generally overlooked.

The main objective of this paper was to analyze the importance of weather variability on model predictions in relation to other sources of uncertainty by the inclusion of different year-to-year variability in the climate input for forest growth simulations. Furthermore, we propose a more stochastic way to analyze and communicate uncertainty.

Materials and methods

ANAFOR model

The ANAFOR model is a detailed mechanistic stand-scale model that dynamically simulates stand carbon (C), water, and nitrogen fluxes; tree growth; and wood tissue development by following a bottom-up approach: leaf-level processes (e.g., photosynthesis and transpiration) are simulated every half hour and implemented into a daily-operating tree architecture and C allocation module (for a full description, see Deckmyn et al. 2008). Trees are simulated as cohorts of identical trees, of the same or different species. Concerning the effects of global change, assimilated C is calculated from photosynthesis modelled with the Farquhar et al. (1980) model in combination with the Dewar (2002) model for stomatal conductance; the model is therefore both sensitive to carbon dioxide (CO₂) concentration and simulates increased

water use efficiency under high CO₂ concentrations. Concerning allocation, C is allocated to roots or shoots depending on the most limiting factor (light, water, or nutrients), and the ratio of crown width to height depends on the stand density and its effect on light availability. The model needs 140 parameters and has been calibrated for deciduous and coniferous species through a Bayesian optimization routine (Deckmyn et al. 2008, 2009, 2011; van Oijen et al. 2013).

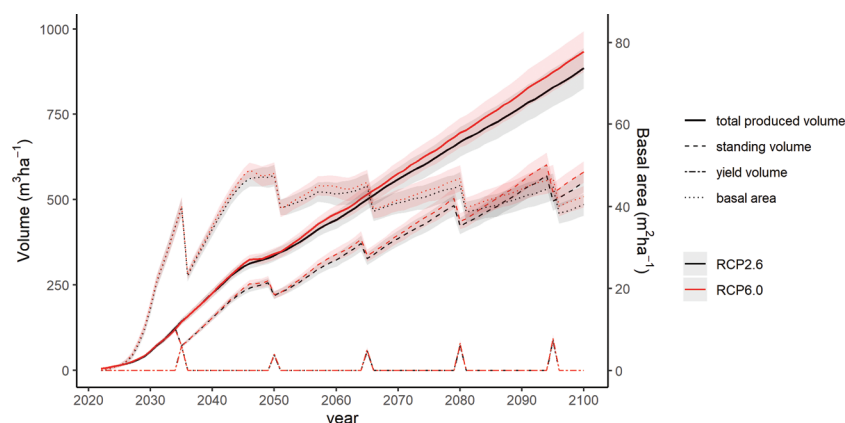
Simulation design

The model runs were performed for a virtual Scots pine (*Pinus sylvestris* L.) forest planted in Peitz, Germany (using data from the PROFOUND database, which includes the long-term monitoring site of Scots pine in Peitz; Lasch-Born et al. 2020), in 2021 (assumed 1-year-old trees) at a density of 10 000 trees·ha⁻¹ and growing for 79 years (tree age: 80 years) until 2100 on a sandy soil (87%–91% sand depending on the soil layer). The management scenario consisted of an initial thinning of a maximum of 50% of the stem number (depending on self-thinning) at 15 years of age (to 5000 trees·ha⁻¹) and subsequent thinning every 15 years. This initial high density was also used in the parameterization run (Brasschaat, Belgium), which affected the early-growth parameters, so our parameter sets were better suited to high-density planting. The amount thinned after the first thinning equalled half of the increase in basal area since the previous thinning and therefore depended on forest growth. This closely reflects the management in Brasschaat, the site for which our model was calibrated, which has climate and soil conditions comparable to those of Peitz. Foresters adjust thinning intensity to the growth intensity.

The climate data for the simulation design, coming from the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP), included two emission or climate scenarios based on greenhouse gas concentration trajectories (Representative Concentration Pathway (RCP)) as defined by the Intergovernmental Panel on Climate Change (IPCC). We used the most stringent mitigation scenario (RCP2.6) and the no-mitigation scenario (RCP6.0). The climate projections were made using three GCMs: MIROC5, IPSL-CM5A-LR, and GFDL-ESM2M. These data were not locally bias corrected. Nine variations of the predicted climate variability were included, hereinafter called “climate shuffles” or simply “shuffles”. They were implemented by changing the order of the different years nine times, but always constricted within a 5-year time period, so as not to change the impact of long-term trends in the climate projections (year 1 could become year 5 but not year 10). For each shuffle, one permutation was carried out in each of the 5-year periods, and these permuted 5-year sequences were then concatenated in their respective order to form one climate input. This was repeated nine times to obtain the different climate shuffles.

For our model runs, we used 10 different parameter sets (which each had 140 parameters) derived from the posterior distribution of a previous model calibration by Bortier et al. (2018) who calibrated ANAFOR using forest biomass and flux data from the Scots pine Brasschaat forest. For that study, a Bayesian approach (van Oijen et al. 2005) was used to calibrate the model parameters (only parameters describing the tree; all soil parameters were fixed) according to the model fit with measured data of diameter at breast height (DBH), tree height, gross primary production, and evapotranspiration from the years 1996–2010 (for full description of the calibration, see Bortier et al. 2018). For the present study, a Latin hypercube sample of 10 parameter sets was taken from the described posterior parameter distribution to reduce the required number of runs. A Latin hypercube sample is partially random but takes more samples from the range with the higher likelihood, so one gets a more representative sample than with random sampling (McKay et al. 1979). The mean variation of the 140 parameters (for values, see Bortier et al. 2018) was 11%, and the likelihood of the 10 parameter sets ranged from –995 (best fit)

Fig. 1 Mean $\pm$ confidence interval of the predicted produced, standing, and yield volume and basal area averaged over all parameter sets, global climate models (GCMs), and shuffles. Black lines represent RCP2.6 (most stringent mitigation scenario), and red lines represent RCP6.0 (no-mitigation scenario). Each line represents a mean of 270 runs. [Colour online.]



to -4588 (worst fit). The simulation design included different climate inputs based on climate projections from three GCMs run for two RCPs and nine shuffles of each of these projections used in combination with a representative sample of parameter sets. This allowed us to explore the uncertainty caused by weather variability in predicting climate change effects on forest growth in the context of other sources of uncertainty. With this ensemble of simulation designs, we simulated several output variables related to the growth and functioning of the forest. For this study, we used the output for basal area; standing volume; yield; DBH; height; and C in wood, roots, leaves, and soil. Produced volume was calculated as the sum of standing volume and cumulative yield.

Variance analyses

The uncertainty assessment was based on a decomposition of the total variance of basal area and produced volume. First, a complete uncertainty assessment was carried out on final simulation output values, which included fixed effects for each of the sources of uncertainty present in the simulation design (i.e., the two RCP scenarios, three GCMs, nine climate shuffles, and 10 parameter sets) and their two-way interactions. After this global analysis, we focused on analyses per parameter set (the dominant source of uncertainty) to compare the importance of the climate-related sources of uncertainty between them, as well as their evolution over time. For this, a separate analysis of variance (ANOVA) was carried out for each decade, using its end value (i.e., value in years 2030, 2040, 2050, 2060, 2070, and 2080). Again, the two-way interactions between the sources of uncertainty were considered. The variance in the output explained by each of the sources of uncertainty was calculated by dividing the sum of squared errors of the factors in the model (the sources of uncertainty) by the total sum of squared error of the response. The statistical analyses and the graphs were made in R version 3.4.3 (R Core Team 2017).

Evaluation of the differences between scenarios

The difference between the no-mitigation scenario RCP6.0 and the stringent mitigation scenario RCP2.6 was calculated for each pair of simulation runs obtained using the same GCM, shuffle pattern, and parameter, taking the mitigation scenario as a baseline. The absolute difference was calculated as $RCP6.0 - RCP2.6$, and the relative difference (%) was calculated as $RCP6.0/RCP2.6 \times 100$. The probability of a decrease of $>10\%$ in a variable in a no-

mitigation scenario compared with a mitigation scenario baseline was calculated for selected variables using the final model output as the proportion of simulation pairs for which the relative difference was $<90\%$. The probability of an increase of $>10\%$ was calculated as the proportion of simulation pairs for which the relative difference was $>110\%$.

Results

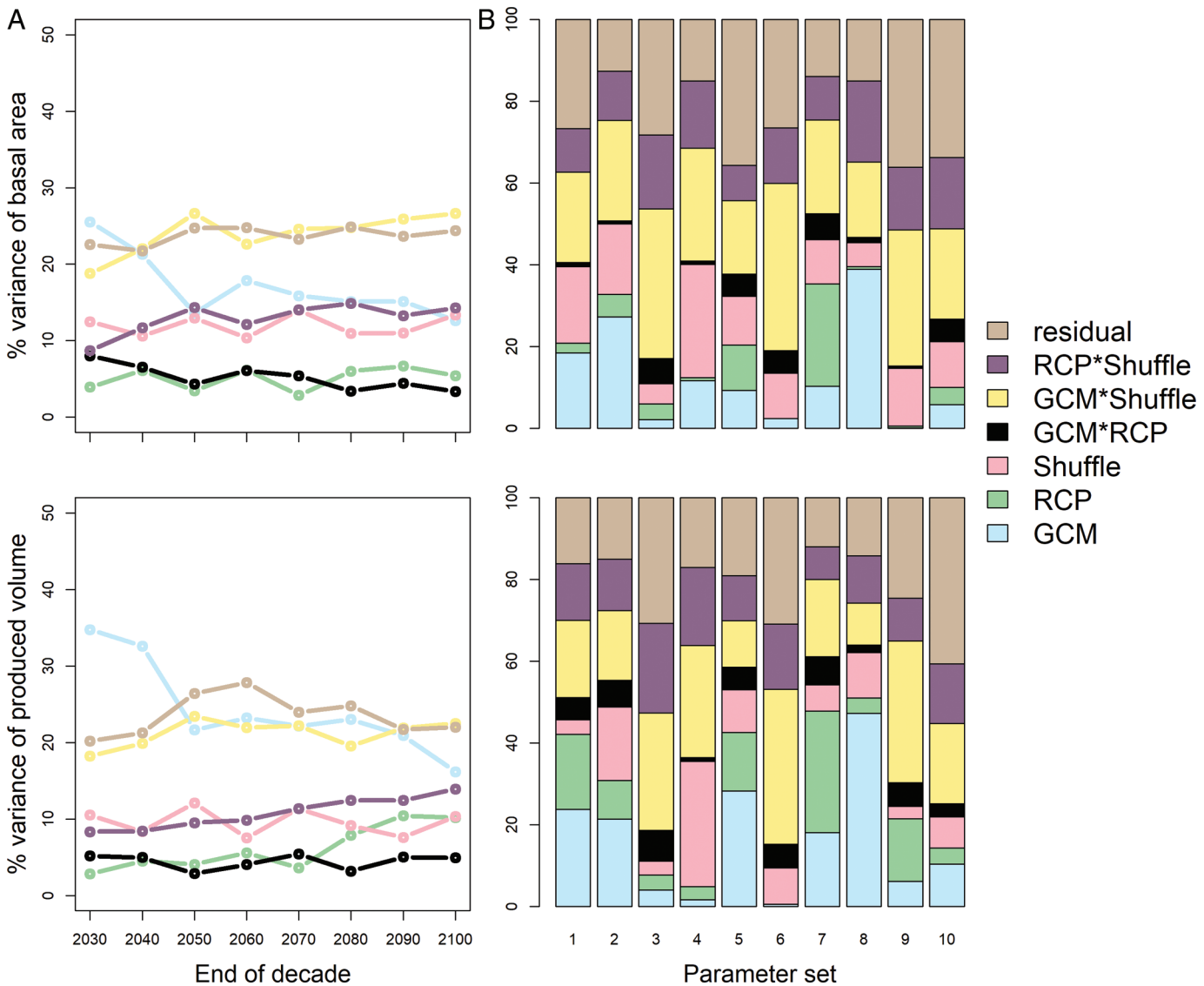
The mean of all simulation runs exhibited expected patterns of steady increase in produced volume (obtained as sum of standing volume and cumulative yield) and saturating basal area responsive to thinning events over the growing cycle (Fig. 1). Both basal area and produced volume were on average higher at the end of simulation under the no-mitigation (RCP6.0) scenario compared with the most stringent mitigation scenario (RCP2.6) (ANOVA, $p < 0.05$; Supplementary Tables S1 and S2¹). However, the main source of uncertainty in our exercise was the use of different parameter sets, which explained 92% and 96% of final basal area and produced volume, respectively (Supplementary Tables S1 and S2¹).

For example, the mean produced volume varied between 304 and 1694 $m^3 \cdot ha^{-1}$ depending on the parameter set used, and a similar pattern was found for basal area (Supplementary Fig. S1¹). Apart from the parameter set and scenario, the type of the GCM model also had a significant main effect ($p < 0.05$) for the final produced volume (Supplementary Table S2¹). Moreover, all three two-way interactions between GCM, scenario, and parameter set had significant effects on both basal area and produced volume.

In the next step, we focused on the climate-related sources of uncertainty by analyzing simulations of each parameter set separately and looked at how their importance changed over the simulation period. Across parameter sets and time, the highest proportion of variance was explained by the GCM and by the interaction of GCM and shuffling for both basal area and produced volume (Fig. 2A). The main effect of GCM decreased over time for both variables and was more important for produced volume. The variance explained by scenario was one of the lowest but tended to increase in time for produced volume. Interestingly, shuffling explained on average more variability than the scenario — across all decades for basal area and in the first five decades for produced volume. Across decades and parameter sets, climate shuffles explained 12% and 10% of uncertainty in the

¹Supplementary data are available with the article at <https://doi.org/10.1139/cjfr-2019-0366>.

Fig. 2. Contribution of the different sources of uncertainty to predicted basal area (top) and produced volume (bottom) (A) at the end of each decade, averaged over 10 parameter sets, and (B) at final harvest (age 80) for each of the 10 parameter sets. For the ANOVA results used for panel B, see Supplementary Tables S1 and S2.¹ [Colour online.]



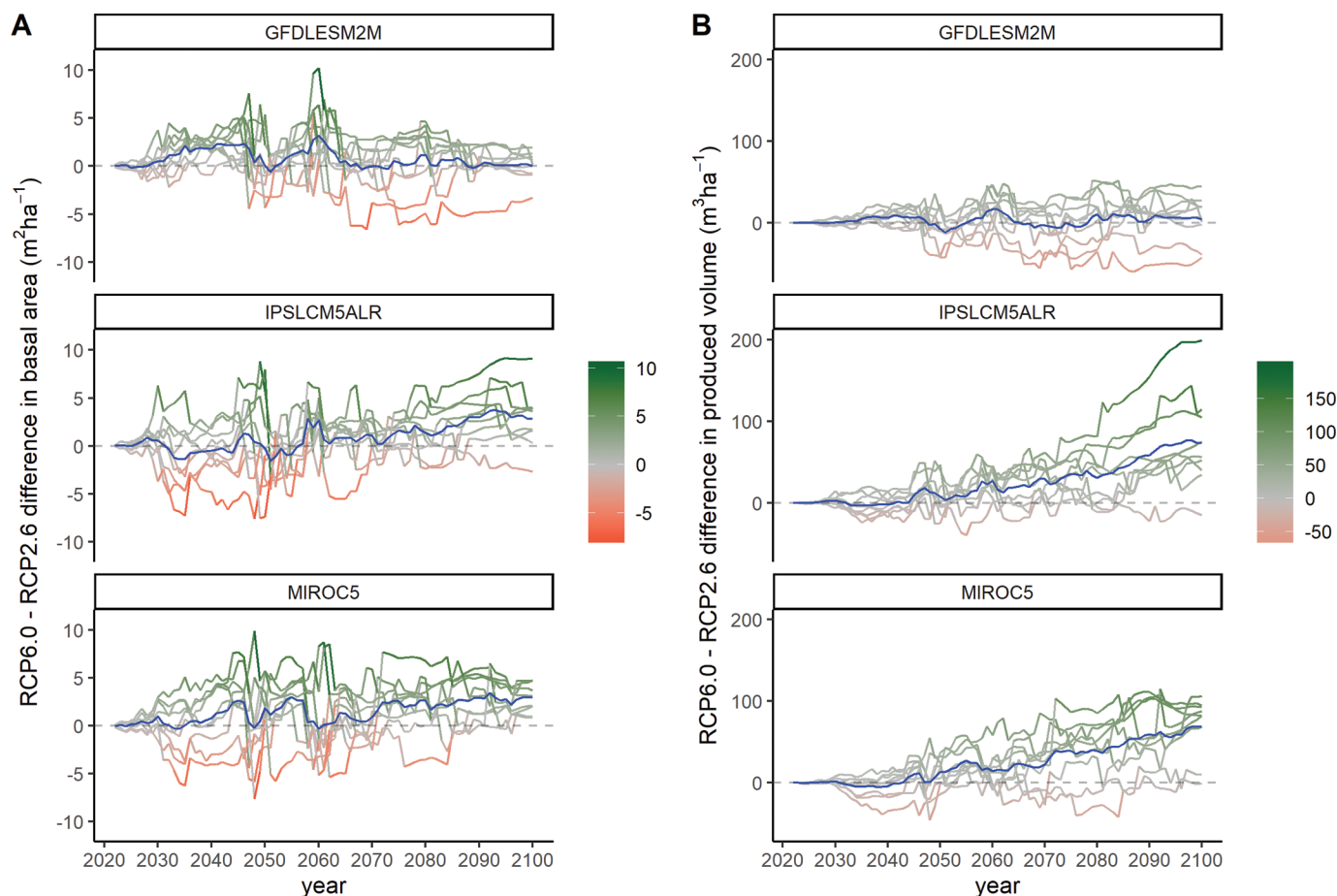
simulated basal area and produced volume, respectively. However, its interaction with GCM and scenario explained an additional 24% and 13%, respectively, with similar but slightly lower values for produced volume (21% and 11%). In total, climate shuffling and its two-way interactions with GCM and scenario were on average responsible for 49% and 42% of the uncertainty not related to parameters in basal area and produced volume, respectively.

As already suggested by the significance of two-way interactions with parameter set in the global ANOVAs, the total explained uncertainty, as well as its composition, differed substantially between parameter sets (Fig. 2B; Supplementary Tables S1 and S2¹). For example, depending on the parameter set, the main effect of shuffle ranged between 5% and 28% for basal area and between 3% and 31% for produced volume (Supplementary Tables S1 and S2¹). However, it was significant ($p < 0.05$) only in two parameter sets (Nos. 2 and 4) for basal area and one parameter set (No. 4) for produced volume (Supplementary Tables S1 and S2¹; Supplementary

Fig. S1¹). Similarly, the interaction between the climate shuffle and the GCM explained 18%–41% of basal area and 10%–38% of produced volume (Fig. 2B) but was significant only in one parameter set for basal area (Supplementary Table S1¹). The most frequently significant effect was GCM, which was significant for only half of the parameter sets for both variables (Supplementary Tables S1 and S2¹). Second in place, the variability explained by RCP scenario was significant in combination with three and five parameter sets for basal area and produced volume, respectively.

To further unravel how the weather variability created by different GCMs and their shuffles affects the simulated response of forest growth to different mitigation scenarios, we looked at the difference between the two selected scenarios using means over all parameter sets for each shuffle (Fig. 3). Depending on the choice of climate input, the model predicted contrasting differences between the two scenarios. The predicted difference in produced volume between the RCP6.0 and RCP2.6 scenarios ranged between -42 and $199 \text{ m}^3 \cdot \text{ha}^{-1}$ depending on GCM and shuffle. On

Fig. 3. The difference in (A) basal area and (B) produced volume between RCP6.0 (no-mitigation scenario) and RCP2.6 (most stringent mitigation scenario) for each of the nine shuffles of three GCMs: GFDL-ESM2M (top), IPSL-CM5A-LR (middle), and MIROC5 (bottom). Each line represents one climate shuffle and is colour-coded based on its y axis value. Green and red represent positive and negative effect, respectively, of the no-mitigation scenario (pronounced climate change) on the predicted variables, compared with the mitigation scenario. Blue lines represent the mean of all shuffles. [Colour online.]



average, the simulations using GFDL-ESM2M model output yielded close-to-zero effect of mitigation scenarios on the final basal area and produced volume, whereas the outputs of the other two GCMs were associated with a mean positive effect of the no-mitigation scenario. Although the mean effect of pronounced climate change on produced volume and basal area was positive, five out of the 27 GCM shuffles (3 GCM $\times$ 9 shuffles) yielded a negative effect on produced volume.

Finally, we investigated the difference between the two scenarios in other simulated variables, for which we used their final values at age 80, across all paired simulations (Fig. 4; Table 1). The probability distribution densities of the differences showed that although a part of the runs yielded high and both positive and negative differences between both scenarios, the highest density of the difference was close to 0 for all the investigated variables. Positive mean effects of no-mitigation scenario were observed for all variables except C in soil and DBH, and the relatively highest difference (123.8%) was found for C in leaves.

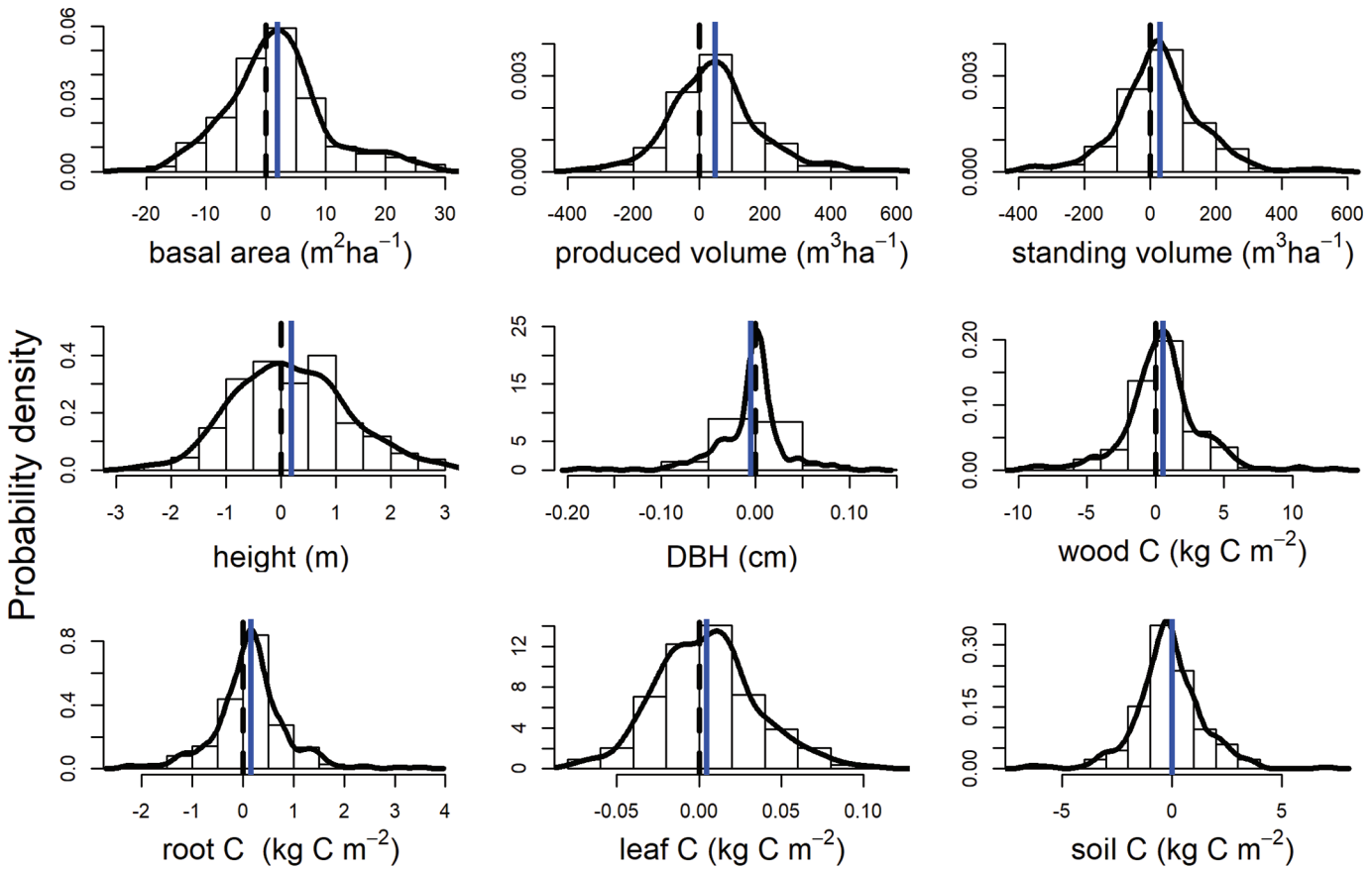
Discussion

Our study revealed some important insights regarding the potential output uncertainty of forest growth models. Firstly, the projected weather variability can have a large effect on the conclusions drawn from a model study (Fig. 3). Although the importance of the inherent variability in climate predictions is rec-

ognized and has been quantified in some studies (e.g., Hawkins and Sutton 2009; 2011), it has been widely neglected in impact studies. We have shown that the variability in the weather or its interaction with the used GCM had a higher effect on the basal area of the forest than the RCP scenario. Overall, the weather variability introduced by shuffles and its two-way interactions with the GCM and RCP scenario were responsible for 42%–49% of the uncertainty in the model output that was not related to parameterization of the model (Fig. 2A). We also showed how very different conclusions concerning the effect of climate change can be obtained by the random choice of a specific order of daily climate data (Figs. 3 and 4). Although we rarely found significant effect of shuffling on the predicted results using the performed ANOVA analyses, this is not surprising because the shuffles were always influenced by being nested within a scenario and GCM. It was therefore not possible to properly statistically test whether they differ, as technically, they were single replicates. However, we could see that shuffling was associated with considerable uncertainty. The shuffles also provided replicates that allowed us to statistically analyze the effect of different GCMs, scenarios, and their interaction on modelled results.

Weather is, and will remain, highly unpredictable. As science progresses, parameter estimation, model structure, and climate predictions improve, and variance analyses can guide us to put

Fig. 4. Histograms and overlaying distribution densities of the difference between RCP6.0 and RCP2.6 at age 80, for all 270 simulation pairs (3 GCMs $\times$ 9 shuffles $\times$ 10 parameter sets) for nine output variables: basal area; produced volume; standing volume; height; diameter at breast height (DBH); and carbon (C) stocks in wood, roots, leaves, and soil. Dashed lines represent zero difference between the two scenarios. Full vertical blue lines represent the mean (for values, see Table 1). [Colour online.]



RCP6.0 - RCP2.6 difference

Table 1. Mean difference, mean percentage (%) of difference, probability (Pr) of a 10% decrease, and probability of a 10% increase of different output variables when comparing the final results at 80 years of age between the no-mitigation scenario (RCP6.0) and the strong mitigation scenario (RCP2.6) over all 270 simulation pairs (3 global climate models (GCMs) $\times$ 9 shuffles $\times$ 10 parameter sets).

Variable	Mean difference	Mean % difference	Pr > 10% decrease (%)	Pr > 10% increase (%)
Basal area ($\text{m}^2 \cdot \text{ha}^{-1}$)	2.0	115.6	20.4	34.4
Produced volume ($\text{m}^3 \cdot \text{ha}^{-1}$)	48.9	112.7	14.4	33.7
Standing volume ($\text{m}^3 \cdot \text{ha}^{-1}$)	29.2	114.0	20.4	37.4
Height (m)	0.2	101.1	1.5	4.8
DBH (cm)	0.0	98.8	21.9	12.6
Wood C ($\text{kg C} \cdot \text{m}^{-2}$)	0.5	115.3	21.1	36.7
Root C ($\text{kg C} \cdot \text{m}^{-2}$)	0.2	119.6	21.5	37.8
Leaf C ($\text{kg C} \cdot \text{m}^{-2}$)	0.0	119.9	39.6	47.0
Soil C ($\text{kg C} \cdot \text{m}^{-2}$)	-0.1	99.8	18.1	18.5

Note: DBH, diameter at breast height; C, carbon.

more effort where we can gain most, but, as suggested by the chaos theory, the complex and chaotic weather system can never be predicted, no matter how good our understanding of climate and weather becomes (Slingo and Palmer 2011). Furthermore and as confirmed by this study, ecosystem simulation models are very sensitive to variation in weather (Olesen et al. 2007). Besides the

uncertainty brought in by environmental disturbances such as extreme weather events that are difficult to implement in impact models (Seidl et al. 2011), our study shows that less extreme weather variability is also an important source of uncertainty in model results. We conclude that this uncertainty is probably larger than previously thought and propose using the shuffling

procedure as one way to introduce interannual climate variability and the associated uncertainty into impact studies.

Secondly, we found that the relative importance of the different sources of uncertainty strongly depended on the parameter set used for the simulation. ANAFORE has been previously shown to be associated with a high parameter uncertainty because it is a very complex model with many parameters (van Oijen et al. 2013). Also, the calibration used (Bortier et al. 2018) was carried out on relatively large-scale data, leaving the uncertainty of parameters linked to stomatal behaviour, photosynthesis, allocation, and soil processes rather wide. This also means that the used prior parameter distributions for the Bayesian calibration were wide; in other words, the prior uncertainty of physiological parameters was large. However, this is not a model-specific problem, but can be generalized to the lack of precise parameter estimates on leaf and stand scales (e.g., Yousefpour et al. 2012). Several authors have reported on the parameter uncertainty (e.g., Horemans et al. 2016; Reyer et al. 2006), and it is now generally included in simulation designs. In many studies, however, only the best fitting parameterization is still used, which of course decreases the reported uncertainty.

Thirdly, the mean of a simulation ensemble is not representative of the possible outcome of specific future emission or climate scenarios and is as useless as the outcome of a single model run. To illustrate this, for our particular study, we found a mean difference of $49 \text{ m}^3 \cdot \text{ha}^{-1}$ in produced volume between the no-mitigation scenario (RCP6.0) and the strong mitigation scenario (RCP2.6), suggesting a small positive effect of climate change on forest growth of the hypothesized forest grown between 2021 and 2100 in Peitz. However, the likelihood of obtaining a 10% increase (33.7%) is only around 19% more than the likelihood of obtaining a 10% decrease (14.4%). The obtained mean differences of 0.5, 0.2, and $0 \text{ kg C} \cdot \text{m}^{-2}$ for the C stocks in wood, roots, and leaves, respectively, is stochastically translated to likelihoods between 37% and 47% of obtaining an increase of $>10\%$. A mean difference of $-0.1 \text{ kg C} \cdot \text{m}^{-2}$ for the C stock in the soil would be stochastically translated to an 18% chance of a decrease of $>10\%$ in the soil C stock. These results are within the described ranges of effects for similar forests (Gustafson et al. 2017), in which both positive and negative effects on growth have been measured and modelled, whereas the effect of global change on soil C tends to be negative (as increased soil temperature increases soil organic matter turnover; Bottner et al. 2000). More generally, we propose that any impact studies should report a probability distribution of the results, as well as a description and quantification of the included sources of uncertainty. By taking into account and reporting on the many uncertainties, forest models can better support decision-making in forest management even if the choice of the sources of uncertainty remains somewhat subjective. Due to the inherent high uncertainties and the fact that managers do not have the accuracy in information they need from simulation studies (Pilkey and Pilkey-Jarvis 2007), new approaches such as, for example, portfolio diversification (Millar et al. 2007; Temperli et al. 2012; Schelhaas et al. 2015) and robust decision-making (McInerney et al. 2012; Yousefpour and Hanewinkel 2016) seem an appropriate solution, even if production concessions have to be made to reduce the risk of a very negative impact.

In summary, we conclude that the variability in weather should be included in simulation ensembles for forest growth and in the accompanying uncertainty assessment. Uncertainty assessment should be part of the modeller's protocol, and the results thereof should always be reported with the complete density distribution of the model results, providing information by which policy-makers and forest managers can base their risk assessments. Scientists should abandon the deterministic dogma and instead show their results in a probabilistic way.

Acknowledgements

This study was financially supported by the Belgian Science Policy Office (BELSPO) through the program BRAIN-be (contract BR/121/A2/MASC), and co-funding by the Slovenian Research Agency through the research program P4-0107 is acknowledged. O.V. was supported by the H2020-MSCA-IF project No. 793485. This work has been conducted under the framework of COST Action FP1304 PROFOUND and under the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP), funded by the German Federal Ministry of Education and Research (reference No. 01LS1201A). We thank Reinhart Ceulemans for providing scientific support and feedback.

References

- Bortier, M.F., Andivia, E., Genon, J.G., Grebenc, T., and Deckmyn, G. 2018. Towards understanding the role of ectomycorrhizal fungi in forest phosphorus cycling: a modelling approach. *Cent. Eur. For. J.* **64**: 79–95. doi:10.1515/forj-2017-0037.
- Bottner, P., Coûteaux, M.-M., Anderson, J.M., Berg, B., Billès, G., Bolger, T., et al. 2000. Decomposition of ^{13}C -labelled plant material in a European $65\text{--}40^\circ$ latitudinal transect of coniferous forest soils: simulation of climate change by translocation of soils. *Soil Biol. Biochem.* **32**(4): 527–543. doi:10.1016/S0038-0717(99)00182-0.
- Deckmyn, G., Verbeeck, H., De Beeck, M.O., Vansteeniste, D., Steppe, K., and Ceulemans, R. 2008. ANAFORE: a stand-scale process-based forest model that includes wood tissue development and labile carbon storage in trees. *Ecol. Modell.* **215**(4): 345–368. doi:10.1016/j.ecolmodel.2008.04.007.
- Deckmyn, G., Mali, B., Kraigher, H., Torelli, N., Op de Beeck, M., and Ceulemans, R. 2009. Using the process-based stand model ANAFORE including Bayesian optimisation to predict wood quality and quantity and their uncertainty in Slovenian beech. *Silva Fenn.* **43**(3): 523–534. doi:10.14214/sf.204.
- Deckmyn, G., Campioli, M., Muys, B., and Kraigher, H. 2011. Simulating C cycles in forest soils: Including the active role of micro-organisms in the ANAFORE forest model. *Ecol. Modell.* **222**(12): 1972–1985. doi:10.1016/j.ecolmodel.2011.03.011.
- Dewar, R.C. 2002. The Ball–Berry–Leuning and Tardieu–Davies stomatal models: synthesis and extension within a spatially aggregated picture of guard cell function. *Plant Cell Environ.* **25**(11): 1383–1398. doi:10.1046/j.1365-3040.2002.00909.x.
- Farquhar, G.V., von Caemmerer, S.V., and Berry, J.A. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species. *Planta*, **149**(1): 78–90. doi:10.1007/BF00386231.
- Friend, A.D., Lucht, W., Rademacher, T.T., Keribin, R., Betts, R., Cadule, P., et al. 2014. Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2 . *Proc. Natl. Acad. Sci. U.S.A.* **111**(9): 3280–3285. doi:10.1073/pnas.1222477110.
- Gaucherel, C., Campillo, F., Misson, L., Guiot, J., and Boreux, J.-J. 2008. Parameterization of a process-based tree-growth model: comparison of optimization, MCMC and particle filtering algorithms. *Environ. Modell. Softw.* **23**(10–11): 1280–1288. doi:10.1016/j.envsoft.2008.03.003.
- Gustafson, E.J., Miranda, B.R., De Bruijn, A.M.G., Sturtevant, B.R., and Kubiske, M.E. 2017. Do rising temperatures always increase forest productivity? Interacting effects of temperature, precipitation, cloudiness and soil texture on tree species growth and competition. *Environ. Modell. Softw.* **97**: 171–183. doi:10.1016/j.envsoft.2017.08.001.
- Hawkins, E., and Sutton, R. 2009. The potential to narrow uncertainty in regional climate predictions. *Bull. Am. Meteor. Soc.* **90**(8): 1095–1107. doi:10.1175/2009BAMS2607.1.
- Hawkins, E., and Sutton, R. 2011. The potential to narrow uncertainty in projections of regional precipitation change. *Clim. Dyn.* **37**(1–2): 407–418. doi:10.1007/s00382-010-0810-6.
- Horemans, J.A., Bosela, M., Dobor, L., Barna, M., Bahyl, J., Deckmyn, G., et al. 2016. Variance decomposition of stem biomass increment predictions for European beech: contribution of selected sources of uncertainty. *For. Ecol. Manage.* **361**: 46–55. doi:10.1016/j.foreco.2015.10.048.
- Korzukhin, D., Ter-Mikaelian, M., and Wagner, G. 1996. Process versus empirical models: which approach for forest ecosystem management? *Can. J. For. Res.* **26**(5): 879–887. doi:10.1139/x26-096.
- Lasch-Born, P., Suckow, F., Reyer, C., Gutsch, M., Kollas, C., Badeck, F.-W., et al. 2020. Description and evaluation of the process-based forest model 4C at four European forest sites. *Geosci. Model Dev.* **13**: 5311–5343. doi:10.5194/gmd-13-5311-2020.
- Matala, J., Hynynen, J., Miina, J., Ojansuu, R., Peltola, H., Sievänen, R., et al. 2003. Comparison of a physiological model and a statistical model for prediction of growth and yield in boreal forests. *Ecol. Modell.* **161**(1–2): 95–116. doi:10.1016/S0304-3800(02)00297-1.

- McInerney, D., Lempert, R., and Keller, K. 2012. What are robust strategies in the face of uncertain climate threshold responses? *Clim. Change*, **112**(3–4): 547–568. doi:10.1007/s10584-011-0377-1.
- McKay, M.D., Beckman, R.J., and Conover, W.J. 1979. Comparison of three methods for selecting values of input variables in the analysis of output from a computer code. *Technometrics*, **21**: 239–245.
- Millar, C.I., Stephenson, N.L., and Stephens, S.L. 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecol. Appl.* **17**(8): 2145–2151. doi:10.1890/06-1715.1.
- Nishina, K., Ito, A., Falloon, P., Friend, A.D., Beerling, D.J., Ciais, P., et al. 2015. Decomposing uncertainties in the future terrestrial carbon budget associated with emission scenarios, climate projections, and ecosystem simulations using ISI-MIP results. *Earth Syst. Dyn.* **6**(2): 435–445. doi:10.5194/esd-6-435-2015.
- Olesen, J.E., Carter, T.R., Díaz-Ambrona, C.H., Fronzek, S., Heidmann, T., Hickler, T., et al. 2007. Uncertainties in projected impacts of climate change on European agriculture and terrestrial ecosystems based on scenarios from regional climate models. *Clim. Change*, **81**(S1): 123–143. doi:10.1007/s10584-006-9216-1.
- Pilkey, O.H., and Pilkey-Jarvis, L. 2007. Useless arithmetic: why environmental scientists can't predict the future. Columbia University Press, New York. p. 230.
- Powell, J.P., and Reinhard, S. 2016. Measuring the effects of extreme weather events on yields. *Weather Clim. Extrem.* **12**: 69–79. doi:10.1016/j.wace.2016.02.003.
- Razavi, T., Switzman, H., Arain, A., and Coulibaly, P. 2016. Regional climate change trends and uncertainty analysis using extreme indices: a case study of Hamilton Canada. *Clim. Risk Manage.* **13**: 43–63. doi:10.1016/j.crm.2016.06.002.
- R Core Team. 2017. R: a language and environment for statistical computing. Version 3.4.3. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.R-project.org>.
- Reyer, C., Lasch-Born, P., Suckow, F., Gutsch, M., Murawski, A., and Pilz, T. 2014. Projections of regional changes in forest net primary productivity for different tree species in Europe driven by climate change and carbon dioxide. *Ann. For. Sci.* **71**(2): 211–225. doi:10.1007/s13595-013-0306-8.
- Reyer, C.P.O., Flechsig, M., Lasch-Born, P., and van Oijen, M. 2006. Integrating parameter uncertainty of a process-based model in assessments of climate change effects of forest productivity. *Clim. Change*, **137**(3–4): 395–409. doi:10.1007/s10584-016-1694-1.
- Schelhaas, M.-J., Nabuurs, G.-J., Hengeveld, G., Reyer, C., Hanewinkel, M., Zimmermann, N.E., and Cullmann, D. 2015. Alternative forest management strategies to account for climate change-induced productivity and species suitability changes in Europe. *Reg. Environ. Change*, **15**(8): 1581–1594. doi:10.1007/s10113-015-0788-z.
- Seidl, R., Fernandes, P.M., Fonseca, T.F., Gillet, F., Jönsson, A.M., Merganičová, K., et al. 2011. Modelling natural disturbances in forest ecosystems: a review. *Ecol. Modell.* **222**(4): 903–924. doi:10.1016/j.ecolmodel.2010.09.040.
- Slingo, J., and Palmer, T. 2011. Uncertainty in weather and climate predictions. *Philos. Trans. R. Soc. London Ser. A*, **369**: 4751–4767. doi:10.1098/rsta.2011.0161.
- Temperli, C., Bugmann, H., and Elkin, C. 2012. Adaptive management for competing forest goods and services under climate change. *Ecol. Appl.* **22**(8): 2065–2077. doi:10.1890/12-0210.1.
- Tennoy, A., Kvaerner, J., and Gjerstad, K.I. 2006. Uncertainty in environmental impact assessment predictions: the need for better communication and more transparency. *IAPA*, **24**: 45–56. doi:10.3152/147154606781765345.
- Uusitalo, L., Lehtikoinen, A., Helle, I., and Myrberg, K. 2015. An overview of methods to evaluate uncertainty of deterministic models in decision support. *Environ. Modell. Softw.* **63**: 24–31. doi:10.1016/j.envsoft.2014.09.017.
- van Oijen, M., Rougier, J., and Smith, R. 2005. Bayesian calibration of process-based forest models: bridging the gap between models and data. *Tree Physiol.* **25**(7): 915–927. doi:10.1093/treephys/25.7.915.
- van Oijen, M., Reyer, C., Bohn, F.J., Cameron, D.R., Deckmyn, G., Flechsig, M., et al. 2013. Bayesian calibration, comparison and averaging of six forest models, using data from Scots pine stands across Europe. *For. Ecol. Manage.* **289**: 255–268. doi:10.1016/j.foreco.2012.09.043.
- Walker, W.E., Harremoës, P., Rotmans, J., van der Sluijs, J.P., van Asselt, M.B.A., Janssen, P., and Kreyer von Krauss, M.P. 2003. Defining uncertainty: a conceptual basis for uncertainty management in model-based decision support. *Integr. Assess.* **4**(1): 5–17. doi:10.1076/iaij.4.1.5.16466.
- Yousefpour, R., and Hanewinkel, M. 2016. Climate change and decision-making under uncertainty. *Curr. For. Rep.* **2**: 143–149. doi:10.1007/s40725-016-0035-y.
- Yousefpour, R., Bredahl Jacobsen, J., Jellesmark Thorsen, B., Meilby, H., Hanewinkel, M., and Oehler, K. 2012. A review of decision-making approaches to handle uncertainty and risk in adaptive forest management under climate change. *Ann. For. Sci.* **69**(1): 1–15. doi:10.1007/s13595-011-0153-4.