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1 **Variance decomposition of predictions of stem biomass increment for**

2 **European beech: contribution of selected sources of uncertainty**

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4 J.A. Horemans^a, M. Bosela^{b,c,f}, L. Dobor^d, M. Barna^{c,e}, J. Bahyl^f, G. Deckmyn^a, M. Fabrika^f, R. Sedmak^{c,f}
5 and R. Ceulemans^a

6
7 ^a Centre of Excellence PLECO, Department of Biology, University of Antwerp, Universiteitsplein 1, B-
8 2610 Wilrijk, Belgium

9 ^b Department of Silviculture and Forest Production, National Forest Centre - Forest Research Institute
10 Zvolen, T.G. Masaryka 22, 960 92 Zvolen, Slovak Republic

11 ^c Department of Forest management, Faculty of Forestry and Wood Sciences, Czech University of Life
12 Sciences, Kamýcká 129, 165 21 Praha - Suchdol, Czech Republic

13 ^d Department of Meteorology, Eötvös Loránd University, Pázmány P. sétány 1/A, H-1117 Budapest,
14 Hungary

15 ^e Institute of Forest Ecology, Slovak Academy of Sciences, Ľ. Štúra 2, 96053 Zvolen, Slovakia

16 ^f Department of Forest Management and Geodesy, Faculty of Forestry, Technical University in Zvolen,
17 T.G. Masaryka 24, 96053 Zvolen, Slovakia

18
19 Correspondence: Joanna A. HOREMANS, Centre of Excellence on Plant and Vegetation Ecology,
20 Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk (Antwerp),
21 Belgium. Ph.: + 32 3265 2279; fax: + 32 3265 2271. E-mail: Joanna.Horemans@uantwerpen.be

23 **Abstract**

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

42 **Keywords** : empirical model, process-based model, climate scenario, forest management, *Fagus*
43 *sylvatica* L.

44 **1. Introduction**

45 As trees grow old, forests unavoidably face the impact of imminent climate change. Forest
46 management measures can contribute significantly to mitigation of and adaptation to these
47 environmental changes. Conventional statistical models implicitly based on the assumption of
48 stationary conditions may not be applicable for forest management decisions, but novel and
49 improved process-based models predict forest growth under changing conditions. Management
50 plans developed using either type of model require appropriate risk assessments (Walker et al.,
51 2003). Uncertainty analysis of forest model results is thus crucial to support management decisions.
52 The model uncertainties partly originate from input variables, including data required for the model
53 set-up and the calibration, as well as from climate and forest management predictions. Uncertainty is
54 also associated with the model boundaries (i.e., the extent of the ecosystem complex covered by the
55 model), with the model structure itself and with the model parameters (Jones, 2000; Reyer *et al.*,
56 2013). Only a part of this model uncertainty, however, is reflected in the variance of the model
57 results. Other sources of error may also contribute to model uncertainty, but may not be
58 quantifiable: either because they are unknown or because they are not included in the model.
59
60 Forest models incorporate aspects of system complexity as well as the non-linear relations and the
61 feedback mechanisms among the system drivers (Tian *et al.*, 2012). Over the last three decades
62 forest models have become more process-driven and they now incorporate a multitude of
63 parameters (Landsberg, 2003; Matala *et al.*, 2003). Process-based models (PBMs) integrate the
64 mechanistic functioning of the ecosystem by reproducing the ecological and physiological processes
65 that drive the system, as well as their responses to external factors (Landsberg, 2003; Kurbatova *et*
66 *al.*, 2008). PBMs are useful tools for understanding the dynamics of an ecosystem and they can
67 provide answers to questions on how ecosystems should be managed under changing environmental
68 conditions (Korzukhin *et al.*, 1996; Matala *et al.*, 2003; van Oijen *et al.*, 2005). However, having a
69 multitude of parameters does not necessarily guarantee that the model predictions will be reliable

70 (Larocque *et al.*, 2014). The complexity of PBMs can be a strength, but also a weakness, because they
71 rarely provide a unique answer to a practical management question (Mohren and Burkhart, 1994;
72 Sands *et al.*, 2000; Matala *et al.*, 2003; van Oijen *et al.*, 2005). Model improvements can result from a
73 better understanding of the internal processes of the system, e.g., carbon allocation processes,
74 nutrient availability in soils, nutrient uptake by trees, and competitive interactions (Seidl *et al.*,
75 2011b). A better knowledge of the external impacts and disturbances – often human-induced – as
76 well as their dependence on site location is also required (Landsberg, 2003; Kearney and Porter,
77 2009; Seidl *et al.*, 2011a). The feedbacks and compensating mechanisms between ecological drivers
78 also create challenges in model development (Ceulemans *et al.*, 1999; Matala *et al.*, 2005; Penuelas
79 *et al.*, 2008).

80

81 In contrast, empirically-based models (EBMs) are built on statistical relationships between forest
82 growth and environmental variables obtained from field measurements (Fabrika, 2007; Hlásny *et al.*,
83 2014; Pan *et al.*, 2014). The choice of the forest model best suited for a particular research or
84 management question is of crucial importance. Efforts have been made to combine the advantages
85 of PBMs (theoretical understanding, flexibility, predictive power under changing conditions) and
86 EBMs (robustness, limited input demand, ease of interpretation) by using multi-model inference
87 (Hlásny *et al.*, 2014) or by developing hybrid models (Makela *et al.*, 2000; Baldwin *et al.*, 2001; Peng
88 *et al.*, 2002; Girardin *et al.*, 2008; Taylor *et al.*, 2009).

89

90 When climate predictions provide an input for forest models, uncertainty is transferred from the
91 climate model to the forest growth simulation (Lindner *et al.*, 2014; Keenan, 2015). The uncertainties
92 in regional climate predictions are caused by three sources: (i) the climate model uncertainty, which
93 is resulting from the model structure and the parameterization and causes different responses to the
94 same radiative forcing, (ii) the scenario uncertainty, which arises from the uncertainty in future
95 environmental changes, as e.g. greenhouse gas emissions, and (iii) the internal variability, which is

96 the inherent temporal randomness of climate in the absence of any radiative forcing (Hawkins and
97 Sutton, 2009, 2010). The relative importance of these three sources of uncertainty changes with the
98 spatial and temporal scale. The internal variability becomes more important with decreasing spatial
99 scale and with an increased occurrence of extreme events (Lindner *et al.*, 2014). Model uncertainty
100 increases with longer prediction periods. Scenario uncertainty increases even more with lead time
101 (Hawkins and Sutton, 2009). Uncertainties from regional climate models (RCMs) can be quantified by
102 using an ensemble approach, combining the results of multiple models to give the statistical
103 probability of possible future climates (Lindner *et al.*, 2014). Beside the physiological aspects, the
104 state of a forest – i.e., its extent, species composition and canopy structure – and its biogeographical
105 location also affect its response to disturbance and vice versa (Allen *et al.*, 2010; Seidl *et al.*, 2011b;
106 Jactel *et al.*, 2012). The effects of forest state and forest history should be correctly understood and
107 taken into account in forest simulation studies, especially for European forests that are generally
108 intensively managed (Spiecker, 2003; Boisvenue and Running, 2006; De Vries *et al.*, 2006; Solberg *et*
109 *al.*, 2009). It is important to correctly estimate the costs and the benefits of different forest
110 management measures and to account for a wide range of forest situations and potential future
111 climate conditions.

112

113 In this contribution we (i) quantified the variance coming from different sources of uncertainty on
114 predictions of tree growth; (ii) tested the significance of these sources of uncertainty; and (iii)
115 assessed the contribution of different RCMs to the total uncertainty in the climate predictions. So,
116 this study only investigated the uncertainty of the model results and it did not consider the effects of
117 the different sources of variance on the actual predictions.

118 As a case study we have modelled the annual stem biomass increment (ASBI) of European beech
119 (*Fagus sylvatica* L.), a dominant tree species in European forests and the most common deciduous
120 species in central Europe (Dittmar *et al.*, 2003). Drought-induced growth reduction and/or a decline
121 of the species have been reported in southern Europe (Ciais *et al.*, 2005; Jump *et al.*, 2006; Piovesan

122 *et al.*, 2008; Bontemps *et al.*, 2010; Charru *et al.*, 2010; Kint *et al.*, 2012; Zang *et al.*, 2014), but for
123 central Europe an accelerated growth has been reported (Pretzsch *et al.*, 2014).

124

125 **2. Materials and Methods**

126 **2.1. Site description and sampling design**

127 The forest site was located in the Kremnické Vrchy Mountains of the Western Carpathians, Slovakia
128 (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
129 slope with a western aspect and an inclination of 13% to 20%. The soil substrate consisted of
130 andesite-tuff agglomerates and the soil type was Andic Cambisol with a high skeleton content (10% -
131 60%). During the measurement period (i.e., the calibration period) of 1989-2003 the annual average
132 temperature was 8.6 °C and the average annual precipitation was 677 mm.

133 At the start of the 1989-2003 calibration period, the forest was 100 years old. Before 1989, it was
134 managed according to usual forestry practice of less intensive thinning interventions from below
135 (mostly the removal of damaged and low-quality trees). In the 30 years preceding the calibration
136 period, the stand was thinned three times. In the period 1963–1972, 54 m³ ha⁻¹ were harvested from
137 the stand. In the following two periods (1973–1982 and 1983–1988) the harvested thinning was 54
138 and 40 m³ ha⁻¹, respectively. European beech (*Fagus sylvatica* L.) was the dominant species (65 -
139 90%) in the forest stand, but hornbeam (*Carpinus betulus* L.), oak (*Quercus robur* L.) and fir (*Abies*
140 *alba* Mill.) were also present. In February 1989 three plots of 0.35 ha each were established. These
141 plots were subjected to strip shelterwood cutting of different intensities. The remaining number of
142 trees per ha was respectively 160 for the heavily thinned plot (H), 243 for the medium thinned plot
143 (M) and 397 for the lightly thinned plot (L). A fourth plot of 0.15 ha was left uncut as a control (C)
144 with 700 trees per hectare. The thinning primarily focused on removing the interbreed species, dying
145 and damaged trees, and trees of very low stem quality. Branches were left on the site to decompose
146 naturally. More detailed information about the forest site and the forest management has been

147 reported previously (Jamnická *et al.*, 2007; Kellerova, 2009; Barna *et al.*, 2010; Janik *et al.*, 2011;
148 Barna and Bosela, 2015).

149
150 During the calibration period stem diameter at breast height (DBH) was measured annually using a
151 diameter tape with a precision of 1 mm. Individual trees and measurement positions were clearly
152 marked to minimize measurement errors. Tree height (h) was measured three times over the
153 calibration period (1998-2003) using a hypsometer (Silva, Clino Master, Sweden in 1989 and 1995;
154 Vertex, Haglöf, Sweden in 2003). For all other years h was interpolated from these measurements.
155 DBH and h were always measured for each individual tree. The volume (v) of stems and branches was
156 estimated using national volume regression equations based on DBH and h. These equations were
157 derived for 12 tree species from the large database assembled in the Czech and in the Slovak
158 Republics (Petráš and Pajtík, 1991). Stem biomass was obtained from the calculated stem volume
159 and the wood density of beech (Pajtik *et al.*, 2009).

160

161 **2.2. Climate data**

162 For the 1989-2003 calibration period, daily temperature, precipitation and wind speed data were
163 obtained from the meteorological station in the village of Sliach (5 km from the forest site). Nitrogen
164 wet deposition was measured at the site by 10 funnel-shaped collectors established on the forest
165 floor of each plot. NO₃ and NH₄ depositions were then obtained by spectrophotometry. For more
166 details about the sampling method see Janík *et al.* (2014) and Dubová and Bublinec (2006). Past CO₂
167 concentrations were obtained from the global values published by Tans and Keeling (2014) .

168 Incoming radiation for the site was estimated using NOAA's JavaScript solar position calculator re-
169 coded for Microsoft Excel (Pelletier, 2014).

170 In view of the limited spatial extent of the forest site under study, we followed the recommendation
171 of Lindner *et al.* (2014) and used a regional (RCM) rather than a general (GCM) circulation model for
172 making climate predictions. Different RCMs were run using the initial and boundary conditions

173 provided by GCMs (Giorgi, 2006) to generate higher resolution meteorological fields. Because of this
174 higher resolution, RCMs can resolve smaller scale features, such as topography and physical weather
175 processes (Wang *et al.*, 2004). Ten high-resolution daily RCMs were used, all disseminated within the
176 framework of the European ENSEMBLES project (Van der Linden and Mitchell, 2009) and based on
177 the same A1B scenario of IPCC (Moss *et al.*, 2008). The A1B greenhouse gas emission scenario
178 provides a balanced emphasis on all energy sources responsible for greenhouse gas emissions. At the
179 ENSEMBLES data portal 30 models were available driven by the A1B greenhouse gas scenario. A total
180 of 23 model output sets fulfilled the criterion of a sufficiently high spatial resolution (25 km x 25 km),
181 but only 14 output sets covered the entire 1951-2100 period. Two other output sets were removed
182 because they used the same RCM-GCM combination as another one, but with high- and low-
183 sensitivity RCM settings. From the remaining 12 models one was not available at the website and
184 another one contained too many data gaps at the end of the simulation period. A list of the 10
185 remaining model combinations (RCM-GCM) is provided by Dobor *et al.* (2015). Note that although
186 the Representative Concentration Pathways have already been adopted by the IPCC for its Fifth
187 Assessment Report (AR5) in 2014, only GCM results were accessible at this time. Time series of
188 maximum temperature (T_{\max}), minimum temperature (T_{\min}), precipitation and wind speed were
189 selected for the closest grid point to the meteorological station from a 25 km \times 25 km horizontal
190 resolution grid. Statistical bias correction was applied to site measurements for the period 1961-2009
191 using the cumulative distribution function fitting technique (also known as the quantile
192 mapping/fitting or histogram equalization), at monthly time intervals. For precipitation, both the
193 amount and the frequency were corrected. Future atmospheric CO₂ concentrations for the model
194 simulations were also adopted from the A1B scenario of IPCC. Future global radiation was
195 estimated with the MT-CLIM model (Mountain Microclimate Simulation Model (Hungerford *et al.*,
196 1989; Thornton and Running, 1999), which adequately estimated the daytime temperature and
197 global radiation. Details of the method and its limitations were described previously by Moss *et al.*
198 (2008) and Dobor *et al.* (2015).

199 Nitrogen deposition was kept equal to the average monthly value over the period 1989-2003 for
200 each plot (20-25 kg ha⁻¹ yr⁻¹) over the whole prediction period (2003-2100). The level chosen was

201 slightly lower than, but close to, the optimal nitrogen deposition for beech, 28 kg N ha⁻¹ yr⁻¹ (Kint *et*
202 *al.* (2012). No nitrogen deposition trends were observed, neither over years nor over seasons during
203 the calibration period. This was concluded from an automated time series forecasting software
204 provided by SAS statistical program (version 9.1, SAS Institute Inc., Cary, NC, USA). Predictions of
205 nitrogen emissions and depositions depend on decisions with regard to land use, to agriculture, to
206 energy policy, etc., as well as on the only partly known feedbacks between changes in the carbon and
207 nitrogen cycles (Lamarque *et al.*, 2011; van Vuuren *et al.*, 2011; Ciais *et al.*, 2013).

208

209 **2.3. Forest model types**

210 **2.3.1. Empirically-based model SIBYLA**

211 SIBYLA (acronym for Simulator of Forest Biodynamics) is an individual tree, distance-dependent and
212 climate-sensitive growth model (Fabrika and Dursky, 2005, 2006). SIBYLA uses the coordinates, DBH
213 and h of every single tree in a stand with the possibility of including different species with different
214 growth rates. In this study the growth, the inter-tree and inter-specific competition and the mortality
215 sub-models were used. The growth and competition sub-models were adopted from the SILVA
216 growth simulator (Pretzsch and Kahn, 1998; Pretzsch *et al.*, 2002) that worked as follows. Species-
217 specific responses of tree increment to climatic and soil variables were based on dose-response
218 functions (Fabrika and Pretzsch, 2013). This made the sub-model suitable for climate impact studies
219 (Fabrika, 2007; Hlásny *et al.*, 2011; Hlásny *et al.*, 2014). Growth increment was then modified by
220 competition pressure. Competitive interactions between trees and among species were described
221 using a competition index based on positions and dimensions of surrounding trees and the light cone
222 principle (Pretzsch, 1995; Bosela *et al.*, 2013). The mortality was simulated via a sub-model of tree
223 survival probability and using the threshold of stand density. The mortality sub-model has been
224 described previously (Ďurský *et al.*, 1996; Ďurský, 1997). To make the SIBYLA model representative of
225 central Europe, it was calibrated using a large-scale database of forest monitoring and inventory data
226 from Slovakia.

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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

253 calibrate ANAFORE using a Bayesian optimization method (van Oijen *et al.*, 2005) produced no
254 reduction in parameter uncertainty. ANAFORE was therefore calibrated by selecting, independently
255 for each plot, 11 parameter sets out of a minimum of 20,000 runs. This selection was made according
256 to the accuracy of the simulated time series with respect to the measured DBH data over the
257 calibration period.

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

260

261 **2.4. Simulation design**

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

- 264 i. FMTYPE (Forest model type): two forest model types were used, an EBM (SIBYLA)
265 and a PBM (ANAFORE).
- 266 ii. MANFOR (management of the forest): four forest study plots were subjected to
267 different thinning intensities in 1989: H, heavily cut; M, medium cut; L, lightly cut;
268 and a control, C, i.e. no thinning.
- 269 iii. CLIMMOD (climate model): 10 RCM results were bias-corrected and used for the
270 simulations up to 2100. All of the RCMs were run based on the A1B SRES scenario of
271 IPCC.
- 272 iv. TIMEWIND (time window): three 15-year time windows were used for the
273 simulations, i.e., 2019-2033, 2049-2063 and 2079-2093. The simulations for each
274 TIMEWIND always started at the same developmental stage of the forest plots.
275 TIMEWIND reflects the contribution of time (in a climate change context) to the total
276 variance and the changes in the relative contributions of the other sources of
277 variance over time. We preferred this splitting method as long term simulations

278 could lead to misinterpretations caused by the change in relative contributions of the
279 sources of uncertainty over time and by the changing interactions among them.

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

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

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

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

295 ii. INTVAR: internal variability of the climate variable.

296

297 **2.5. Statistical analysis**

298 Variance decomposition of the forest model results was realized by performing an analysis of
299 variance (ANOVA) with the average annual stem biomass increment (ASBI; in dry mass of an average
300 tree) over the 15 years of simulation as the response variable for each of the simulation designs. The
301 analysis was first made for the dataset including results of both FMTYPEs together (complete
302 dataset) and subsequently for ANAFORE and SIBYLA, individually. The studied sources of uncertainty

303 were FMTYPE, CLIMMOD, MANFOR, TIMEWIND and STARTSET. After the ANOVAs for the main
304 effects of FMTYPE (complete dataset), CLIMMOD, MANFOR and TIMEWIND only, their interacting
305 effects were also added as covariates. Two different approaches were thus used. In the first
306 approach these interactions were ignored and their effect was entirely included in the residual error
307 of the model. In the second approach significant two-way interactions were retained. STARTSET
308 (nested in MANFOR) was only added as a covariate in an additional ANOVA analysis and was in all
309 former analyses treated as a completely random source of variance, i.e. part of the residual error.

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

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

321 An additional variance decomposition was performed on the RCM climate variable predictions. As all
322 RCMs used the same scenario (A1B), only the model uncertainty and the internal variability were
323 estimated for climate predictions from 2000 until 2100. The averaged climate model results,
324 computed as the annual average of all RCMs were expressed as changes compared to the average of
325 the reference period 1971-2000 and were fit with a fourth-order polynomial using ordinary least
326 squares calculations. A reference period of 30 years was used in line with the definitions of climate
327 by the World Meteorological Organization. The RCM predictions were compared to the polynomial

328 (fitted for the averaged climate model results) and the variance of the differences was calculated per
329 decade; then these variances were averaged through the RCM models. The model uncertainty was
330 defined as the variance of the different models in a given decade. The residual error of the analysis
331 was attributed to the inherent randomness of climate (INTVAR). The fractions of the total variance
332 explained by RCM and INTVAR were calculated and reported as percentages of the total variance.

333

334 **3. Results**

335 **3.1. Quantification of uncertainty in biomass increment predictions**

336 The total variance of ASBI in the complete dataset, i.e., the dataset including both FMYPEs, was
337 382.4×10^3 (std. dev. 618). The main effect ANOVA and the two-way interaction ANOVA models
338 explained 74.9% and 86.2% of the total variance, respectively. These ANOVA models provided the
339 SSE values for the calculation of the fractions of the total variance explained by each of the sources
340 of uncertainty, i.e., FMYPE, CLIMMOD, MANFOR and TIMEWIND, their eventual interactions and the
341 residual error.

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

349 For the ANOVA model including only ASBI data from ANAFORE, 72.0% of the variance was explained
350 by the main effect model and slightly more (76.8%) by the two-way interaction model (Fig. 1). For
351 SIBYLA the explained variance was higher, ranging from 89.0% for the main effect model to 95.6% for
352 the two-way interaction model. The total variance of the responses of ANAFORE was 10 times larger

353 than the total variance of the responses in SIBYLA (209.7×10^3 against 20.18×10^3). TIMEWIND was a
354 more important source of variance for SIBYLA than for ANAFORE (36.3% against 23.3%). Nearly half
355 of the variance was explained by MANFOR for both models (48.7% for SIBYLA against 47.4% for
356 ANAFORE). The residual error, was smaller for SIBYLA (11.0%) than for ANAFORE (28.0%).

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

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

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

374 **3.2. Effect of simulation design**

375 For both FMTYPES the effect of the simulation design on ASBI, in particular the effect of the
376 interactions between FMTYPES and CLIMMOD, between FMTYPES and MANFOR, and between
377 FMTYPES and TIMEWIND are shown in Fig. 2. In relative terms, the effect of the simulation design on

378 ASBI was similar for both growth models, as evidenced by the significant correlations between both
379 FMTYPES with correlation coefficients of 0.978 ($p < 0.0001$), 0.969 ($p = 0.0313$) and 0.939 ($p = 0.2240$),
380 respectively, for the category averages of CLIMMOD, MANFOR and TIMEWIND. However, the
381 interaction effects between two of these sources of uncertainty – MANFOR and TIMEWIND – with
382 FMTYPE were significant sources of uncertainty in the ANOVA of the complete dataset (Fig. 1). This
383 means that in absolute values, the effect of the simulation design was not the same for both
384 FMTYPES.

385 **3.3. Quantification of uncertainties for regional climate predictions**

386 The decadal evolution of the predicted T_{max} , T_{min} and precipitation, expressed as change compared to
387 the average of the reference period 1971-2000, depended on the RCM used (Fig. 3). For T_{max} and T_{min}
388 the percentage of the variance explained by the internal variability was small during the entire
389 prediction period from 2000 to 2100. It decreased from 16.5% to 6.8% for T_{max} , and from 10.2% to
390 7.9% for T_{min} . The remaining variance was explained by the use of the 10 RCMs changing from 83.5%
391 to 93.2% for T_{max} , and from 89.8% to 92.1% for T_{min} . In absolute values, the total variance of the T_{max}
392 predictions increased from 0.35°C to 0.85°C, and the total variance of T_{min} increased from 0.40°C to
393 0.52°C.

394 For precipitation, the fraction of the total variance explained by the internal variability decreased
395 from 32.5% to 16.0% over the prediction period. The fraction of the total variance explained by the
396 use of different RCMs increased from 67.5% in the decade 2000-2010 to 84.0% in the decade 2090-
397 2100. The total variance of the predicted change in precipitation over the different RCMs was 275.85
398 mm in the decade 2090-2100, compared with 119.19 mm in the decade 2000-2010.

399

400 **4. Discussion**

401

402 A major part of the variance of ASBI was explained by FMTYPE. This is explained by the large absolute
403 differences in ASBI results between both FMTYPES and the large uncertainty in the ASBI results of the

404 process-based model ANAFORE. PBMs and EBMs significantly differ in the way that uncertainty is
405 generated and they do this at each place in the model environment where uncertainty is generated
406 (Walker *et al.*, 2003). First, the 'context uncertainty' of the model has to be considered. Although
407 PBMs and EBMs represent the forest system by the incorporation of external climatological variables,
408 state variables (defining the initial forest situation) and eventually the consideration of forest
409 management measures, the system boundaries of both model types are different. For example,
410 ANAFORE defined the soil system in great detail, while SIBYLA didn't. On the other hand, SIBYLA
411 defined the forest structure by describing each individual tree, and thus by including inter-tree and
412 inter-specific interactions.

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

423 Thirdly, uncertainty differences came with the input data (input uncertainty) and the way they were
424 used in the models. Several of the climate variables were introduced into both models with the same
425 uncertainty, generated by the climate predictions. Other climate variables differed between the
426 models or were not introduced in the same way, thus creating different uncertainties. The
427 differences in climate effects on model results were enhanced by the way in which they were used
428 afterwards (the model structure uncertainty). State variables were imported differently in both
429 models, leading to differences in their effect on the uncertainty. With poor information about the

430 state variables, there is a lot of unknown uncertainty, not reflected in the results. In the context of
431 comparing a PBM and an EBM the 'parameter uncertainty' is also a very important cause of
432 differences in model result uncertainty. In PBMs the parameter uncertainty is determined by the
433 multivariate distribution of the parameters (van Oijen *et al.*, 2013). For ANAFORE the parameter
434 uncertainty was reflected in the post-calibration parameter space and could be described
435 statistically. On the other hand EBMs are deterministic in nature. Parameter uncertainty is often
436 represented by the confidence intervals for the input regression functions, which is not the true
437 uncertainty representative of the population. It was thus impossible to quantify the real parameter
438 uncertainty of the SIBYLA model. The parameter uncertainty becomes more important as the site
439 conditions deviate more strongly from the calibration conditions. All the aforementioned
440 uncertainties together are reflected in the final 'model uncertainty'.

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

452

453 Notwithstanding the conclusion that input climate predictions are an important source of uncertainty
454 in ecological impact studies (Olesen *et al.*, 2007; Ruffault *et al.*, 2014), the use of different RCMs did
455 not introduce much variance in the forest model results. By deliberately limiting the climate

456 scenarios to local variants of scenario A1B, the uncertainty from climate scenarios was not fully
457 reflected in this study. Additional sources of unknown uncertainty, not captured in the variance
458 decomposition, could have changed the absolute and relative importance of the sources of
459 uncertainty. Although tree growth varies as a function of nitrogen deposition in a non-linear way
460 (Magnani *et al.*, 2007), we did not include any nitrogen deposition scenario in the study. Further, no
461 climate extremes were included in the predictions. The uncaptured and unknown uncertainties
462 depend on the forest model used and on the choices of sources of uncertainty to be included in the
463 variance decomposition.

464 The similar relative effect of the studied sources of uncertainty on ASBI results for the EBM and the
465 PBM is encouraging, however, caution is needed. To make growth predictions that apply outside the
466 range of the environmental conditions of calibration, the tree physiological processes must be
467 modelled realistically. In all aspects of modelling, there are inherent risks in extrapolating empirical
468 relationships outside the environmental conditions of the calibration data set. However, in the
469 context of this study ANAFORE was too complex, in other words, over-parametrized for the data
470 available. The significant interaction effects of STARTSET with both TIMEWIND and MANFOR in the
471 ANOVA model confirmed this. Furthermore, ANAFORE has been developed for newly planted young
472 forests; we observed an overestimation of the growth rate when simulating the adult forest plots of
473 the present study. The accuracy, the context and the structure of the model have to be aligned with
474 the management questions and the range of environmental conditions over which the model should
475 be applied (Battaglia and Sands, 1998). This emphasizes the need for intensive collaboration between
476 forest managers and modellers in defining the best model for answering specific questions. The
477 model requirements for input and calibration data as well as their spatial and temporal scales have to
478 be matched to the data available, with a focus on providing answers to the practical questions under
479 specific environmental and management conditions. Purely PBMs or EBMs, or hybrid models could
480 all be useful.

481 Future research on forest growth predictions should be designed to enable better risk evaluation by
482 decision makers and forest managers. This research would benefit from: (i) open-access databases
483 containing a large range of forest and environmental variables measured at different spatial and
484 temporal scales to enable correct model calibration and validation. The concept of ‘supersites’ is
485 useful for calibrating parameter-rich models; (ii) ongoing efforts at comparing model structures and
486 their sensitivity to (interacting) external driving variables; (iii) proper communication about the
487 sources of uncertainty, about the quantity of these uncertainties and about the place in the model
488 where these uncertainties are generated.

489

490 **5. Conclusions**

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

500

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742 Table 1: Synoptic description of the main characteristics of the empirically based SIBYLA and the
743 process-based ANAFORE models. * climate data input in daily or monthly time steps are downscaled
744 by the model to half hourly time steps. **depending on data availability the modeller can choose to
745 use either stand-level or tree-level input data. If only stand-level data are available, the model
746 generates tree-level data (coordinates, diameter at breast height and height distribution) to use in
747 the simulations.

Input	Spatial resolution	Temporal resolution	Contents, remarks
ANAFORE			
stand	stand	initial	site information (long., lat., slope), cohort information
species	tree/cohort	initial	number of species (up to 10)
tree	tree/cohort	initial	dimensions, carbon content in pools
branch	tree/cohort	initial	separate information about branches for each whorl
soil biota	stand	initial	information about mycorrhizae, saprotrophic fungi and soil microbes
soil physics	stand	initial	maximum volumetric water content and water potential, pH, thickness, texture
soil organics	stand	initial	thickness according to litter biomass and a constant organic matter density
element concentration and fraction	stand	initial	carbon and nitrogen contents divided in fractions of size and availability in each layer
management	stand	year	thinning timing and rules, rotation cycle
climate	stand	half hour, day or month *	incoming solar radiation, temperature, humidity deficit, wind speed, precipitation, CO ₂ , nitrogen deposition
wood grading	tree/cohort	initial	classes of wood quality (European standards)
log quality assessment species	tree/cohort	initial	four categories for which maximum norms can be given for 10 parameters (European standards)

SIBYLA

stand**	tree	annual	depends on data available (species, vertical layer, density, age, site index, etc.)
tree	tree	annual	diameter at breast height, height, crown dimension, crown depth
soil	stand	annual	soil moisture and nutrient content in simple categories
climate	stand	annual	temperature, temperature amplitude, length of growing season, precipitation
management	stand/tree	annual	different management options

Output	Spatial resolution	Temporal resolution	Contents, remarks
ANAFORE			
stand	stand	day	wood biomass, root biomass, height, maximum leaf area index, soil carbon
stand scale fluxes	stand	day	gross primary production, netto primary production, heterotrophic respiration, soil respiration, evaporation
tree output	tree cohort	day	number of trees, carbon allocation (day), carbon content per pool (year), height, basal area, dimensions
fluxes	tree cohort	half hour	water and carbon fluxes
Posphorus (P)	stand	day	organic P, minimum P, P uptake by mycorizhae, P uptake by tree, P transfer by mycorizhae, total tree P, Carbon:P in organic layer
soil	stand	day	carbon, nitrogen, P, water, carbon:nitrogen ratio
nitrogen uptake	tree/cohort	day	available nitrate, nitrate transfer by mycorizhae, available ammonia
harvest	tree cohort	year	standing and transported carbon, nitrogen all pools, harvested number of trees
monetary	stand	year	yield, particulate matter, water, carbon, nitrogen, prices
particulate matter	tree cohort	day/year	deposited, re-suspended, removed, on leaf particulate matter concentration, precipitation, evaporation, throughfall, water on leaf, wind speed above trees, canopy LAI
wood	tree/cohort	day	stem sapwood, stem heartwood, branches sapwood, branch heartwood

SYBILA

stand	stand	annual	mean height, mean diameter, wood biomass, root biomass, foliage biomass, chemical content, biodiversity of tree species, forest density and other wood production characteristics
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tree output	tree	annual	height, diameter, wood biomass, root biomass, foliage biomass, chemical content, timber type.
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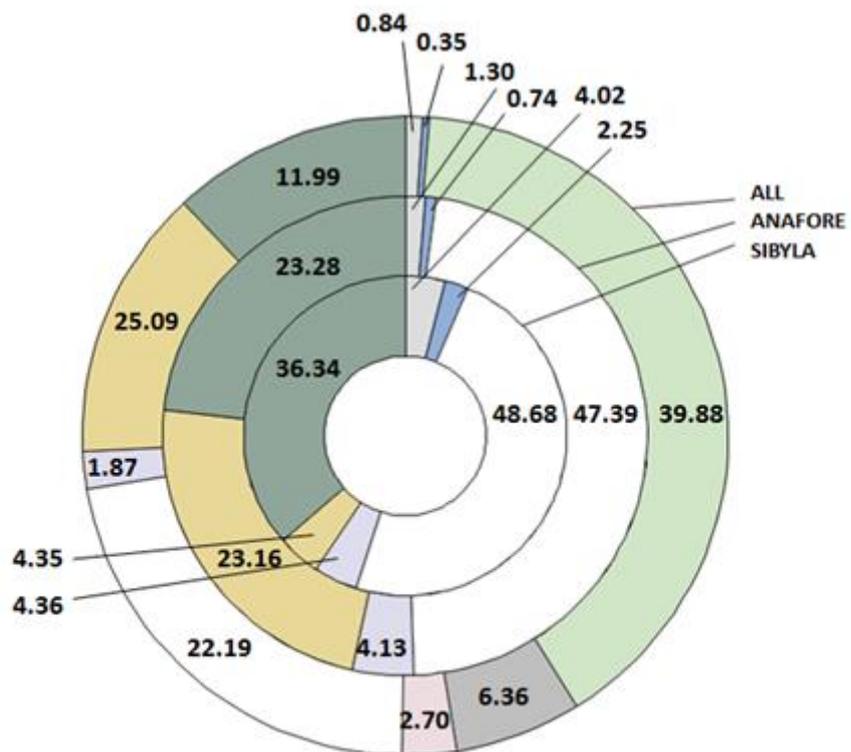
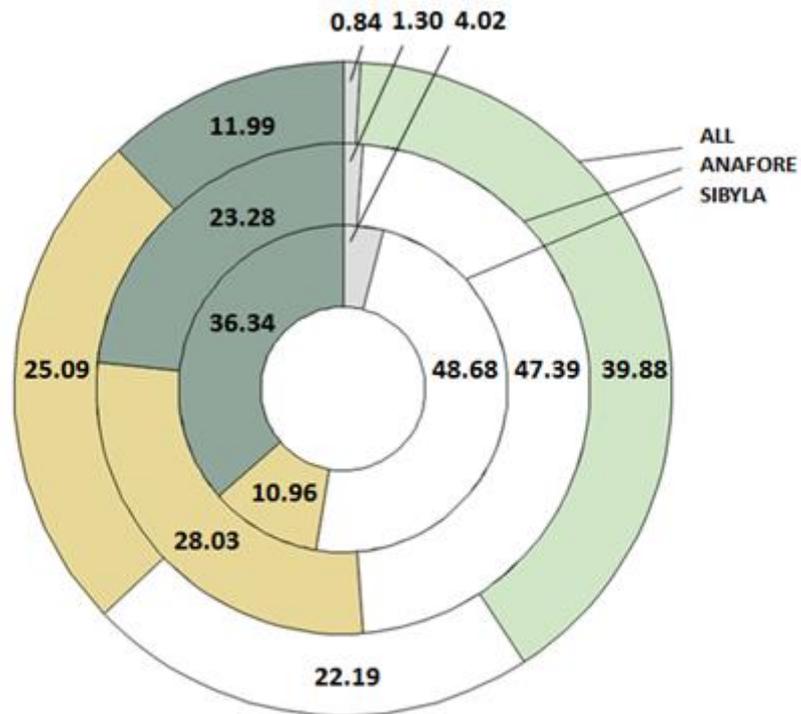
750 FIGURE LEGENDS

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

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

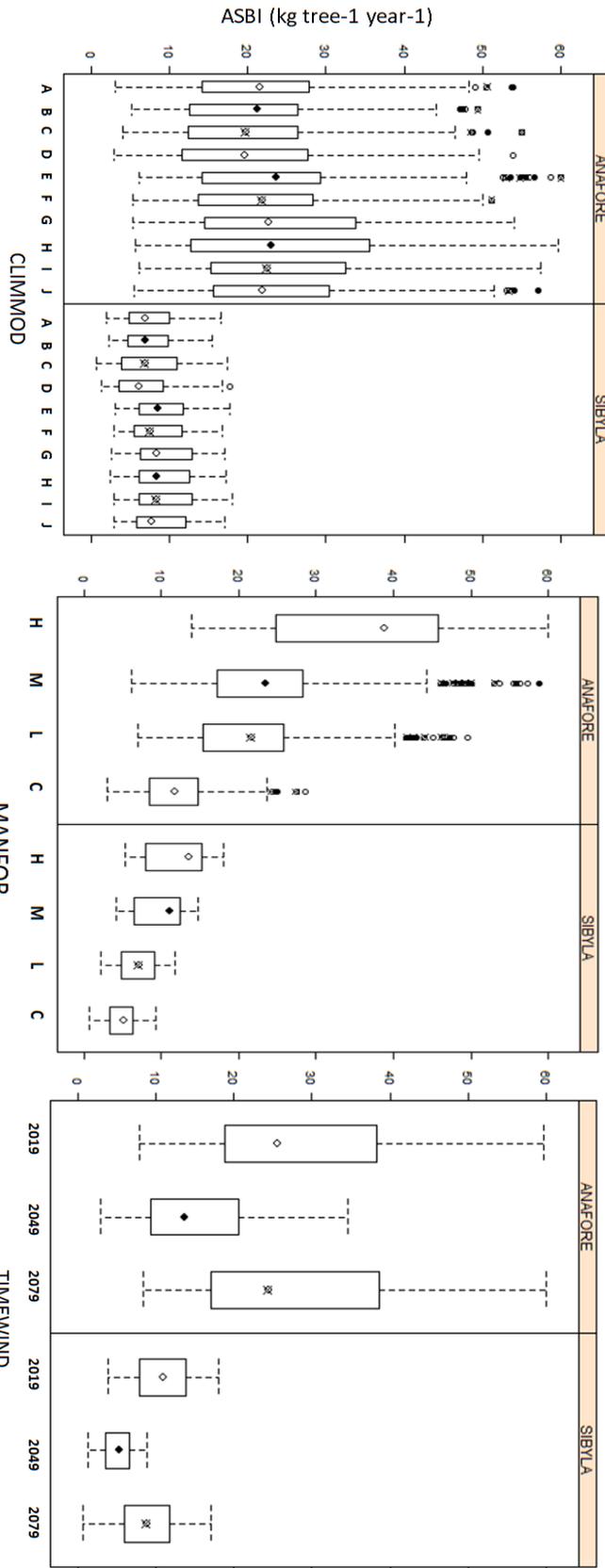
758 Figure 3: Regional climate model predictions for minimum temperature, maximum temperature and
759 precipitation, all expressed as changes according to the average of the reference period for climate
760 predictions 1971-2000. The model uncertainty and the internal uncertainty are shown as insets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

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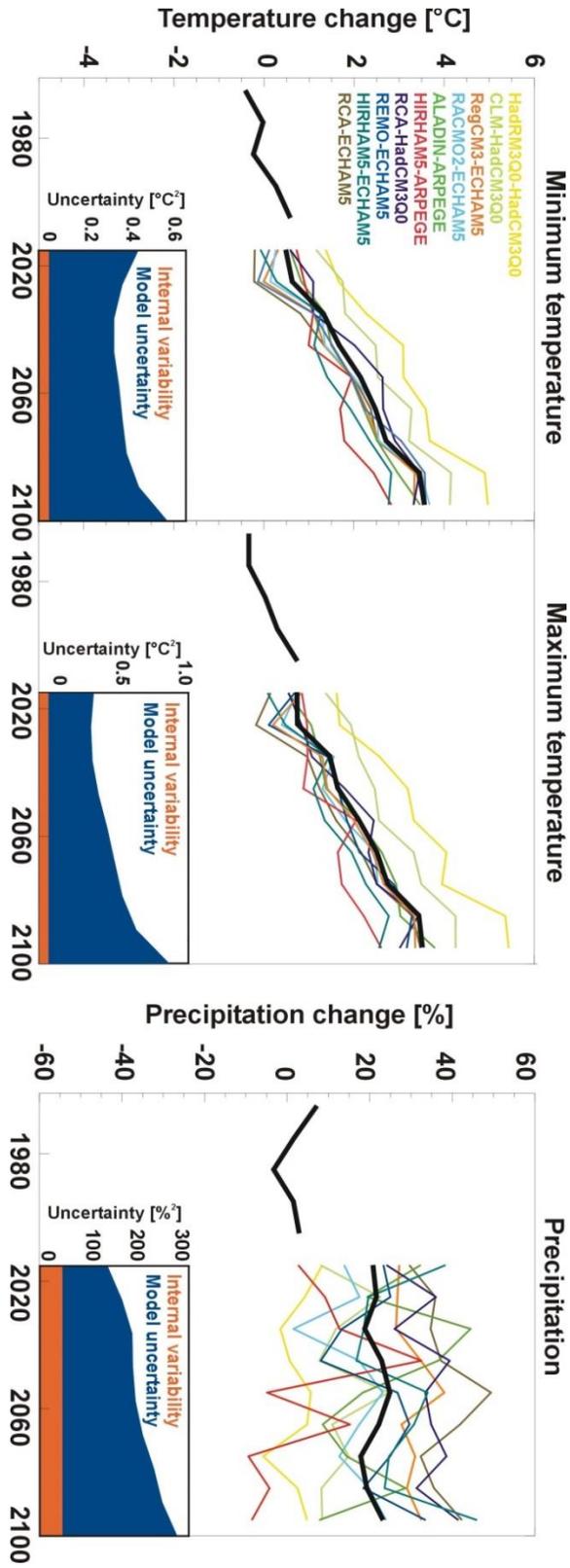


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