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1 **Decomposing sources of uncertainty in climate change projections of boreal forest**
2 **primary production**

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19 **Highlights**

- 20 • We predict GPP and water balance of Finnish forests by simple ecosystem model PRELES
- 21 • We show how different sources of uncertainty propagates to ecological impacts.
- 22 • Global Circulation Model (GCM) variability was the major source of uncertainty until 2060.
- 23 • We need to improve our mechanistic understanding of long-term CO₂ fertilization effect on
- 24 GPP.
- 25 • A thorough assessment of uncertainties in the projections of the impacts is important for
- 26 drawing robust conclusions.

27

28 **Abstract**

29 We are bound to large uncertainties when considering impacts of climate change on forest productivity.
30 Studies formally acknowledging and determining the relative importance of different sources of this
31 uncertainty are still scarce, although the choice of the climate scenario, and e.g. the assumption of the
32 CO₂ effects on tree water use can easily result in contradicting conclusions of future forest productivity.
33 In a large scale, forest productivity is primarily driven by two large fluxes, gross primary production
34 (GPP), which is the source for all carbon in forest ecosystems, and heterotrophic respiration. Here we
35 show how uncertainty of GPP projections of Finnish boreal forests divides between input, mechanistic
36 and parametric uncertainty. We used the simple semi-empirical stand GPP and water balance model
37 PRELES with an ensemble of downscaled global circulation model (GCM) projections for the 21st
38 century under different emissions and forcing scenarios (both RCP and SRES). We also evaluated the
39 sensitivity of assumptions of the relationships between atmospheric CO₂ concentration (C_a),
40 photosynthesis and water use of trees. Even mean changes in climate projections of different
41 meteorological variables for Finland were so high that it is likely that the primary productivity of forests
42 will increase by the end of the century. The scale of productivity change largely depends on the long-
43 term C_a fertilization effect on GPP and transpiration. However, GCM variability was the major source
44 of uncertainty until 2060, after which emission scenario/pathway became the dominant factor. Large
45 uncertainties with a wide range of projections can make it more difficult to draw ecologically
46 meaningful conclusions especially on the local to regional scales, yet a thorough assessment of
47 uncertainties is important for drawing robust conclusions.

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49 **KEY WORDS:** Photosynthetic efficiency, Ecosystem response, Environmental change, Ecophysiology

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57 1. INTRODUCTION

58

59 Understanding the development of forest productivity in a changing environment is pivotal for making
60 decisions about forest use in the future. Such understanding is also needed for improving the climate
61 projections themselves, as a large proportion of uncertainty of global warming projections arises from
62 uncertainties in modelling terrestrial phenomena and their biophysical interactions with climate (Bonan
63 2008). Boreal forests play a large role in determining the global mean temperature (Snyder et al. 2004,
64 Snyder and Liess 2014), and are generally assumed to provide climate mitigation potential due to
65 projected increased growth and carbon sequestration under climate change (IPCC 2013), although the
66 biophysical effects like albedo or biogenic volatile organic compounds (BVOCs) may change the net
67 impact (Bright 2014, Unger 2014). Opposing trends may also emerge as a result of increased utilization
68 of forests for the production of bioenergy and new bio-based products (Ollikainen 2014). For example
69 in Finland, recent impact studies suggest an increase of 5-27% in productivity of Norway spruce until
70 end of this century (Ge et al. 2013 using SRES A2 scenarios, Reyer et al. 2014 using SRES A1B).
71 However, all impact studies include a lot of uncertainty related to model structure, parameter values,
72 and climate input data, which has not been systematically analysed in boreal forest studies. The lack of
73 including these in the assessment of uncertainty may lead to suboptimal decision-making from the
74 climate change mitigation perspective.

75 In a large scale comparison, forest productivity is primarily driven by two large fluxes, gross primary
76 production (GPP), which is the source carbon for all carbon in forest ecosystems (Ma et al. 2015), and
77 heterotrophic respiration. Correlations can therefore be found along environmental gradients between
78 GPP and Net Primary Production (NPP; Waring et al. 1998, Mäkelä and Valentine 2001, Dewar et al.
79 1998), litter fall (Reich et al. 2014, Mäkelä et al. 2016) and carbon accumulation in the soil (Liski et al.
80 2006). Recent decades have witnessed a profound development of models of canopy GPP, thanks to
81 improved measurements and data from eddy flux networks where carbon and water fluxes are measured
82 globally over different land cover types (e.g.FLUXNET, <https://fluxnet.fluxdata.org>). This has

83 considerably improved the reliability of GPP predictions under current climate as a function of weather
84 and canopy type (e.g. Novick et al. 2015, Wagle et al. 2016), sometimes also with generic models that
85 do not require site-specific parameterisation (Minunno et al. 2016). Model-data assimilation techniques
86 such as Bayesian model calibration also provide an improved understanding of the uncertainties of
87 model parameters and how they propagate to model predictions (van Oijen et al. 2013, Minunno et al.
88 2016). The significance of GPP for ecosystem functioning, combined with a sound understanding of
89 the process under the current climate, makes GPP simulations an appropriate example case for exploring
90 the types of uncertainty we are bound to face in future impact projections in a changing climate.

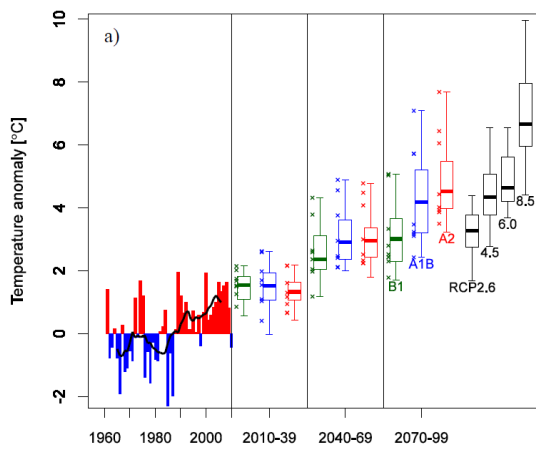
91 Uncertainties in model predictions generally originate in input uncertainty and model uncertainty (cf.
92 Uusitalo et al. 2015). In climate change projections, input uncertainty includes uncertainties about
93 climate scenario and climate development under a given scenario, demonstrated in the differences
94 between climate models. In addition, there is uncertainty caused by natural variability of weather.
95 Model uncertainty consists of parametric and structural uncertainty.

96 An important structural uncertainty for GPP prediction arises from the fact that the interactions of
97 elevated atmospheric CO₂ concentrations (C_a) with changing climate are still poorly understood due to
98 the limited possibilities of theory and model testing in experimental and natural conditions. In modelling
99 studies, even more than half of the projected forest productivity has been attributed to increasing C_a
100 (Bergh et al. 2005, Reyer et al. 2014) while without C_a fertilization, simulated forest productivity has
101 even been predicted to decrease under climate change (Ollinger et al. 2007, Medlyn et al. 2011). While
102 it is generally accepted that elevated C_a increases the water use efficiency of plants (WUE), the extent
103 and mechanisms of this effect are not clear. Analyses of eddy-covariance measurements of the past 15
104 years have suggested even larger improvements of WUE than predicted by prevailing theories (Keenan
105 et al. 2013). While studies where C_a concentration has been increased in the field (Free-Air Carbon
106 dioxide Enrichment, FACE) have shown that trees increase their photosynthetic rates and still reduce
107 stomatal conductance (Ainsworth and Rogers 2007), the long-term ecosystem level responses depend
108 on ecosystem type. Direct responses of trees to elevated C_a may become diluted in time, as physiological
109 processes and tree structure acclimate to new conditions (Norby and Zak 2011). For example, some

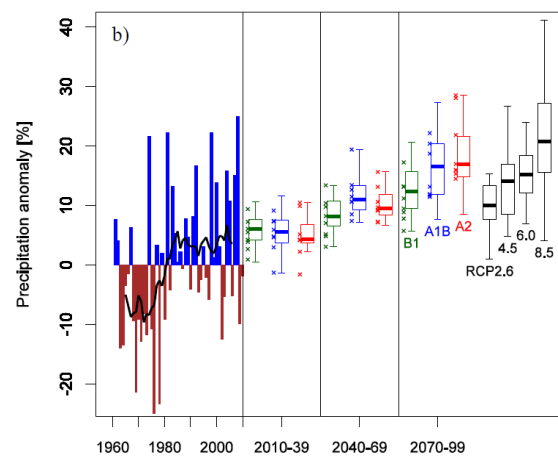
110 studies have predicted spruce decline in southern Finland (Kellomäki et al. 2008, Ge et al. 2013), but
 111 the result strongly depends on the assumptions of C_a effects on transpiration.

112 The impact uncertainty arising from uncertainties in global circulation model (GCM) outputs has
 113 largely been ignored in (forest productivity in the boreal zone, although it has been investigated in the
 114 context of e.g. disturbances (Lehtonen et al. 2016). It is well known that projections of climate models
 115 can differ more between each other than projections of one specific climate model between emission
 116 scenarios (e.g. van Vuuren et al. 2011, Ahlström et al. 2012, Nishina et al. 2015). In the case of Finland,
 117 only few GCMs project mean annual temperature changes below 2 °C between the periods 1971-2000
 118 and 2070-2099, even when assuming a low emission scenario (SRESB1) or a low emission
 119 Representative Concentration Pathway (RCP2.6) (Fig.1). The respective changes in the high-end
 120 scenarios reach up to 10 °C (under RCP8.5 forcing, see Jylhä et al. 2009, Rötter et al. 2013, Ruosteenoja
 121 et al. 2016). The change in winter temperatures in January may be twice as large as the change in
 122 summer temperatures in July. Uncertainties in precipitation changes are much larger, but increases are
 123 expected especially in winter (Rötter et al. 2013, Jylhä et al. 2009). The frequent approach of using the
 124 ensemble mean of climate model variables as input to ecosystem models (e.g. Peltola et al. 2010,
 125 Veijalainen et al. 2010, Sievänen et al. 2014) is questionable since it may violate the coherence between
 126 different climate variables.

127



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131 Figure 1. Observed anomalies in average annual (a) air temperature and (b) precipitation and
132 projected changes for 30-year mean periods during the 21st century for Finland for SRES scenarios
133 B1, A1B and A2 simulated with 8 GCMs selected for this study (stars) and for the full ensemble of 24
134 Coupled Model Intercomparison Project phase 3, CMIP3, models (boxplots), modified from Rötter et
135 al. (2013). GCMs are listed in Table SA.1 in the supplementary material. Similar projected changes
136 for RCP scenarios projected by CMIP5 GCMs are shown for last 30-year period.

137

138 The objective of this study was to predict gross primary production (P) and plant-water relations of
139 boreal forests in Finland using climate scenarios for the 21st century from ensembles of GCMs with
140 different forcings (both RCP and SRES). By showing both scenario families we acknowledge the fact
141 that SRES scenarios are still used in impact studies, and even more so in policy analyses. Comparing
142 the two sets of scenarios will help us put the SRES scenario results in perspective with those obtained
143 from the RCP scenarios. We calculated P using a simple ecosystem flux model, PRELES, (Peltoniemi
144 et al. 2015) with a generic boreal parameterisation (Minunno et al. 2016). We then quantified and
145 compared the different sources of uncertainty, including the parametric uncertainty obtained from data-
146 model assimilation, the structural uncertainty of C_a fertilization and water use effects, and input
147 uncertainties originating in stochastic variability of weather and uncertainty created by the choice of
148 climate model and forcing scenario. Using our study on GPP as an example, we discuss the implications
149 more broadly in the framework of ecological impact model applications that are subject to large
150 uncertainties.

151

152 2. MATERIALS & METHODS

153 2.1 The PRELES model

154 The PRELES model (Peltoniemi et al. 2015) describes P and water exchange (evapotranspiration, E)
155 of forest canopies on the basis of light use efficiency (LUE), expressed as a multiplicative model of
156 potential LUE and environmental modifiers f_i ($0 < f_i < 1$). It inherits its photosynthesis part from
157 Mäkelä et al. (2008) while a simple description of daily soil water balance was made in Peltoniemi et
158 al. (2015). The model has been calibrated to eddy-covariance derived data on P , E , and measurements

159 of soil water in Scots pine stands (Peltoniemi et al. 2015), and a generic, species-independent
 160 parameterisation for boreal stands has been prepared (Minunno et al. 2016). While the existing model
 161 parameterisation has been carried out in current climate under constant C_a , here we extend the model to
 162 be applicable to future environment by incorporating an additional C_a modifier. Here we first outline
 163 the structure of the model, then introduce our treatment of the sources of mechanistic and input
 164 uncertainty. The details of PRELES are presented in Peltoniemi et al. (2015).

165

166 The photosynthetic production P ($\text{gC m}^{-2} \text{ day}^{-1}$) is predicted in PRELES as:

$$167 \quad P = f_{\text{aPPFD}} P_0 \equiv \beta f_{\text{aPPFD}} \sum_d \Phi_d \prod_i f_{id} \quad (1)$$

168 where f_{aPPFD} is the fraction of photosynthetic photon flux absorbed by the canopy, P_0 is the potential
 169 photosynthetic production when all radiation is absorbed ($f_{\text{aPPFD}} = 1$), β is the potential light use
 170 efficiency (gC mol^{-1} , Table 1), Φ_d is photosynthetic photon flux density of day d (PPFD, $\text{mol m}^{-2} \text{ day}^{-1}$),
 171 and f_{id} are values on day d of environmental modifiers related to variable i ($i =$
 172 L, S, D, W representing light, temperature, vapour pressure deficit and soil water, respectively). The
 173 product of Φ and the light modifier f_L takes the form of rectangular hyperbola, which describes the
 174 saturating light effect on stand P , the temperature modifier f_S calculates the seasonal temperature
 175 potential for P . It is calculated using daily mean temperatures and over the course of the year the
 176 response typically takes a form resembling a cut sine wave where the peak values during summer are
 177 flattened to 1, while during the off-season (currently November-March in southern-most Finland) there
 178 is marginal or no potential to photosynthesize and its values are zero or close to zero. Impacts of the
 179 water vapor pressure deficit of atmosphere, D (VPD), and soil moisture, are implemented as $f_{D,W} =$
 180 $\min(f_D, f_{W,P})$. Here, f_D describes a modest exponential decrease of P with increasing D , and $f_{W,P}$ describes
 181 the decrease of photosynthesis with decreasing soil moisture content (Table 2 and Table 1 in appendix).

182 In order to calculate $f_{W,P}$, soil water balance and relative extractable water (W) are predicted using a
 183 simple bucket model where the water balance is controlled by precipitation, evapotranspiration,
 184 snowmelt, throughfall, and drainage. The modifier $f_{W,P}$ is then defined as $f_{W,P} = \min(1, W/\rho_P)$, i.e.,
 185 low W below fitted parameter ρ_P thus potentially decreases $f_{D,W}$. The simple soil water model does not

186 describe lateral water flows, except that, above field capacity (θ_{FC}), a fraction of water is lost as runoff
187 every day and becomes inaccessible to roots.

188 Evapotranspiration (E) is predicted using an empirical model, which is sensitive to P prediction, D , Φ ,
189 temperature, and f_{aPPFD} .

$$190 \quad E = \alpha P f_{W,P}^{\nu} D^{1-\lambda} + \chi(1 - f_{aPPFD}) \phi f_{W,E} \quad (2)$$

191 where parameters α , ν , λ and χ are fitted parameters, which partially determine the fraction of the two
192 water fluxes (the two components of the sum, eq. 2) that correspond to transpiration and evaporation.

193 The modifier $f_{W,P}$ of the P equation is raised to the power ν because P and E fluxes are not similarly
194 influenced by drought. Modifier $f_{W,E}$ reduces evaporation under dry soil; formulation of $f_{W,E}$ modifier
195 follows $f_{W,P}$ but has its own (fitted) threshold ρ_E , i.e. $f_{W,E} = \min(1, W/\rho_E)$. The model also includes a
196 storage for surficial water (θ_{surf}) and snow (θ_{snow}), which are accounted for in the stand water balance.
197 If $\theta_{surf} > 0$ or $\theta_{snow} > 0$ then $f_{W,E} = 1$.

198 For incorporating the CO_2 response in the model, the C_a effects on stand P were estimated using
199 summary functions emulating the SPP stand photosynthesis model with Farquhar equations (Farquhar
200 et al. 1980, Leuning 1995) for leaf photosynthesis (Mäkelä et al. 2006, Kolari et al. 2009). The SPP
201 model simulations were done with using the SMEAR II stand as representative of typical middle-aged
202 managed Scots pine stand (see Ilvesniemi et al. 2009 for detailed description of the site and stand
203 structure).

204

205 The C_a influences both P and E through their own modifiers. The effects of soil moisture are partially
206 influenced by C_a .

207

208 P is influenced by CO_2 of air in two ways. Firstly, if ambient CO_2 increases above its reference level
209 $C_{a,ref}$, the photosynthetic efficiency will increase in a nonlinear manner which is described with the
210 following modifier function:

211
$$f_{CO_2, P_0} = 1 + \frac{C_a - C_{a,ref}}{C_a - C_{a,ref} + C_{Sat}} \quad (3)$$

212 At the same time, however, the VPD response is also altered by decreasing the slope of the VPD
 213 response in increasing C_a due to partial closure of stomata, described as follows:

214
$$f_{CO_2-D} = e^{\kappa_f \left(\frac{C_{a,ref}}{C_a} \right)^{0.4}} \cdot D \quad (4)$$

215 Finally, the above responses are combined in the following CO_2 modifier of photosynthesis:

216
$$f_{P, CO_2} = f_{CO_2, P_0} f_{CO_2-D} / f_D \quad (5)$$

217 which describes the overall effect of C_a on photosynthesis.

218 The evapotranspiration, E , is also influenced by CO_2 . Implementation of E changes under changed CO_2
 219 concentration was made with a multiplier modifying the transpiration, i.e the first part of the model
 220 function for E (see Eqn 2 above):

221
$$f_{Tr, CO_2} = 1 - \frac{C_a - C_{a,ref}}{C_a - C_{a,ref} + C_{Sat}} \quad (6)$$

222

223 For more details, consult Mäkelä et al. (2008), Peltoniemi et al. (2015) and Minunno et al. (2016).

224

225 **2.2 Standard set of model parameters**

226 A standard set of parameters at reference C_a was obtained from the previous Scots pine stand
 227 parameterisation (Peltoniemi et al. 2015). The parameterisation under changing C_a was based on this
 228 reference case and the simulations of relative changes in the more detailed SPP model, as explained
 229 above (Table 1).

230

Tree species	Effective soil water holding capacity [§]	κ^*	β^\ddagger	
<i>Pine</i>	167	0.13	0.75	Parameter set from Hyytiälä eddy-site that compared well with Sodankylä eddy-covariance site parameterization.
<i>Spruce</i>	210	0.4	0.75	
<i>Birch</i>	260	0.4	0.94	

231 § The column height (mm) of extractable soil water roots of the trees have access to.

232 * Parameter of VPD sensitivity f-modifier, $f_D=e^{-\kappa D}$

233 ‡ Deciduous species have clearly higher foliar [N] than conifers, which promotes higher β (Peltoniemi et al.,
234 2012). Deciduous species LUE were predicted assuming a linear relationship between LUE and (Peltoniemi et
235 al. 2012) mean needle N concentration ($1.27 \text{ mgN (gDM)}^{-1}$ for pine and $2.40 \text{ mg (gDM)}^{-1}$ for birch, updated
236 dataset of Merilä and Derome 2008). Mean pine needle N concentration in this dataset was assumed to generate
237 the LUE estimated for Hyytiälä.

238

239 Table 1 Definition of tree species using model parameters. All other parameters were kept as defaults
240 (Peltoniemi et al. 2015).

241

242 We further modified these pine (*Pinus sylvestris* L.) parameters on the basis of the literature (Mäkelä et
243 al. 2008, Linkosalo et al. 2008, Minunno et al. 2016) to represent Norway spruce (*Picea abies* [L.]
244 Karst.) and silver birch (*Betula pendula* Roth.) in the analysis (Table 1). In Minunno et al. (2016), the
245 authors found no significant differences in the parameter estimates between Scots pine and Norway
246 spruce dominated stands. Because spruce and birch generally occupy moister sites than pine, we
247 increased the soil water holding capacity for them. The aim was to provide a realistic description of the
248 typical growth sites of the different species. In addition, the parameter modifications assumed that
249 spruce and birch had higher sensitivity to D than pine. Birch also has a higher light-use efficiency than
250 pine and spruce (Peltoniemi et al. 2012). A description of the phenology of leaf budburst for birch was
251 adopted from Linkosalo et al. (2008). This phenology model is an on-off variable which determines the
252 date on which the temperature modifier f_S is activated. The phenology model does not account for

253 autumn phenology, i.e. there is no description of leaf-senescence and its potential effect on
 254 photosynthesis.

255 The fraction of absorbed photosynthetic photon flux density, f_{aPPFD} , essentially depends on forest
 256 structure. To screen the impact of structure on P we used three values (0.5, 0.75, and 1, Fig. SB.1 –
 257 SB.3), representing sparse, typical and theoretical stands that harvest different proportions of PPFD.
 258 The f_{aPPFD} also has a minor impact on the total amount of evapotranspiration and on the ratio of
 259 transpiration to evaporation.

260 **2.3 Estimating PRELES parametric uncertainty**

261 For estimating the parametric uncertainty of the impact model, we used a posterior distribution of
 262 parameters obtained with Bayesian inversion, and by applying the above adaptive Markov Chain Monte
 263 Carlo (MCMC) algorithm in the model calibration study (Peltoniemi et al. 2015). We used the
 264 differential evolution Markov chain (DEMC, ter Braak (2006)) algorithm to sample from the posterior
 265 distribution. The algorithm combines a global optimization algorithm, the differential evolution method
 266 of Storn and Price (1997), with an MCMC simulation step. A few Markov chains are run in parallel
 267 learning from each other. We used the DEMC version (ter Braak & Vrugt 2008) that uses a reduced
 268 number of chains (3) and a snooker updater implemented in the R package BayesianTools (Hartig et
 269 al., 2017). Here we varied 13 parameters of the posteriori (Table 2).

Parameter	Symbol	Unit	Used range
Potential light use efficiency	β_P	$\text{g C mol}^{-1} \text{ m}^{-2}$	0.685...0.810
Delay parameter for the response of temperature acclimation state to the changes in ambient temperature	τ	-	11.43...15.74
Threshold above which the state of acclimation increases	X_0	$^{\circ}\text{C}$	-4.56...-2.97
Threshold at which the acclimation modifier reaches its maximum	S_{\max}	$^{\circ}\text{C}^{-1} \text{ d}^{-1}$	17.75...20.08
Sensitivity parameter of f_D to D	κ	kPa^{-1}	-0.196...-0.070
Light modifier parameter for saturation with irradiance	γ	$\text{mol}^{-1} \text{ m}^{-2}$	0.029...0.041
Threshold for W effect on P in modifier $f_{W,P}$	ρ_P	-	0.397...0.902
Transpiration parameter	α	$\text{mm (g C m}^{-2} \text{ kPa}^{-1} - \lambda)^{-1}$	0.308...0.358

Parameter adjusting transpiration with D	λ	$\text{mol}^{-1} \text{m}^{-2}$	0.100...0.919
Evaporation parameter	χ	mm mol^{-1}	0.023...0.059
Threshold for W effect on evaporation in modifier $f_{W,E}$	ρ_E	-	0.0002...0.9983
Parameter adjusting transpiration with W	ν	-	0.013...0.685
Surfacial water storage maximum	$\theta_{\text{surf,max}}$		0.422...5.000

270

271 Table 2. Parameters sampled from the posteriori of Peltoniemi et al. (2015) and their ranges used in the
 272 simulations.

273

274 We deemed 60 posteriori samples sufficient for characterizing the uncertainty of model parameters,
 275 their co-variation, consequent predictions of the model, as well as the distribution characterizing the
 276 distribution of residuals. The subset of the parameter vectors used in the simulations was sampled with
 277 even sized step from the posteriori distribution in such a manner that the whole parameter space formed
 278 by the posteriori was sampled. Figure SB.5 shows how the obtained subset covers the total variation of
 279 posteriori distribution of each parameter. The uncertainty of the mean response of the model (i.e. daily
 280 P) was generated using model parameters in the posterior sample. The uncertainty attributed to model
 281 parameters only partially captures the uncertainty of daily P . Around the mean response, there is
 282 variation of residuals, which stems from the uncertainties of observations used in the model calibration
 283 and inability of the model structure to describe the true variation. Therefore, for each day of the year in
 284 each simulated run, we drew a sample from the normal distribution with standard deviation s , centered
 285 on the simulated P for that day. Values of s were specific to the model parameters used; they were
 286 obtained from the same posterior sample as model parameters.

287

288 **2.4 Structural uncertainty**

289 The largest structural uncertainty of the model is related to the increased WUE due to C_a fertilization
 290 effect. The C_a effect was added to the model on the basis of a more detailed model (cf. Kolari et al.

291 2009), while the other environmental effects have been calibrated against data (Minunno et al. 2016).
292 To quantify this uncertainty, we explored four alternative assumptions. Firstly, we assumed a full
293 impact of the model described above, implying direct effects on photosynthesis and evapotranspiration
294 and indirect effects on soil moisture through effects on evapotranspiration. Secondly, we assumed no
295 effect on soil moisture, because it is possible that any reduction in transpiration due to C_a effects could
296 be counteracted by increased evaporation (Allen et al. 2010). Thirdly, some studies have indicated a
297 strong downregulation of photosynthesis even if C_a increases (Ellsworth et al. 2004); we therefore
298 considered the possibility that C_a influences neither P nor evapotranspiration. Finally, we considered
299 the hypothetical case that there was no effect of C_a on P and that soil moisture did not affect the
300 processes at all. In this case, all effects are primarily caused by temperature increase.

301 These assumptions gave rise to the following model settings:

302

303 1. *All factors*

304 The full model, including the effects of daily mean temperature (T , °C), vapor pressure deficit
305 (D , kPa), photosynthetic photon flux density above the canopy (ϕ , mol m⁻²), C_a (ppm) and
306 effective rooting zone soil water (θ , mm).

307 2. *All factors less soil water: the case - soil water*

308 The effects of soil moisture constraint on P were removed, i.e. we set the soil water modifier in
309 the model, $f_{W,P}$, to unity.

310 3. *All factors less C_a : the case - C_a*

311 Here $C_a = C_{a, \text{ref}}$, which forces the f_{P,CO_2} and f_{E,CO_2} modifiers to 1.

312 4. *All factors less soil water and C_a : the case - CO_2 - soil water*

313 Here $C_a = C_{a, \text{ref}}$, and constraints of soil moisture on P through soil water deficit were removed.

314

315 **2.5 Input uncertainties: baseline and future climate data**

316 Baseline daily weather data on a regular 10 km x 10 km grid covering Finland for the period 1971-2000
317 were obtained from the Finnish Meteorological Institute for mean temperature, precipitation, global

318 radiation and vapour pressure (Venäläinen et al. 2005). The estimation of PPFD and VPD from these
319 data is described in Suppl. A. Climate scenarios for the 21st century were prepared by downscaling
320 GCM simulations of the SRES emission scenarios (IPCC 2007) and the more recent Representative
321 Concentration Pathways (RCPs, IPCC 2013) that took part in the Coupled Model Intercomparison
322 Project (CMIP) phases 3 (for SRES, Meehl et al. 2007) and 5 (for RCP, Moss et al. 2010). Subsets of
323 the full CMIP3 and CMIP5 ensembles were selected for which the required set of variables was
324 available and which we regarded as representative for spanning the range of projected changes in the
325 full ensembles. The criteria for representative ensembles were that they covered a sufficient range of
326 uncertainty from a larger ensemble, and that the biases between the historical simulation and observed
327 climate were not judged to be too large (Ruosteenoja 2011). For the SRES-based scenarios, eight GCM
328 simulations of the B1, A1B and A2 emission scenarios were selected (cf. Figure 1 and Rötter et al.
329 2013). For RCP-based scenarios, 5 GCMs were selected, all covering the low RCP2.6, moderate
330 RCP4.5 and high RCP8.5 forcing scenarios (Suppl. A Fig. SA.1, IPCC 2013).

331

332 Two alternative downscaling approaches were used: a simple change factor approach for the SRES
333 simulations and bias-adjustment for the RCP simulations.

334

335 In the change factor approach, simulated monthly long-term changes in climate variables for the periods
336 2011-2040, 2041-2070 and 2071-2100 relative to 1971-2000 (Suppl. A Table SA.1) were used to adjust
337 daily observed time series. The GCM grid cell centre point values were re-projected to the projection
338 of the grid of the observed database and monthly changes were bi-linearly interpolated to estimate
339 values for the centre points of the 10 x 10 km grid cells. For each grid cell, monthly changes were
340 linearly interpolated to daily changes, which were added to the observed time-series. The development
341 of C_a during 21st century was taken from simulations with the BERN carbon cycle model (Suppl. A Fig.
342 SA.1, IPCC 2007). It is also assumed that the climate model bias remains the same in the simulations
343 of future climate (Ruosteenoja et al. 2011). For further illustrations of the climate scenarios see
344 Supplement A and details of the construction of climate scenarios see Rötter et al. (2013).

345

346 The dataset obtained from Finnish Meteorological Institute consisted of RCP-based simulations of
347 climate input variables for the period 1980-2100. These data were bias-adjusted with observed daily
348 data (Aalto et al. 2013) on a 10 x 10 km grid over Finland using quantile mapping (Suppl. A). The bias-
349 adjusted model output was interpolated, using the bilinear method, onto a 10×10 km grid covering the
350 area of Finland.

351

352 The bias-adjusted simulations represent a transient time-series from 1980 to 2100, whereas the SRES-
353 based scenarios are not strictly a continuous, transient time-series, but 30-year time-series separate for
354 baseline and three future periods.

355

356 **2.6 Decomposition of sources of uncertainty**

357 We estimated the uncertainty of GPP and ET projections arising from the impact model (parametric
358 and structural uncertainty) and its weather inputs (scenario, climate model variation). The analysis was
359 done separately for the RCP emission pathways and SRES emission scenarios.

360

361 We had $S = 3$ emission descriptions either in RCP (RCP2.6, RCP4.5 and RCP8.5) or SRES (A2, A1B,
362 B1). For producing the climate projections we had an ensemble of $M = 5$ GCMs (CMIP5) for RCP and
363 $M = 8$ GCMs (CMIP3) for SRES. We also included the parametric uncertainty of impact model ($K =$
364 60 parameter vectors). The parameter vectors were the same for both RCP and SRES analyses. For
365 each year t we therefore calculated $S \times M \times K$ values of the predicted variable, i.e. annual mean GPP
366 or ET value, denoted by x_{kms}^t . The total variation could be described as a set of values, X^t , for each
367 year:

$$368 X^t = \{x_{kms}^t | k = 1, \dots, K; m = 1, \dots, M; s = 1, \dots, S\} \quad (7)$$

369 Here s is either concentration pathway in RCP or SRES emission scenario, m is GCM, and k is parameter
370 vector of PRELES. We then reduced the variation in three steps. First, we calculated the average over
371 parameter vectors for each scenario and climate model and year, yielding values denoted by x_{ms}^t and
372 defining the set X_k^t :

373 $X_k^t := \{x_{ms}^t | m = 1, \dots, M; s = 1, \dots, S; \}$ (8)

374 The variability in X_k^t is therefore smaller than the overall variability, and the difference is accountable
 375 to parameter uncertainty. Similarly, we averaged these over the GCMs, yielding

376 $X_{km}^t := \{x_{.s}^t | s = 1, \dots, S\}$ (9)

377 The difference between X_{km}^t and X_k^t accounts for the GCM uncertainty. Finally, we defined the
 378 following overall annual mean:

$$\hat{x}_t = \frac{1}{S} \times \frac{1}{M} \times \frac{1}{K} \sum_k \sum_m \sum_s x_{kms}^t \quad (10)$$

379 The variability around the mean created by X_{km}^t accounts for variability in concentration pathway /
 380 emission scenario.

381 We then found minima and maxima in the sets X^t , X_k^t , and X_{km}^t for all years t . Combined with the
 382 overall mean, this procedure gave us seven time series over the simulation period. We assumed that
 383 these time series described the different components of variability in our predictions. We further fitted
 384 smooth time functions to these discrete time series using linear functions or log-log transforms. For
 385 estimating the natural variability of climate, we used the reference period (1980-2010) as a basis.

386

387 The above method for decomposing the uncertainty is descriptive and does not account for possible
 388 interactions between the components. We therefore followed the approach of Nishina et al. (2015) and
 389 carried out a three-way analysis of variance (ANOVA) for the annual GPP / ET for describing the
 390 relative importance of the different sources of variation and their interactions as

391 $SS_{overall_t} = SS_{S_t} + SS_{m_t} + SS_{k_t} + SS_{S \times m_t} + SS_{S \times k_t} + SS_{m \times k_t} + SS_{S \times m \times k_t}$ (11)

392 in which t is year. $SS_{overall}$ is the total variability around the mean (sum of squares), and the other
 393 symbols are as above. Here we also considered interaction effects between the components. We did
 394 this analysis of decomposing uncertainty only for one grid point (10 km x 10 km) corresponding to the
 395 location of Hyytiälä Forest station (southern Finland; 61°50.845N, 24°17.686E, 181 m a.s.l.).

396

397 3. RESULTS

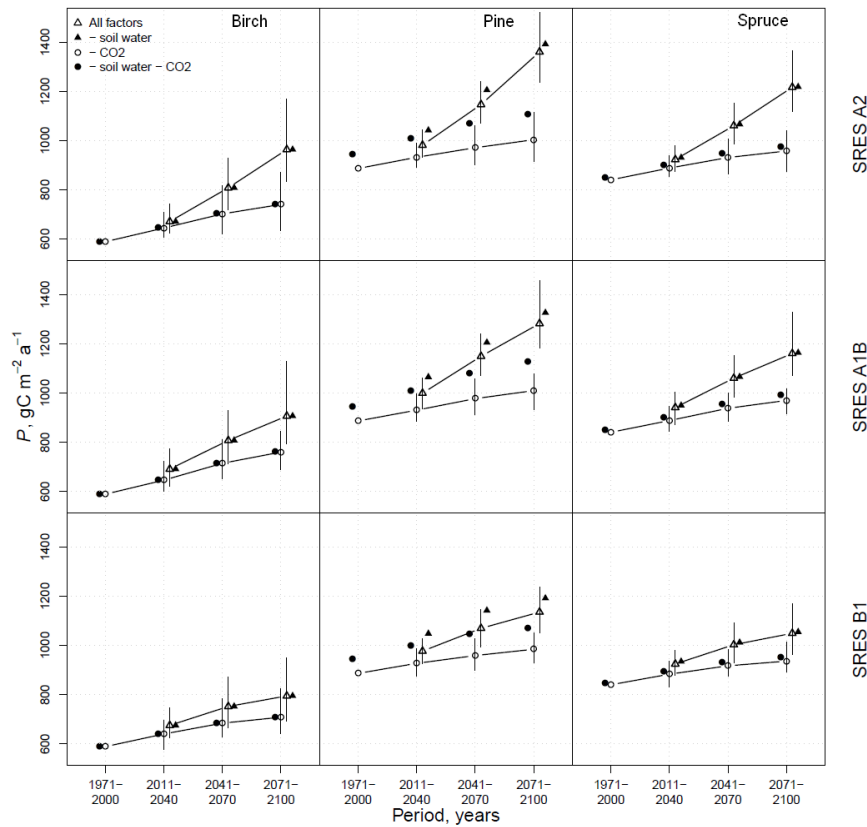
398

399 3.1 Projections of GPP and ET for SRES-based climate scenarios

400 Climate change increased the species specific ensemble mean GPP in all simulation cases (cf. section
401 2.4) within all SRES scenarios and the magnitude of the changes followed the projected emissions in
402 the scenarios, being largest in A2 (in average 36%) and lowest in B1 (25%), while A1B was closer to
403 A2 (Fig. 2). The predicted GPP driven with projections of SRES and CMIP3 ensemble had a large
404 range which nearly corresponded to the change itself (relative range was 88% across scenarios at the
405 end of the period, Table 3). Considering the structural uncertainty, the C_a fertilization effect alone was
406 decisive for the overall impact on GPP in all species, regardless of what was assumed about soil
407 moisture (Fig. 2, Table 3).

408 If C_a fertilization effect was excluded (section 2.4, case 3.) and species pooled the average GPP increase
409 was almost the same in A2 (19%) and A1B (18%) and only slightly smaller in the B1 (14%) scenario.
410 Therefore, in B1 the ensemble range was much larger relative to the mean change itself (170%),
411 meaning that the most conservative climate change predictions yielded only conservative increases of
412 GPP by the end of the century.

413 Changes of other climatic factors, mostly temperature, also increased GPP in all scenarios (Fig. 2, black
414 filled circles). In the climate model projections with the largest increases in temperature, the effects of
415 other climatic factors roughly equalled those of C_a (Table 3). The minimum GPP estimates in B1
416 suggested that without the C_a effect, none of the species would benefit from climate change during the
417 first simulated period 2011-2040 (Fig. 2).



418

419 Figure 2. Effect of climate change on gross primary production (P) of forests in Finland with the
 420 fraction of absorbed photosynthetic photon flux density (f_{aPPFD}) 0.75. Symbols show the mean
 421 prediction obtained using the downscaled projections of eight CMIP3 global circulation models in
 422 different SRES emission scenarios. Horizontal lines connect the symbols of “All factors” and “-CO₂”
 423 simulation cases (see section 2.4). Vertical lines show the range of predictions obtained with these
 424 projections (min – max), for clarity only for the same two simulation cases as in case of horizontal
 425 lines.

426 Most of GPP increases can still be attributed to the increases of GPP in summer (May-Aug). Increases
 427 of GPP in the winter-spring period (Jan-Apr) were approximately as high as increases of GPP in autumn
 428 (Sep-Dec), suggesting that summer season radiation conditions dominate as drivers of annual GPP
 429 increase (data not shown).

430 In the climate projections, the change in precipitation was less pronounced than change in e.g.
 431 temperature (Fig. 1). Anyhow, the soil water constraint was relaxed due to decreasing transpiration in
 432 the conifers (Fig. 3). This effect was clearest in pine which was the species most constrained by soil
 433 water in reference climate due to low soil water holding capacity. This effect was only slight in spruce,

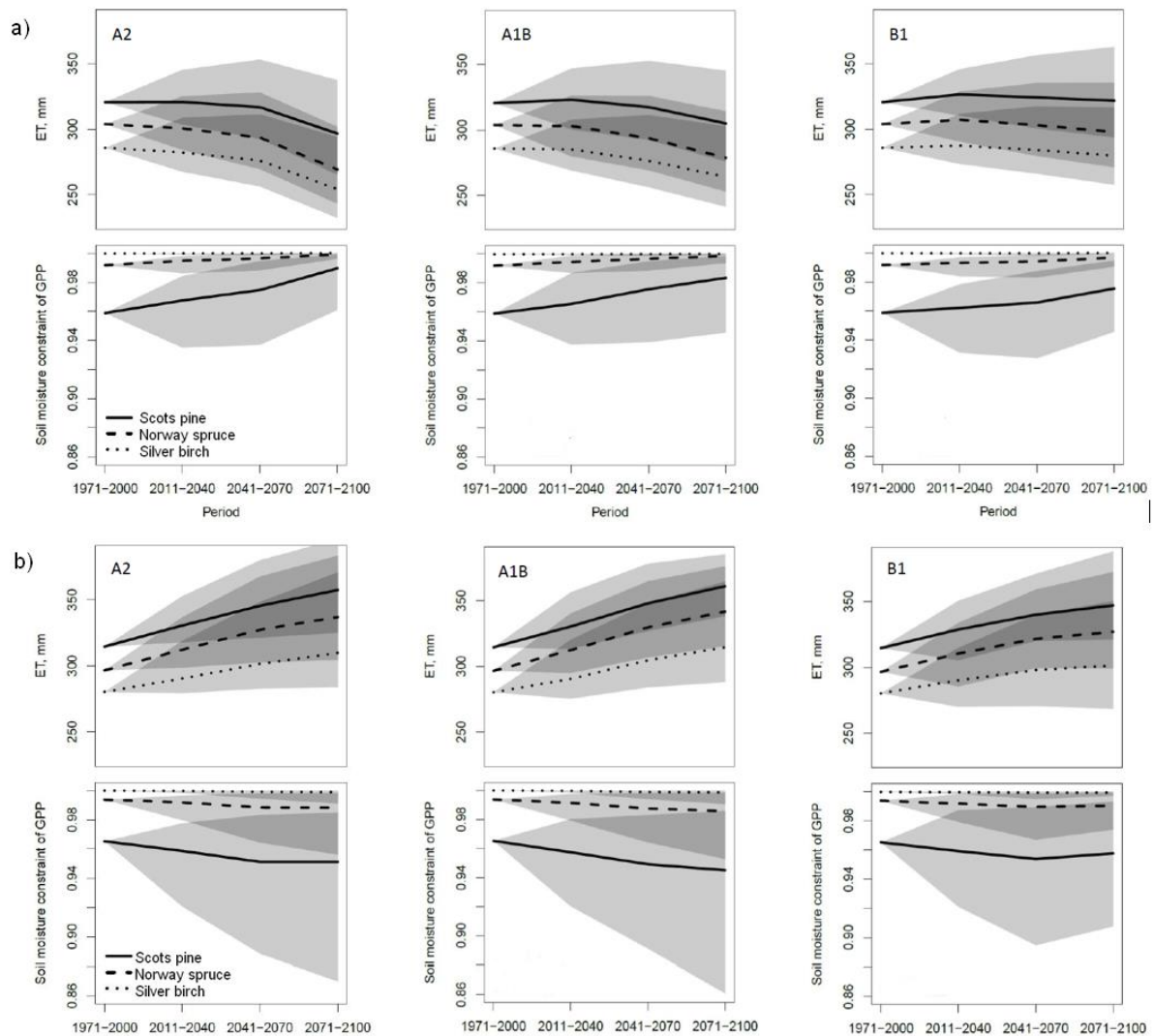
434 while birch GPP was not affected by soil moisture deficit in any of the time periods in any SRES
 435 emission scenario. When the C_a effect was excluded, the increased evapotranspiration exceeded the
 436 effect of larger rainfall and thus, GPP of pine was more constrained by soil water deficit in all SRES
 437 scenario climates than in the reference period (Fig. 3). In spruce this effect was much less pronounced
 438 and in birch it could not be detected.
 439

Species	Scen	Case	Period	Mean	Max	Min	Relative			
							Mean	Max	Min	
Birch	B1	All_factors	2011-2040	676	748	625	0.17	0.30	0.09	
			2041-2070	752	873	665	0.31	0.52	0.16	
			2071-2100	795	948	694	0.38	0.65	0.21	
		No_CO2	2011-2040	641	696	576	0.09	0.18	-0.02	
			2041-2070	685	785	630	0.16	0.33	0.07	
			2071-2100	709	826	643	0.20	0.40	0.09	
		A1B	All_factors	2011-2040	691	773	621	0.20	0.34	0.08
				2041-2070	807	930	714	0.40	0.62	0.24
				2071-2100	907	1129	795	0.58	0.96	0.38
	No_CO2	2011-2040	646	723	602	0.10	0.23	0.02		
		2041-2070	715	809	651	0.21	0.37	0.10		
		2071-2100	760	846	687	0.29	0.44	0.17		
	A2	All_factors	2011-2040	671	741	623	0.17	0.29	0.08	
			2041-2070	808	930	718	0.41	0.62	0.25	
			2071-2100	964	1168	834	0.68	1.03	0.45	
		No_CO2	2011-2040	645	710	608	0.09	0.21	0.03	
			2041-2070	702	817	622	0.19	0.39	0.06	
			2071-2100	741	871	634	0.26	0.48	0.08	
Spruce	B1	All_factors	2011-2040	925	979	880	0.13	0.20	0.07	
			2041-2070	1003	1094	931	0.22	0.34	0.14	
			2071-2100	1050	1169	964	0.28	0.43	0.18	
		No_CO2	2011-2040	884	935	831	0.05	0.11	-0.01	
			2041-2070	918	984	876	0.09	0.17	0.04	
			2071-2100	937	1013	891	0.11	0.21	0.06	
		A1B	All_factors	2011-2040	941	1002	873	0.15	0.22	0.07
				2041-2070	1060	1154	984	0.29	0.41	0.20
				2071-2100	1161	1328	1072	0.42	0.62	0.31
	No_CO2	2011-2040	888	948	844	0.06	0.13	0.00		
		2041-2070	938	1002	886	0.12	0.19	0.05		
		2071-2100	970	1016	915	0.15	0.21	0.09		
	A2	All_factors	2011-2040	923	981	875	0.13	0.20	0.07	
			2041-2070	1061	1153	985	0.29	0.41	0.20	
			2071-2100	1217	1366	1117	0.49	0.67	0.36	
		No_CO2	2011-2040	888	937	854	0.06	0.12	0.02	
			2041-2070	931	1008	865	0.11	0.20	0.03	
			2071-2100	958	1042	875	0.14	0.24	0.04	
Pine	B1	All_factors	2011-2040	977	1027	926	0.14	0.20	0.08	
			2041-2070	1070	1146	996	0.25	0.34	0.16	
			2071-2100	1136	1238	1052	0.33	0.45	0.23	
		No_CO2	2011-2040	928	986	874	0.05	0.11	-0.01	
			2041-2070	959	1029	898	0.08	0.16	0.01	
			2071-2100	985	1052	928	0.11	0.19	0.05	
		A1B	All_factors	2011-2040	1000	1061	935	0.17	0.24	0.09
				2041-2070	1150	1242	1070	0.34	0.45	0.25
				2071-2100	1283	1458	1184	0.50	0.70	0.38
	No_CO2	2011-2040	931	999	886	0.05	0.13	0.00		
		2041-2070	977	1057	913	0.10	0.19	0.03		
		2071-2100	1010	1080	931	0.14	0.22	0.05		
	A2	All_factors	2011-2040	981	1044	932	0.15	0.22	0.09	
			2041-2070	1147	1239	1070	0.34	0.45	0.25	
			2071-2100	1361	1520	1238	0.59	0.78	0.45	
		No_CO2	2011-2040	932	989	890	0.05	0.12	0.00	
			2041-2070	971	1059	902	0.10	0.19	0.02	
			2071-2100	1004	1115	915	0.13	0.26	0.03	

440

441 Table 3 Changes of gross primary production (P , $\text{g C m}^{-2} \text{ a}^{-1}$) with default parameter set of PRELES
442 and the downscaled projections of the ensemble of eight CMIP3 -GCMs over Finland separately in
443 SRES B1, A1B and A2 scenario with the fraction of absorbed photosynthetic photon flux density
444 (f_{aPPFD}) 0.75.

445



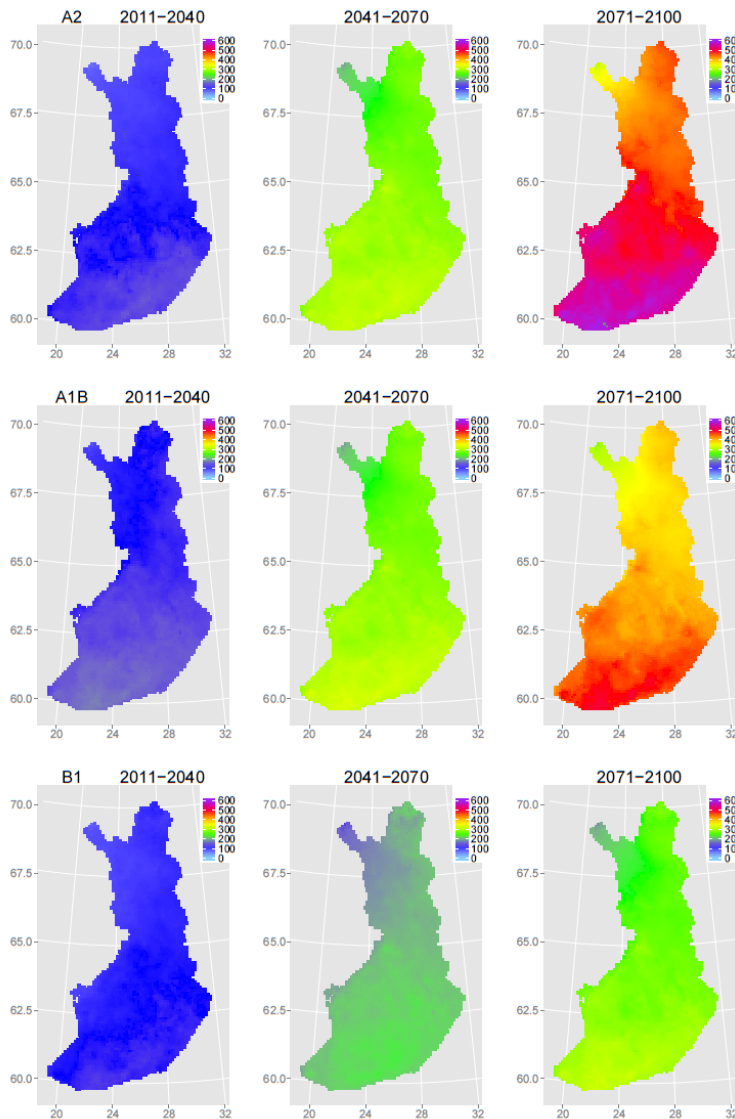
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447

448 Figure 3. Simulated evapotranspiration E and soil moisture constraint in SRES scenarios during 21st
449 century in simulation cases A) 'All factors' and B) 'All factors less C_a '. The gray-shaded bands are the
450 range of the response variable obtained with the downscaled projections of eight CMIP3 GCMs in
451 different SRES scenarios.

452

453 The increase of GPP was in absolute terms only slightly larger in southern than in northern Finland in
 454 all simulated SRES cases. Relative increases were thus higher in the north in all modelled species and
 455 the range of GPP predictions was also larger in northern than in southern Finland (Fig. 4).



456

457 Figure 4. The range of change of gross primary production (P , $g C m^{-2}$) predictions for Scots pine in
 458 simulation case 'All factors' with the downscaled projections of the ensemble of eight CMIP3 8-
 459 GCMs and with faPPFD = 0.75 in the different SRES emission scenarios.

460

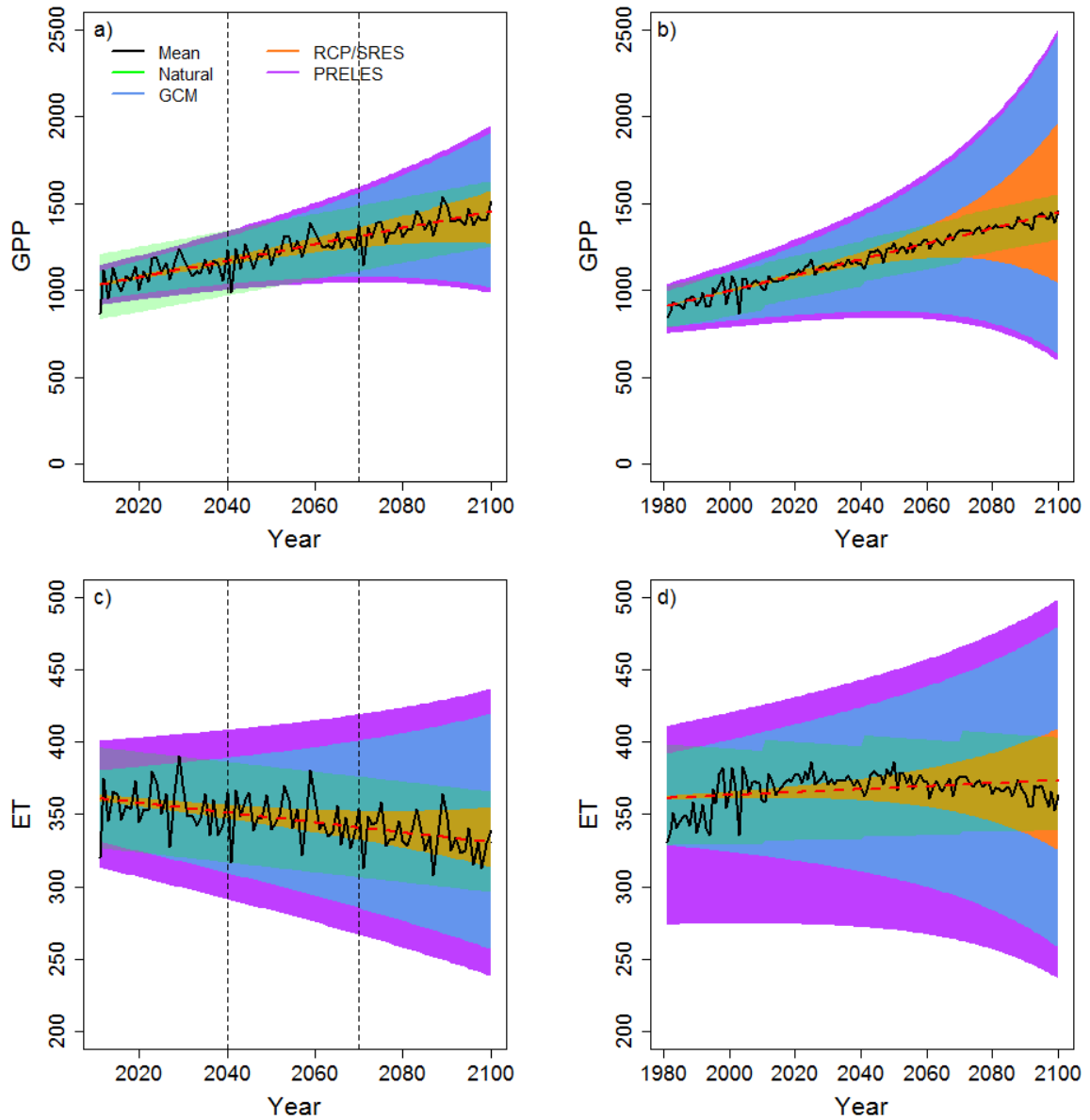
461 The relative change in GPP was the highest in birch in North Finland, up to 80% (44% – 127%) in the
 462 A2 scenario at the end of the century (Table 3). Larger increases of GPP in birch than in other species
 463 were predominantly caused by a stronger effect of the temperature increases. This was illuminated by

464 the result that when C_a fertilization effect (case 3.) was excluded the changes were still the most
465 pronounced for birch, 33% (7% – 69%, Table 3).

466

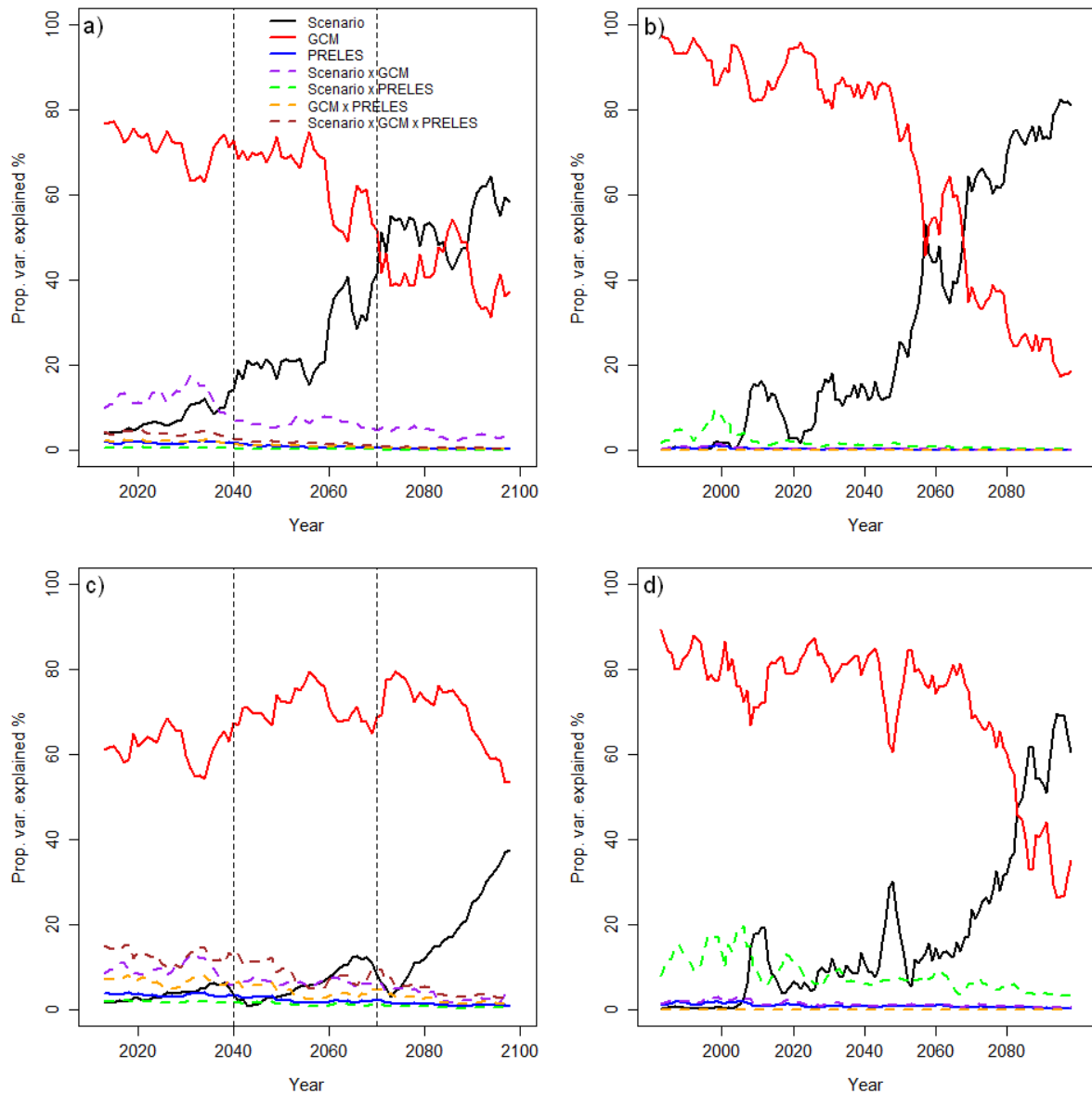
467 **3.2 Contribution of different uncertainty sources to GPP and ET**

468 In absolute terms, the overall uncertainty increased greatly over time both in GPP and ET and differed
469 clearly between SRES and RCP simulations (Fig. 5, Fig. SA.5). However, the pattern of the GPP in
470 terms of the fraction of uncertainty for each variable was quite similar in both (Fig. 6). The year to year
471 variation was large being ca. 55% in SRES and 48% in RCP and could be detected even in smoothed
472 five years average (Fig. 6). The relative importance of the different sources of uncertainty changed over
473 time in both the predictions of GPP and ET. For GPP, the GCM uncertainty dominated roughly before
474 2060 and emission uncertainty thereafter. For ET, GCM uncertainty remained the largest throughout
475 21st century in SRES while RCP emission uncertainty exceeded that of GCMs only around 2080. In
476 GPP of the SRES, the emission uncertainty never exceeded the natural variability while in RCP this
477 occurred already around 2060 (Fig. 5). A significant interaction effect between emission scenario
478 uncertainty and GCM uncertainty was found for SRES but not for RCP. The uncertainty due to PRELES
479 parameters was almost negligible in predictions of GPP but much larger in the predictions of ET in both
480 SRES scenarios and RCP pathways. In ET also, the dominant role of variation between GCMs was
481 eminent (Fig. 6).



482

483 Figure 5. Role of different sources of uncertainty (see eqs. 7-10) on the predicted Scots pine GPP and
 484 ET in one grid cell (Hyttiälä Forest Station). The different colors are additive and total uncertainty
 485 ($S \times M \times K$) is illustrated by total colored area. The colors indicate removing one source of
 486 uncertainties stepwise, starting from PRELES parametric and structural uncertainty (purple area, $K =$
 487 60 parameter vectors, same vectors for both RCP and SRES), GCM variability (blue area, $M = 5$
 488 CMIP5 GCMs for RCP and $M = 8$ CMIP3 GCMs for SRES), and emission pathways/scenarios
 489 (orange area, $S = 3$ emission descriptions separately for RCP [RCP2.6, RCP4.5, RCP8.5], and SRES
 490 [A2, A1B, B1]). The lighter color in the middle indicates the natural climatic variability. a) GPP in
 491 SRES, b) GPP in RCP, c) ET in SRES, d) ET in RCP. The vertical dashed lines illustrate the climate
 492 periods used in SRES (1980-2010, 2011-2040, and 2041-2100). In RCPs, transient climate data were
 493 used (1980-2100).



494

495 Figure 6. ANOVA (see eq. 11) for Scots pine GPP and ET in one grid cell (Hyttiälä Forest Station)
 496 separately for RCP [RCP2.6, RCP4.5, RCP8.5], and SRES [A2, A1B, B1]). a) GPP in SRES b) GPP
 497 in RCP, c) ET in SRES and d) ET in RCP. The vertical dashed lines illustrate the climate periods used
 498 in SRES (1980-2010, 2011-2040, and 2041-2100). In RCPs, transient climate data were used (1980-
 499 2100).

500

501 **4. DISCUSSION**

502 The starting point for any model based analysis of the carbon cycles is the reliable description of gross
 503 primary production. We covered a broad envelope of predictions, multiple GCMs and multiple emission
 504 scenarios with one impact model, allowing us to make conclusions on the types of change that seem

505 likely for different species or sites. Moreover, our results revealed the sensitivity of predictions of the
506 PRELES model to input uncertainty and how the variability of GPP and ET propagates from emissions
507 scenarios to the assumptions of the impact model CO₂ response function. The most general finding was
508 that the selection of the climate change projection had a profound influence on both the predicted GPP
509 and ET of boreal forests of Finland. Many studies concerning different ecological impacts of climate
510 change, e.g. disturbances (e.g. Lehtonen et al. 2016, Seidl et al. 2017) have noted this. We considered
511 here a continuous variable whereas disturbance is always discrete which emphasizes the need for
512 specific analysis for different impacts. However, in both cases the wide range of projections may lead
513 to difficulties in drawing ecologically meaningful conclusions (Cavanagh et al. 2017). Real uncertainty
514 is even larger due to feedback loops between climate and vegetation (e.g. Forzieri et al. 2017) which
515 we could not account for with a simple tool like PRELES.

516

517 The highest predictions of GPP were almost double compared with present day observations, while the
518 lowest predictions without C_a fertilization effect did not increase GPP during the next decades and
519 barely during the whole century. The species specific mean GPP increased in all simulated cases and
520 was generally in the same scale as found in earlier studies with more mechanistic models (Wamelink et
521 al. 2009, Ge et al. 2013, Reyer et al. 2014). Our finding that the decomposition of uncertainty hardly
522 differed between combinations of older SRES emission scenarios and CMIP3 projections and the
523 currently used RCPs and CMIP5 GCMs lends support to the robustness of this result. The difference of
524 the climate projections for Finland between SRES and RCP scenarios seems to be quite modest (Fig.
525 1) especially if compared with the high variability between projections of individual GCMs (Fig 6).
526 Thus, from the viewpoint of forest impact studies SRES and RCP projections essentially cover the same
527 range (van Vuuren and Carter 2014). Our results were consistent with earlier studies in the sense that
528 GCMs were the dominant sources of uncertainty for GPP until around 2060, while uncertainty of the
529 temporal development of emissions, either driven by RCP or SRES scenarios, dominated later in the
530 projection period (2060–2100, Nishina et al. 2015, Horemans et al. 2016). We note that this uncertainty
531 analysis only covered one grid point (Hyttiälä forest station), but extending it to the whole country

532 would likely not create more than marginal changes to the decomposition of uncertainty, due to the
533 small parametric variation in PRELES.

534

535 The difference of variation between RCP and SRES observed here was partly due to the fact that
536 selected pathways of RCPs were more extreme than emission scenarios of SRES (RCP2.6 vs SRESB1
537 and RCP8.5 vs SRESA2). In addition, GCMs have developed from CMIP3 to CMIP5. However,
538 although characteristics of the CMIP5 models have changed from CMIP3, e.g. they may have higher
539 resolution, their atmospheric or ocean components may have changed in order to improve their ability
540 to describe the fluxes between ecosystems and the atmosphere, the models in the new ensemble are
541 neither independent of each other nor independent of the earlier generation (Knutti et al. 2013). From
542 the impact viewpoint, one could thus argue that the characteristics of input uncertainty have not changed
543 that much between these two generations of GCMs. Additional variability between RCP and SRES in
544 our analysis was created by the fact that we did not have the same GCMs in the compiled subset of
545 projections (see Suppl. A), and that the method for downscaling the results of GCMs for Finland
546 differed between RCP and SRES. In SRES thirty-year periods of historical data were coupled with
547 GCM projections to produce the climate for the whole century, while in the case of RCPs, the GCM
548 projections directly provided the transient climate change from 1980 to 2100. This contributed to fairly
549 different natural variability between RCP and SRES (Fig. 6, Suppl. A).

550

551 The dominant role of GCM over emission scenario as a driver of uncertainty of the impact studies
552 outcome has not been pointed out in earlier Finnish studies (e.g. Kellomäki et al. 2008. Ge et al. 2013).
553 In boreal-forest related studies this is of special importance due to the fact that the time perspective of
554 tree growth approaches that of climate change. Our results demonstrate that impact studies with a single
555 GCM projection may not expose the full range of possible changes and thus, may lack information
556 about local/regional scale impacts that would be essential for decision making (e.g. Lung et al. 2013).
557 Our understanding is that forest related climate mitigation policies do pose a risk that actions are based
558 on mean response not on the range of scenarios, the relative probabilities of which cannot be specified

559 at this point of time. It would therefore be extremely helpful for coherent decision-making if reporting
560 overall uncertainty and its component sources was standard practise in scientific impact studies.
561
562 Structural uncertainty of the model, i.e., uncertainty due to our deficient scientific understanding of the
563 process at hand, was represented here by the response of gas exchange to long-term CO₂ fertilization.
564 Under the default assumptions, the direct influence of C_a on GPP (species pooled) was 50% of the total
565 impact in A2 scenario and roughly 40% in A1B scenario and up to 38% in B1 at the end of the century,
566 but the increase was sensitive to assumptions of C_a effects on WUE. Severe production limitations due
567 to soil moisture availability seem unlikely if transpiration of trees is moderated by increased C_a . Without
568 the assumptions of C_a -induced reductions of transpiration, there would be more sites suffering from
569 drought in the future (Fig. 3b). Relative humidity (RH%) has been found to be a critical factor to
570 differentiate the projected NPP among different Global Vegetation Models (Nishina et al. 2015). We
571 derived vapor pressure deficit (D) using RH% predicted by the GCMs, while earlier Finnish studies
572 have assumed unchanged RH% of air (e.g. Kellomäki et al. 2008, Ge et al. 2013), but both approaches
573 lead to increased D . Earlier research concerning Finland has warned about vulnerability to climate
574 change of spruce growing on dry sites. However, based on our study, a crucial aspect for species
575 management is that, species responsive to D and occupying moist sites will perform well. Drought-
576 vulnerable sandy dry or uphill sites (Muukkonen et al. 2015) tend to be Scots-pine dominated already
577 in the current climate. The species-specific responses of our study must be interpreted with caution, as
578 the parameter adjustments were made subjectively on the basis of available but insufficient information.
579 Concerning conclusions of these water effects, one has to keep in mind the weak ability of GCMs to
580 represent within-year, seasonal and day-to-day variability of weather. This issue is the most critical one
581 for rainfall since rains could become more sporadic and intense in the northern hemisphere (e.g. Jylhä
582 et al. 2009, Rummukainen 2012, 2013), with possibility off increased frequency of longer periods of
583 drought. Neither we nor earlier studies accounted for this specific property of input uncertainty.
584

585 The applied PRELES model has been parameterized with several years of eddy-covariance data
586 including considerable within-year variability of fluxes. We have found that the model also performs
587 well at warmer and colder eddy-covariance sites (Minunno et al 2016). Further support for plausible P
588 predictions has been obtained through a comparison with the JSBACH model (Reick et al. 2013) at the
589 scale of Finland (Peltoniemi et al. 2015). In this study, we found that the proportion of PRELES
590 parametric uncertainty from total uncertainty was almost marginal in the projections of GPP. This
591 indicates that lots of data were used in the calibration and the most important parameters were well
592 constrained. We acknowledge that under the changing environmental conditions we were not able to
593 fully separate model structural uncertainty from the parametric uncertainty but PRELES uncertainty
594 here only describes the variability included in the calibration dataset (Minunno et al. 2016) and, thus,
595 did not increase over time. This is a general challenge in calibration, especially in the case of simple
596 models. It could be that processes not important in the current environment become major issues in the
597 future, and thus the impact model uncertainty is not reflected coherently. One way forward could be to
598 test PRELES with different CO_2 response functions against data from FACE experiments, and/or to
599 calibrate the functions in such data sets. This could be very informative bearing in mind that the
600 structural uncertainty related to this driver had a prominent effect on the model predictions. Our results
601 also do not account for the possible increase in canopy size as a result of increasing GPP which could
602 also lead to increasing ET and hence more pronounced drought effects, however, a comparison of
603 simulations with different f_{aPPFD} values may provide a cue. In our simulations increasing f_{aPPFD} from
604 0.75 to 1 had an effect on E comparable to the (opposite) C_a -induced reduction of transpiration (Fig.
605 SB2).

606

607 There are numerous effects we did not consider in our analysis. Restriction of tree response due to soil
608 nitrogen limitation may downregulate the CO_2 fertilization effect. Long-term growth stimulation has
609 been found only under high nutrition (e.g. fertilized sites or on former agricultural land) or explained
610 as a result of priming effects (see references in Palacio et al. 2014). The main effects of nutrients
611 (particularly nitrogen as the main limiting nutrient in boreal forest) are (1) increased photosynthetic
612 capacity of foliage (Reich et al. 1998, Peltoniemi et al. 2012), and (2) increased carrying capacity, i.e.,

613 the total foliage that can be supported by the stand (Ladanai and Ågren 2004, Mäkelä et al. 2008). In
614 boreal conifers the increased photosynthetic capacity due to variation in foliar N concentration is
615 relatively modest (e.g. Peltoniemi et al. 2012), whereas the impacts of changes in carrying capacity
616 could be considerable. The effects of increasing canopy cover and consequently f_{aPPFD} were already
617 discussed above. However, whether or not the canopy cover will increase under climate change also
618 depends on the response of nutrient availability to climate, as the increased CO₂ fertilisation is known
619 to strengthen the carbon sink below ground under N limitation (Norby et al. 2010). Here, more
620 information is needed on trends in N deposition, implications of the priming effect, as well as impacts
621 of weather drivers on soil organic matter decomposition. In order to account for the nutrient cycle
622 which could either up- or down-regulate the predicted increases in GPP, e.g. nitrogen modifier could
623 be included in PRELES based on approaches like Peltoniemi et al. (2012). We also did not include any
624 nitrogen deposition scenario. However, nitrogen deposition does not play a big role in Finland when
625 compared with e.g. Central Europe. Also the effect of climate extremes and especially their connection
626 to the changing disturbance regimes we did not include in the predictions. When considering the carbon
627 cycling the increasing disturbances may have a much bigger role in the future than in current conditions
628 (Seidl et al. 2017). All these additional effects will further increase the uncertainty of GPP projections
629 into the future.

630

631 **5. CONCLUSIONS**

632 We consider it very likely that primary production of Finnish forests will be higher in the future than it
633 is now. However, uncertainty around this mean response is very large and our decomposition of its
634 sources demonstrates that more constraining information is needed equally on the biological
635 mechanisms and on the expected environmental drivers before the projections can be made more
636 conclusive. Regarding the mechanisms, we need to improve our scientific understanding of the
637 interactions of CO₂ fertilization with water and nutrient fluxes (Figs. 2 and 3). At the same time, our
638 analysis underlines the need of transparency in modelling studies about how input uncertainty from
639 emission scenarios and different GCMs and their assumptions propagates to ecological impacts (Figs.

640 5 and 6). Transparency is easier to reach if the modelling approach is relatively simple, such as in the
 641 present study. It is encouraging in this respect that our results were much in line with previous studies
 642 obtained with highly mechanistic, complex models. We believe that these general methodological
 643 conclusions can be extended to more comprehensive models, such as models of the full vegetation
 644 carbon budget, although our example model only considered gross primary production.

645

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651

652 Appendix List of the variables and functions of PRELES model.

653 Variable (model input or estimated by the model)	654 Symbol	655 Unit
655 Daily precipitation (water or snow)	R	mm
656 Drainage	F	mm
657 Drainage from surfacial water storage to soil (after $\theta_{\text{surf,max}}$ is reached)	F_{surf}	mm
658 Evapotranspiration from snow storage	E^{snow}	mm
659 Evapotranspiration from soil storage	E^{soil}	mm
660 Evapotranspiration from surficial water storage	E^{surf}	mm
661 Fraction of absorbed photosynthetic photon flux density	f_{aPPFD}	–
662 Gross primary production	P	gCm ⁻²
663 Leaf area index	L_A	–
664 Light modifier	f_L	–
665 Minimum of vapour pressure deficit and soil water modifier	$f_{\text{DW,P}}$	–
666 Modifier for temperature acclimation state, cf. S	f_S	–
667 Photosynthetic photon flux density	Φ	mol ⁻¹
668 m ⁻²		
669 Rainfall, as rain	R^1	mm
670 Relative extractable water	W	–
671 Soil water modifier for evaporation	$f_{\text{W,E}}$	–
672 Snow/ice water content (in water equivalents)	θ_{snow}	mm
673 Snowfall	R^0	mm
674 Snowmelt	M	mm
675 Soil water content	θ	mm
676 Soil water modifier for gross primary production	$f_{\text{W,P}}$	–
677 State of acclimation to temperature	S	°C
678 Surficial water content, e.g. on leaf and soil surfaces (has an upper limit defined by subscript 679 ‘max’)	θ_{surf}	mm
680 Temperature, daily mean	T	°C
681 Vapour pressure deficit, daily mean	D	kPA
682 Vapour pressure deficit modifier	f_D	–
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892 **Supplementary material A: Climate scenarios and derivation of weather variables**

893

894

895 Table SA1. List of General Circulation Model (GCM) simulations from the CMIP5 project for the
896 RCP2.6, RCP4.5 and RCP8.5 scenarios, and from the CMIP3 archive (Meehl *et al.*, 2007) for three
897 SRES emission scenarios (B1, A1B, A2) (Nakicenovic *et al.* 2000, IPCC 2007, Table 8.1).

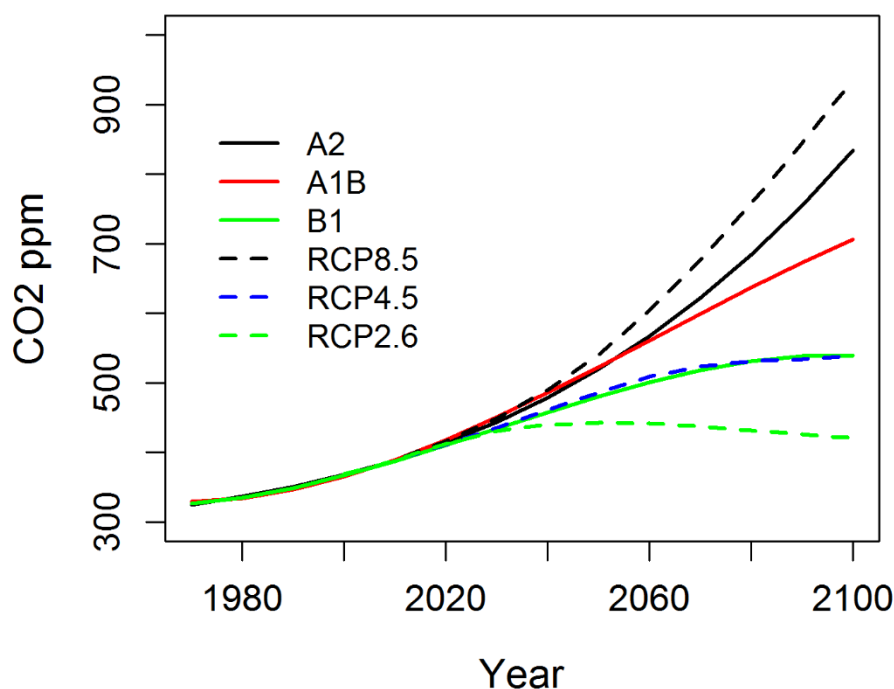
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Pathway/Scenario	GCM	Institution
RCP	CanESM2	Canadian Centre for Climate Modelling and Analysis
	CNRM-CM5	Centre National de Recherches Meteorologiques / Centre Europeen de Recherche et Formation Avancees en Calcul Scientifique
	GFDL-CM3	Geophysical Fluid Dynamics Laboratory
	HadGEM2-ES	Met Office Hadley Centre (additional HadGEM2-ES realizations contributed by Instituto Nacional de Pesquisas Espaciais)
	MIROC5	Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for

SRES	BCCR-BCM2.0	Bjerknes Centre for Climate Research, Norway
	CCCMA- CGMC3.1(T47)	Canadian Centre for Climate Modelling and Analysis
	CNRM-CM3	Météo-France
	CSIRO-Mk3.5	CSIRO Atmospheric Research, Australia
	GISS-ER	Goddard Institute for Space Studies, USA
	INM-CM3.0	Institute for Numerical Mathematics, Russia
	IPSL-CM4	Institut Pierre Simon Laplace, France
	MIROC3.2 (medres)	Center for Climate System Research, National Institute for Environmental Studies and Frontier Research Center for Global Change, Japan

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904 Figure SA.1 The development of atmospheric CO₂ concentrations (C_a in ppm) in atmosphere over the
905 21st century. RCP2.6 by integrated assessment model IMAGE, RCP4.5 by MiniCAM, and RCP8.5 by

906 MESSAGE. SRES curves (A2, A1B, B1) were drawn with parameters fitted on estimates of BERN
907 carbon cycle model (IPCC, 2007).

908

909

910 *On the differences between bias correction and delta change approaches*

911

912 The main difference between these two methods is that the bias correction method is based on
913 the modelled climate whereas delta change method uses historical data. This difference means
914 that in delta change method the observed interannual variability does not change in the
915 projected future climate while in bias correction temporal properties such as autocorrelation
916 could change over time and thus interannual variability may change in the projected climate
917 from the historical one. From the viewpoint of ecological impact study, the delta change
918 method could be more relevant in near-term projections, e.g. up to 2040, and especially if
919 expected changes in the phenomena of interest are small. The bias correction method is
920 regarded more preferable for the projections of further in the future, e.g. 2050-2100., or where
921 expected changes are large.

922

923 *Estimation of water vapour pressure deficit, VPD*

924

925 For the model simulations, we converted grid estimates of daily vapour pressures to vapour
926 pressure deficits (VPD) according to Cambell and Norman (2000).

927

928 Water vapour pressure deficit (Pa) is given by the difference between actual water vapour
929 pressure e_a and its saturation value e_s

930

$$931 \quad VPD = e_a - e_s$$

932

933 The vapour pressure of saturated air was obtained from the Tetens formula

934

$$935 \quad e_s(T) = a \times \exp\left(\frac{bT}{T + c}\right)$$

936

937 where T is temperature, and constants are $a = 0.611$, $b = 17.502$, and $c = 240.97$.

938

939 In the scenario climate i , new actual water vapour pressure e_{ai} was calculated from the observed
940 vapour pressures (VP_a) and vapour pressure deltas (ΔVP_i) obtained from same ensemble of 8
941 GCMs as temperature deltas (ΔT_i).

$$942 \quad e_{ai} = VP_a + \Delta VP_i$$

943

944 Saturated vapour pressure e_{si} in the scenario climate i was calculated accordingly

945

$$946 \quad e_{si} = e_s(T + \Delta T_i)$$

947

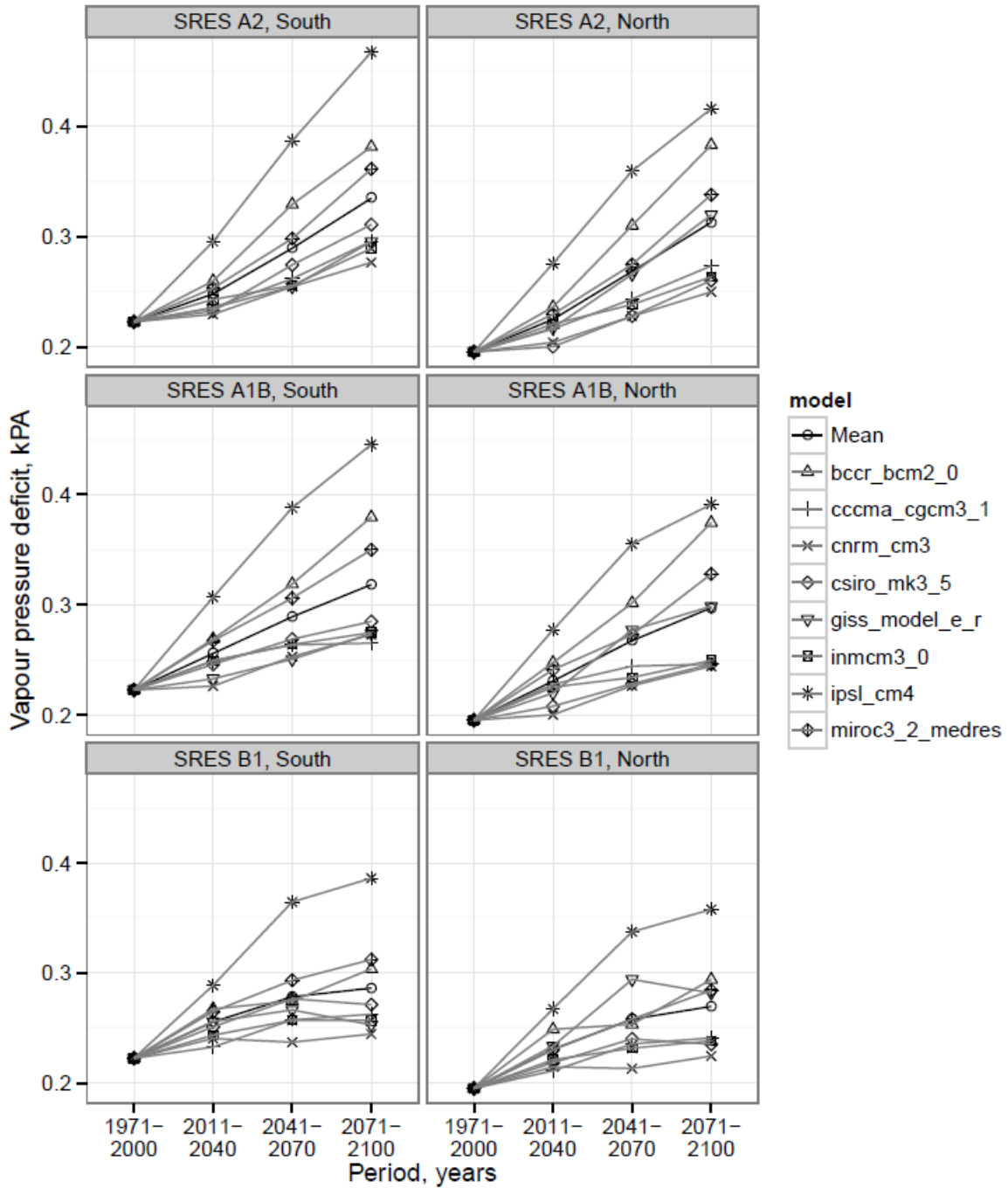
948 Thereafter, VPD in scenario climate i was obtained from

949

$$950 \quad VPD_i = e_{si} - e_{ai}$$

951

952 The obtained VPDs are presented in Figure SA2. The scenarios of climate change by climate
953 model used in the gross primary productions (P) simulations are given for southern and
954 northern (south and north from 65°N) Finland separately. The entire latitudinal range of
955 Finland is 59°30'N - 70°05'N.



956

957 Figure SA.2 Scenarios of annual VPD in southern and northern Finland using eight climate models,
 958 and their average estimate during the 30 year periods.

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963 *Photosynthetic photon flux density, PPFD*

964 Reference period values of global radiation did not represent plausible interannual variation.
965 Therefore we produced reference period radiation data in SRES projections with the method
966 presented in Oker-Blom et al. 1989 based on the sun elevation. We applied this method for
967 each day and hour of the year and calculated theoretical clear sky radiation, which we further
968 converted to estimates of actual PPFD, based on its relationship with weather variables in
969 Hyttiälä. The following decomposition of actual PPFD was used:

$$970 \quad \phi = \phi_m + \phi_D + \varepsilon_i$$

971 where ϕ_m is the mean overall daily ϕ estimated from hourly (k) sun radiations ξ_k estimated with
972 the method of Oker-Blom et al. (1989)

$$973 \quad \phi_m = c_m \sum_{k=0}^{23} \xi_k$$

974 Integrating diurnal hourly values of theoretical radiation yielded daily theoretical PPFD (ϕ_t),
975 which was converted to mean daily PPFD by multiplication with a fitted coefficient, $c_m=2.051$,

$$976 \quad \phi_m = c_m \phi_t.$$

977 To represent co-variation of PPFD with daily weather, we added a second term to the model
978 that represented VPD-dependency of ϕ :

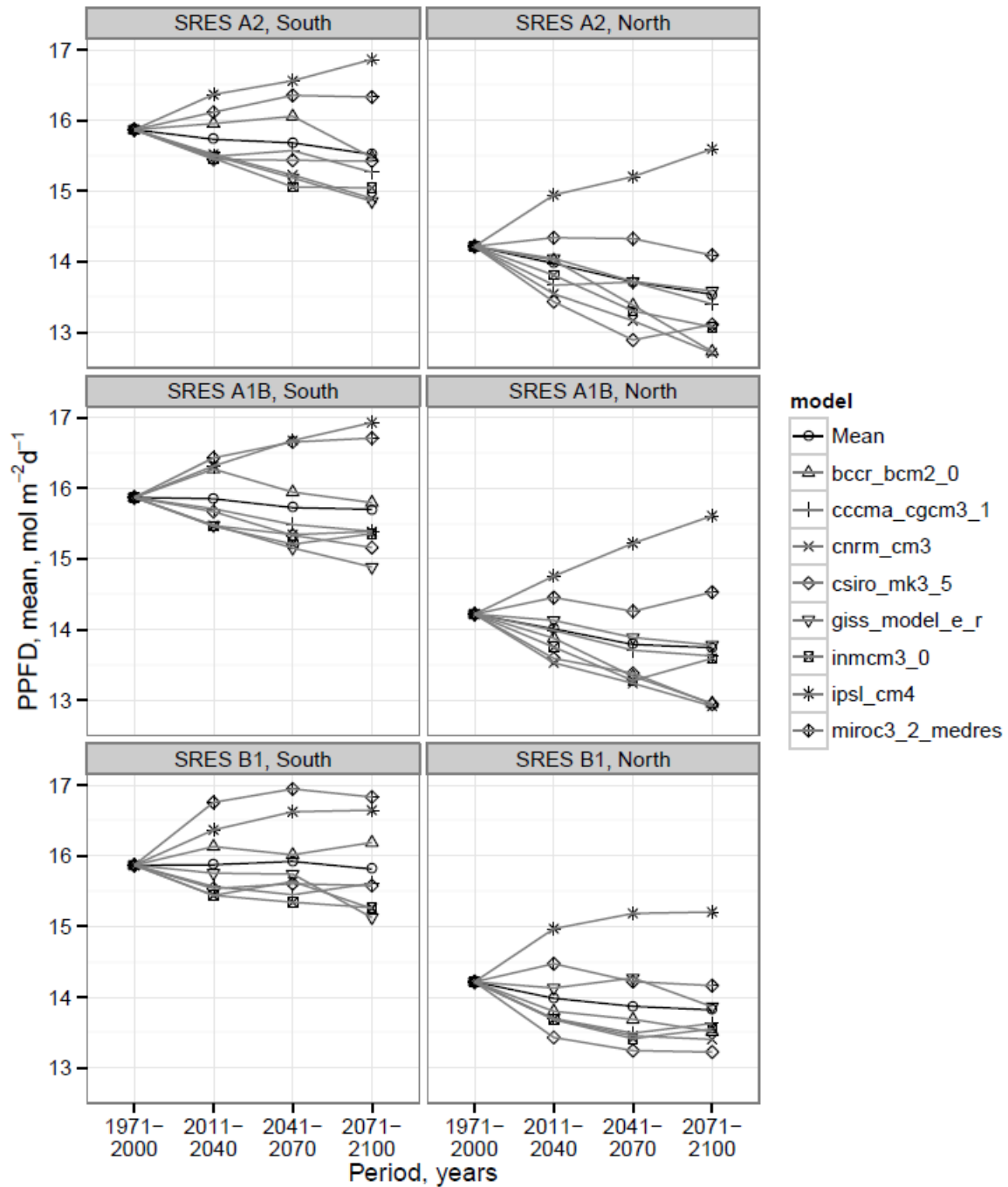
$$979 \quad \phi_D = \frac{a_1}{a_2 D + 1} - a_3$$

980 where all a are fitted coefficients. Residuals of this fit has a seasonal D relationship, so we
981 finally replaced the ε_i term with their means estimated for four types of days, those with high
982 and low sun mean radiation ($\phi_m < 5 \text{ mol m}^{-2}$), $\phi_m < 5 \text{ mol m}^{-2}$, respectively) and high and
983 low VPD ($D < 0.1 \text{ kPa}$ and $D < 0.1 \text{ kPa}$).

984 The obtained radiation is presented in Figure SA3. The scenarios of climate change by
985 climate model used in the gross primary productions (P) simulations are given for southern
986 and northern (south and north from 65°N) Finland separately. The entire latitudinal range of
987 Finland is 59°30'N - 70°05'N.

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991 Figure SA.3 Scenarios of annual radiation in southern and northern Finland using eight climate models,
 992 and their average estimate during the 30 year periods.

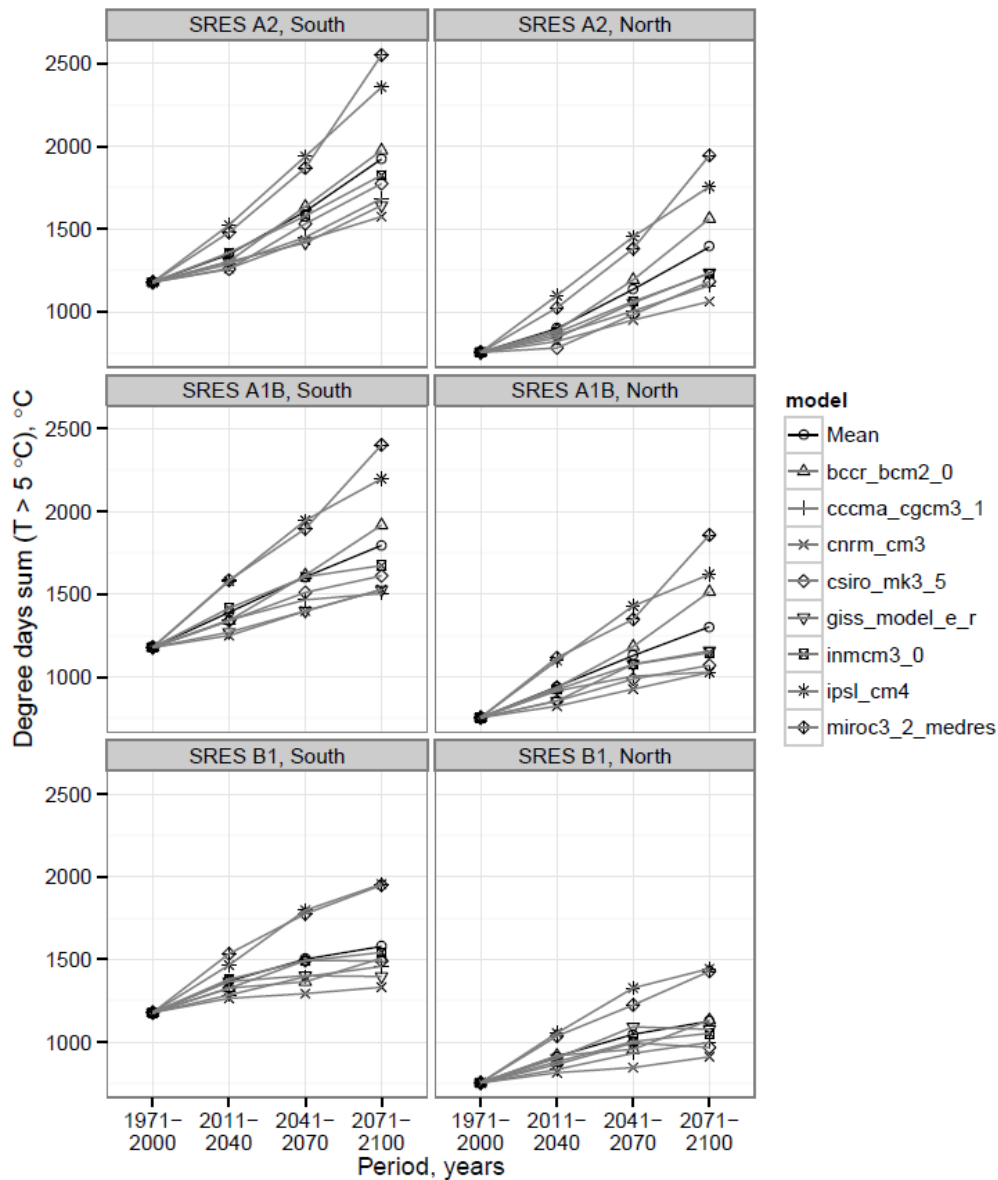
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996 *Effective temperature sum, ETS*

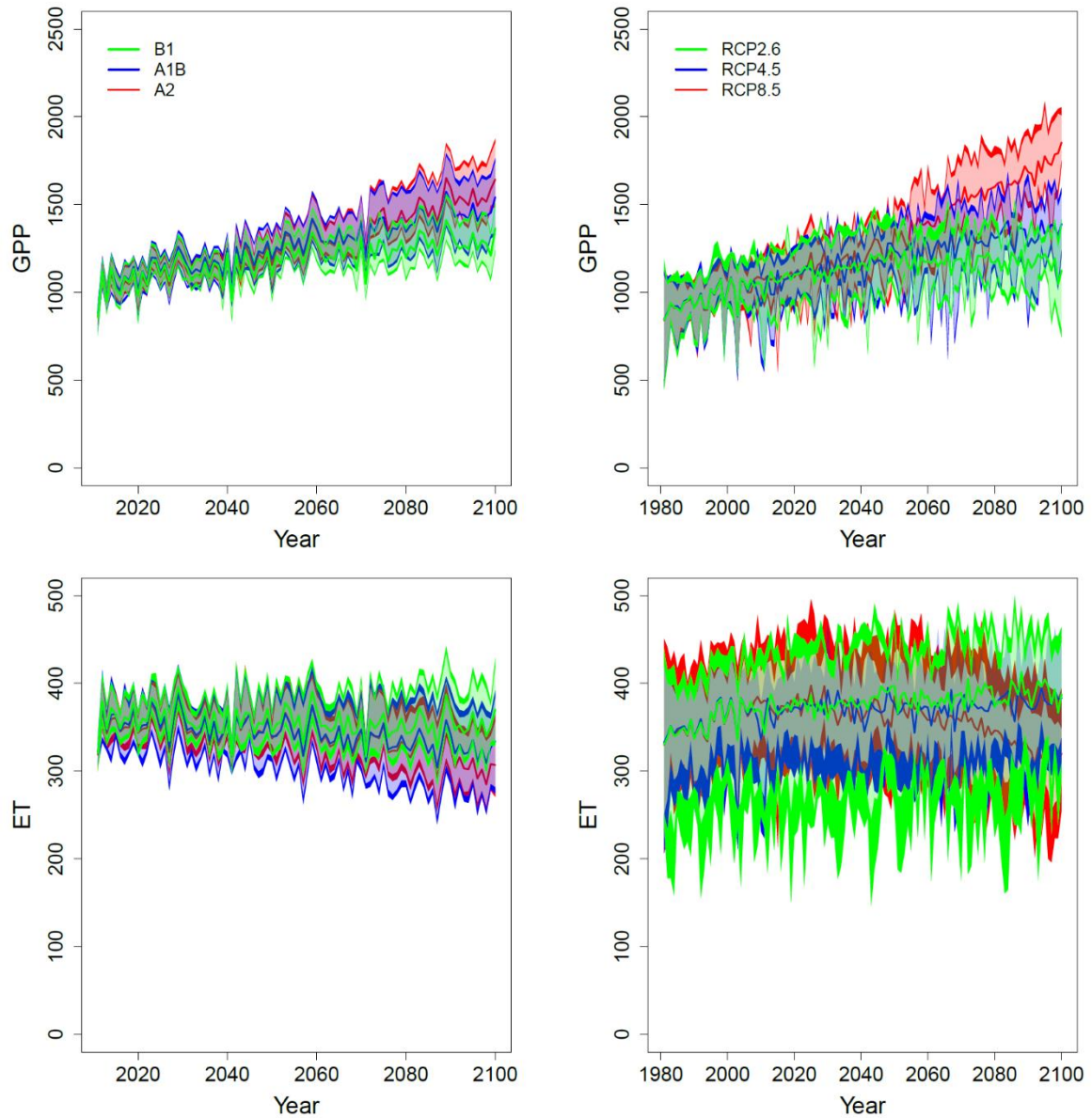
997 We calculated effective temperature sum as the sum of degrees by which the daily average
 998 temperature exceeds +5 °C. A threshold of +5 °C is a commonly used standard when
 999 calculating the effective temperaturesum in forestry and agriculture in the Nordic countries.
 1000 Figure SA4 shows the development of annual temperature sum projected by different climate
 1001 models.



1002

1003 Figure SA.4 Scenarios of annual temperature sum in southern and northern Finland using eight
 1004 climate models, and their average estimate during the 30 year periods.

1005



1006

1007 Figure SA.5 The emission scenario/pathway specific gross primary production (GPP) and
 1008 evapotranspiration (ET). The lighter shade of the coloured area around each curve shows the
 1009 GCM variability and the outermost darker shade indicates PRELES parametric and structural
 1010 uncertainty within each emission scenario.

1011

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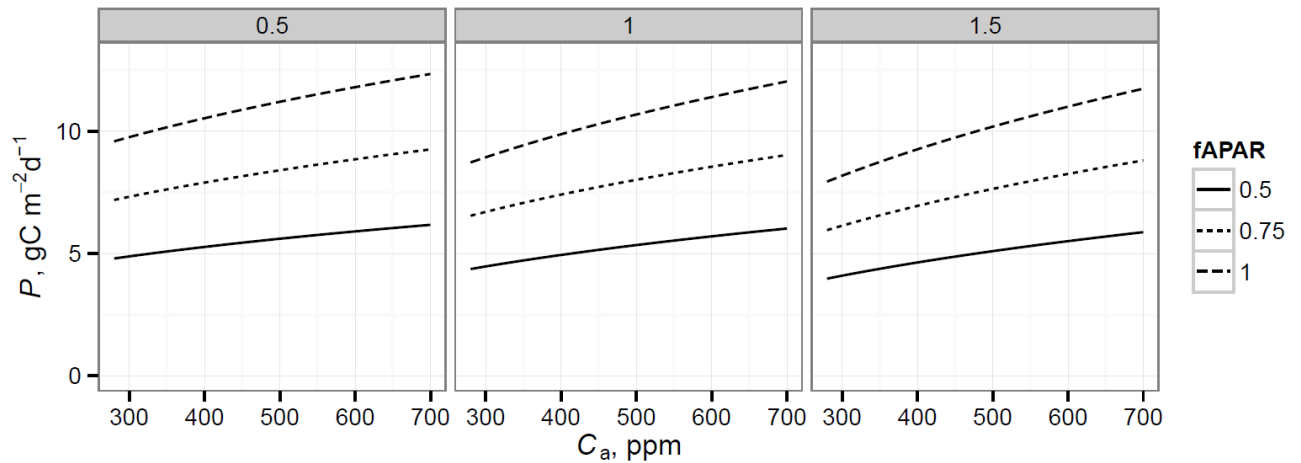
1040 **Supplementary material B: Model responses to synthetic climate forcing**

1041

1042 The model predicts increases of P with increasing C_a , which slightly saturate under high C_a (Fig. SB.1).

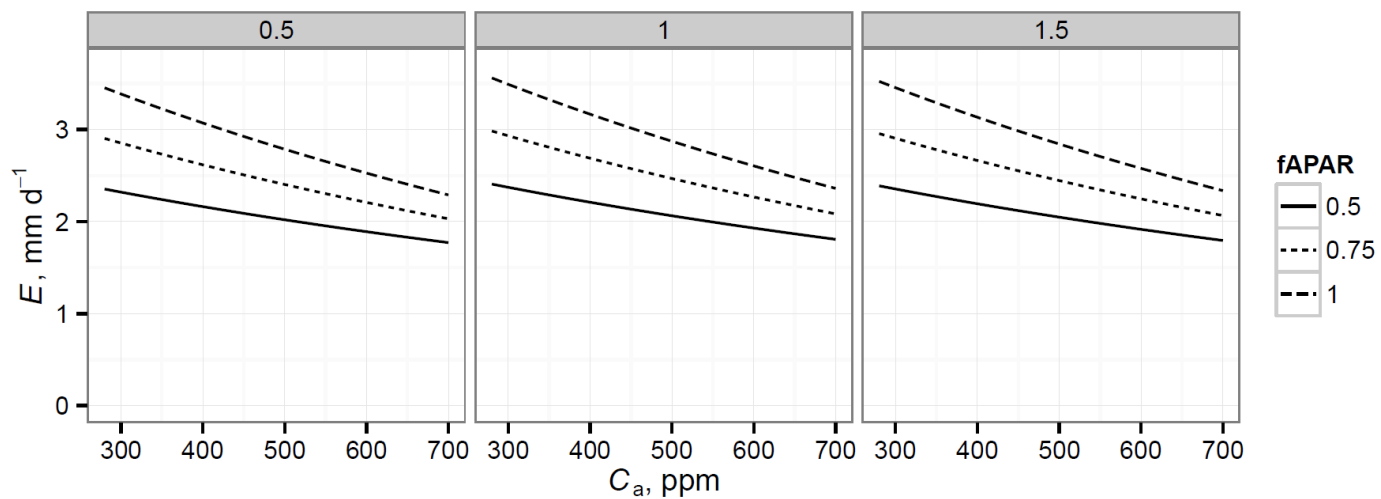
1043 The absolute increases are proportional to f_{aPPFD} . Changes are more pronounced under high D . The

1044 model predicts decreases of E with increasing C_a (Fig. SB.2). The absolute increases are proportional
1045 to f_{aPPFD} . Changes are more pronounced under high f_{aPPFD} , where the fraction of transpiration of E is
1046 larger. The changes of P and E lead to increase of ecosystem WUE (water use efficiency, P/E), which
1047 are nearly linear (Fig. SB.3). We also applied the model with Hyytiälä eddy-covariance site weather
1048 data, in order to show how model predicts under hypothetical weather scenarios whereby we modified
1049 the input variables in a systematic manner (Fig. SB.4). Assuming that precipitation does not increase,
1050 T and PAR remain unchanged, we find an increase of annual mean P from 2.7 to 3.4 gC m⁻² d⁻¹ when
1051 C_a increases from 380 to 700 ppm. If this change is accompanied with an increase of 5° C in all annual
1052 daily temperatures, the corresponding increase of P is from 3.05 to 4.2 gC m⁻² d⁻¹. Under increasing T ,
1053 the role of precipitation increases, due to the increasing evapotranspiration and decreasing soil moisture
1054 content (not shown). If irradiance upon canopies decreases, the role of soil moisture limitation
1055 decreases. Effects of C_a have been implemented in the form of empirical equations fitted to a detailed
1056 stand level model that implements the biochemical photosynthesis model (Farquhar et al. 1980, Leuning
1057 1995). Our model predicted 11 and 15% increase of P and E when exposed to 550 ppm ($D = 0.5$ kPa,
1058 $f_{aPPFD} = 1$) (*ceteris paribus*). Light-use efficiency should increase 25% when C_a increases from current
1059 levels to 550 ppm in a closed canopy forest without the effects of photosynthetic down-regulation
1060 (Medlyn et al. 2011). Warren et al. (2011) found in a FACE experiment that the annual canopy
1061 transpiration decreased 10-16% due to elevated C_a , while in a multimodel comparison the range of stand
1062 transpiration among models was from -31 to +10% (De Kauwe et al. 2013). Our model estimates are,
1063 thus, roughly comparable to these.



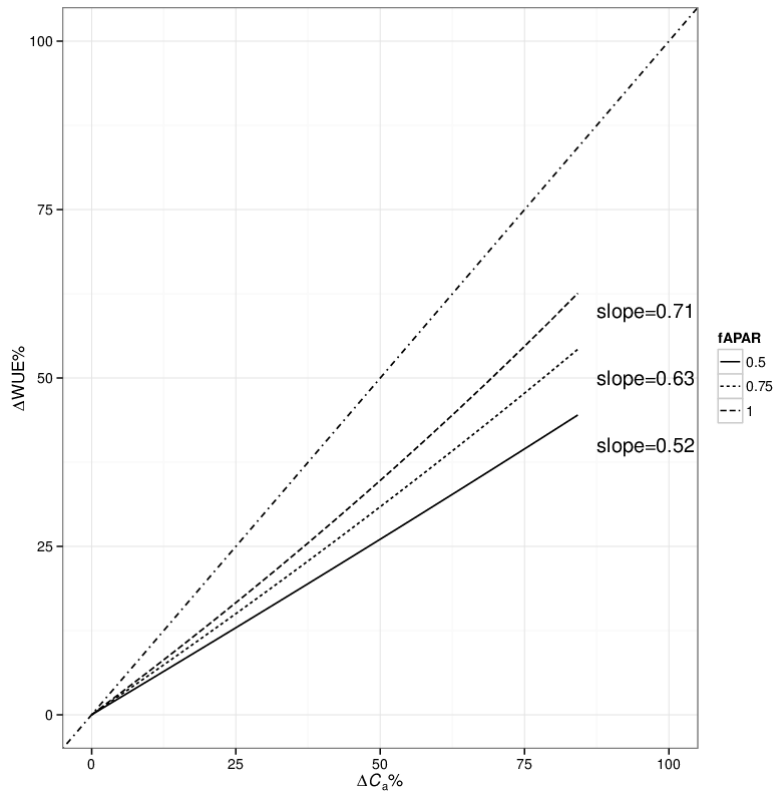
1064

1065 Figure SB.1 Increase of model predicted daily P with increasing C_a and by D and f_{APAR} . The values of
 1066 D on the upper grey panel (0,5 – 1,5). In these simulations, the effect of T and seasonality term of the
 1067 model (S) was saturated, and soil moisture did not play role. PAR upon canopy was set to 30 mol/m².
 1068 Default model parameters (for Scots pine) were used.



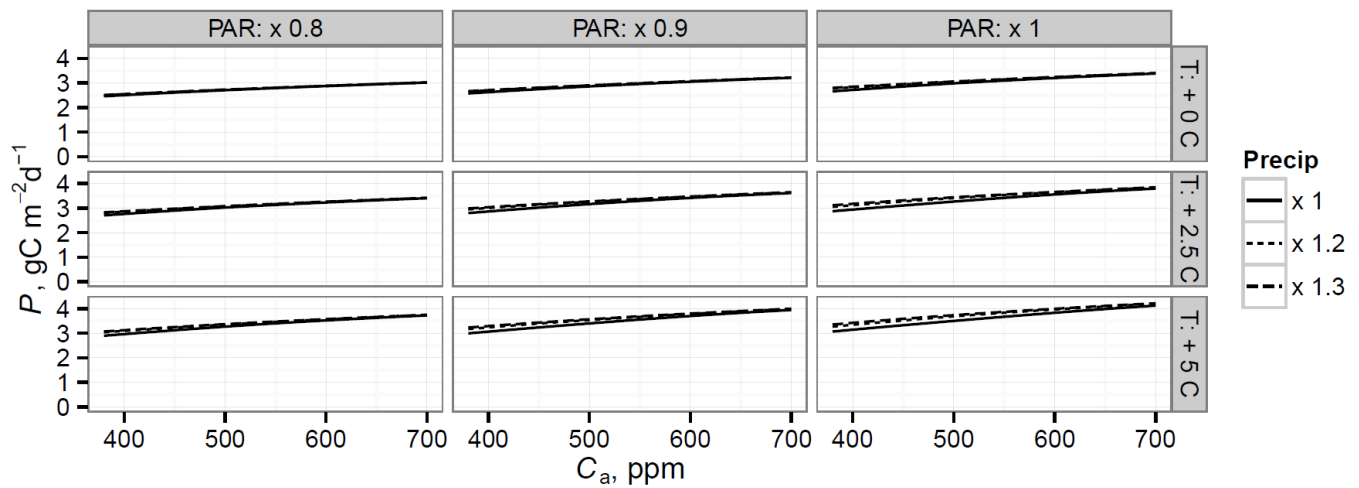
1069

1070 Figure SB.2 Change of model predicted daily E with increasing C_a and by D and f_{APAR} . The values of
 1071 D on the upper grey panel (0,5 – 1,5). In these simulations, the effect of T and seasonality term of the
 1072 model (S) was saturated, and soil moisture did not play role. PAR upon canopy was set to 30 mol/m².
 1073 Default model parameters (for Scots pine) were used.



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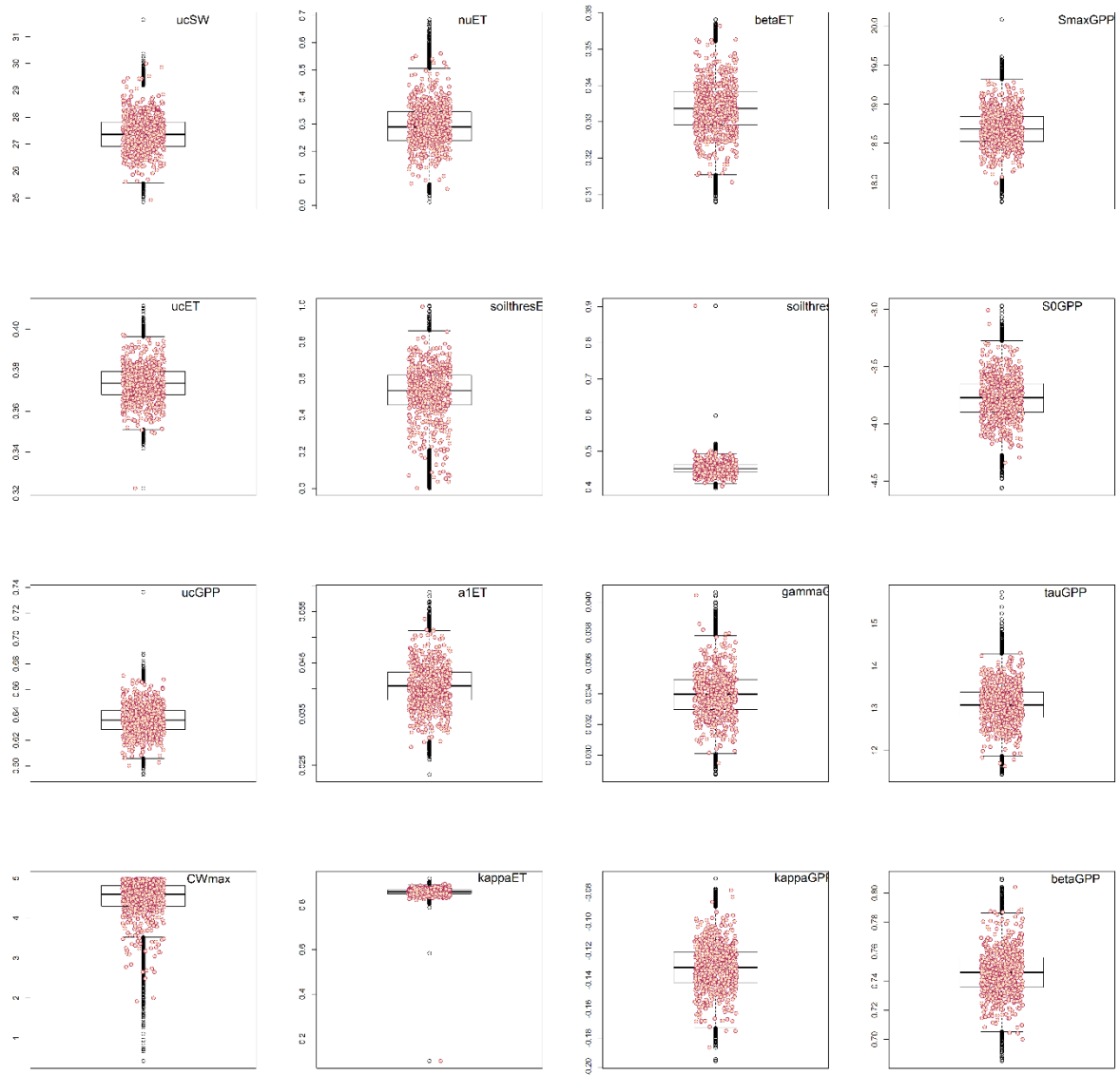
1075 Figure SB.3 Relative change of ecosystem WUE with relative change of C_a at different f_{APAR} . Dash
 1076 dot line is the 1:1 relationship. D was set to constant 0.5 kPa, air temperature to 20 C and PAR to 30
 1077 mol/m². WUE is sensitive to D : slope at $f_{APAR} = 1$ increases from 0.63 to 0.97 when daily average D
 1078 increases from 0 to 2 kPa.



1079

1080 Figure SB.4 Annual mean P (across simulation period of 10 years) in Hyytiälä. Default model
 1081 parameters (for Scots pine) were used.

1082



1083

1084 Figure SB.5 The boxplot of each parameter showing the total variation of posteriori. Red circles
 1085 indicate the parameter values sampled from the posteriori for the description of PRELES parametric
 1086 uncertainty in the simulations.

1087 **References**

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