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# 15 Mining ecophysiological responses of European beech ecosystems to 16 drought

## 17 Abstract

18 The most accurate understanding of forest functioning during drought is crucial to improve the forecast  
19 of future forest productivity. Here we investigate the ecophysiological responses (i.e. primary  
20 production, evapotranspiration and water use efficiency) of European beech to drought events with the  
21 ecosystem model MuSICA, using as benchmark the observed fluxes at the experimental forest Hesse  
22 (France). We show that MuSICA is able to realistically simulate observed drought-induced limitations.  
23 Subsequently we use simulation experiments to provide: (1) a quantification of the reduction of  
24 ecosystem fluxes during the 2003 drought, (2) a partitioning of heat stress and water limitations during  
25 droughts, (3) an analysis of the impact of specific drought trajectories, and (4) an evaluation of the  
26 potential impact of projected climate change on the studied forest and (5) over the beech distributional  
27 range. Our results show that the 2003 drought resulted in a 17% reduction of annual gross primary  
28 production and in a 21% reduction of evapotranspiration at Hesse. The studied forest ecosystem is  
29 mostly sensitive to negative precipitation anomalies (82% of the reduced forest productivity in 2003)  
30 and almost insensitive to heat stress due to high temperatures (16%). Moreover, we show that the  
31 ecosystem fluxes are limited more by fast drought onsets in the early growing season (June-July) than by  
32 onsets later in the season. Deciphering the impact of future climate change on beech productivity is  
33 complicated by large uncertainties in projected future precipitation and in the severity of extreme dry  
34 years. Drastic reduction of ecosystem fluxes is only predicted with climate projections that show marked  
35 reductions in precipitation. However, increased CO<sub>2</sub> fertilization in the future will counterbalance  
36 negative drought impacts. This modelling-based study improves our understanding of the functioning of

37 an emblematic European tree species during extreme events and informs on potential future forest  
38 responses to projected climate change.

## 39 Keywords

40 Drought; carbon flux; *Fagus sylvatica* L.; ecosystem model; MuSICA; projected climate change

## 41 1. Introduction

42 The frequency of extreme climate events, and especially of droughts, is supposed to increase with future  
43 climate change (Prudhomme et al. 2014; Zhao and Dai 2017). Central and Southern Europe in particular  
44 are regional hotspots where drought severity and frequency will increase the most (Prudhomme et al.  
45 2014). This implies that European forest ecosystems will face new and extreme conditions driving  
46 changes in species productivity and distribution (Lindner et al. 2010). Indeed, severe droughts are linked  
47 to significant reductions of forest productivity (Granier et al. 2007; Reichstein et al. 2007). Species-  
48 specific responses to drought should hence be analyzed thoroughly, in addition to possible interactions  
49 between the impact of drought and other projected changes (e.g. increased plant water use efficiency  
50 with elevated CO<sub>2</sub>; Battipaglia et al. 2013).

51 Among the emblematic European tree species, European beech (*Fagus sylvatica* L.) may be severely  
52 impacted by drought during the growing season, resulting in xylem embolism and reduced productivity  
53 (Gessler et al. 2007). Beech has already experienced locally increased growth limitations over the 20<sup>th</sup>  
54 century due to drought, which has reduced tree competitiveness in relation to other species  
55 (Scharnweber et al. 2011). This loss of competitiveness is especially evident at the southern edge of the  
56 species distributional range (Peñuelas et al. 2007). A process-based assessment of the ecophysiological  
57 responses of European beech to drought would allow an analysis of the species vulnerability to climate

58 change and would potentially improve future projections of beech growth performance over its  
59 distributional range.

60 Such process-based assessment could be performed with ecophysiological models. These models can  
61 play an important role in investigations and forecasts of drought impacts on forests because they ensure  
62 a coupled representation of the processes behind carbon and water fluxes (Bonan and Doney 2018;  
63 Ogée et al. 2003). The selected models should guarantee plausible simulations also at the margin or  
64 outside of their calibration environment. Indeed, plausible extrapolations beyond the observed  
65 boundary conditions are crucial to accurately predict future ecosystem functioning and carbon budget  
66 during extreme events, such as future droughts (Clark et al. 2011).

67 Some studies have already quantified the impact of drought on ecosystem productivity globally (Zhao  
68 and Running 2010), on specific regions (Ciais et al. 2005), or on specific forest ecosystems (Reichstein et  
69 al. 2007). However, droughts are the result of two components: an increase in temperature-induced  
70 plant stress (e.g. effects of temperature on vapor pressure deficit, or the effects on carboxylation rate)  
71 and a decrease in water availability driven by low precipitation (Zhao and Dai 2017). The partitioning of  
72 heat stress and water limitations during drought events for specific ecosystems is still to be further  
73 analyzed. Moreover, each drought has its own climate trigger and its timing of occurrence during the  
74 year (Mo 2011), potentially inducing a very specific impact on forests. For example, fast drought onsets  
75 in spring followed by average summer conditions can have different impacts on annual ecosystem  
76 performance than lesser but constant reduction in water availability during the whole growing season.  
77 Impacts due to different drought trajectories should also be better analyzed. Here we focus on the  
78 ecophysiological responses (i.e. forest water and carbon fluxes, and ecosystem water use efficiency) of  
79 European beech forests using simulation experiments. First, we ensure that the used ecosystem model  
80 (MuSICA; Ogée et al. 2003) is able to realistically simulate drought-induced flux reductions at an  
81 experimental site, even for much drier periods than used during model calibration. Second, we re-

82 compute the local impact of the 2003 drought on ecosystem fluxes using a novel simulation-based  
83 approach. Third, we quantify the partitioning of heat stress and water limitations during drought.  
84 Fourth, we investigate the impact of different drought trajectories. Fifth, we evaluate the potential  
85 impact of projected climate change on the productivity and water use of beech forests locally and, sixth,  
86 evaluate the potential impact over the entire species distributional range in Europe.

## 87 2. Materials and Methods

### 88 *2.1. The Hesse forest experimental station*

89 We used the data of the Hesse forest experimental station (Granier et al. 2008) to optimize the MuSICA  
90 ecosystem model for beech forests. The Hesse site (+48.7° latitude, +7.1° longitude, 300 m elevation) is  
91 a European beech forest located in north-eastern France (Moselle) in the center of the species  
92 distributional range. Hesse belongs to the ICOS infrastructure ([www.icos-ri.eu](http://www.icos-ri.eu)) and there are 20 years of  
93 ecosystem fluxes and ecophysiological measurements available at the site. Hesse is a drought-sensitive  
94 ecosystem and extreme dry years, such as 2003, produce significant anomalies on the observed carbon  
95 dynamics (Granier et al. 2007). We used measured ecophysiological traits for the initialization of the  
96 model parameters (Dufrêne et al. 2005) and soil water content at three soil depths (SWC; 0.1, 0.3 and  
97 0.55 m), carbon fluxes (net ecosystem exchange - NEE; and gross primary production - GPP; NEE was  
98 partitioned into GPP and ecosystem respiration using the night-time approach of Reichstein et al. 2005)  
99 and evapotranspiration (ET) for further parameter optimization and validation.

### 100 *2.2. The MuSICA ecosystem model*

101 MuSICA is a mechanistic ecosystem model primarily developed to simulate water, carbon and energy  
102 exchanges over the soil-vegetation-atmosphere continuum (Domec et al. 2012; Giuggiola et al. 2016;  
103 Klein et al. 2014; Ogée et al. 2003; Ogée et al. 2004; Wingate et al. 2010). MuSICA discretizes the  
104 ecosystem in several air and soil layers. In this project, we used 15 layers in the soil and 10 layers in the

105 vegetation. Carbon fluxes depend on the coupling between photosynthesis (Farquhar et al. 1980) and  
106 stomatal conductance (Leuning 1995), as well as on the simulation of respiration, leaf light interception  
107 (Sinoquet et al. 1990), convection and turbulent transport (Raupach 1989) in each air layer. Soil water  
108 fluxes are a mixture of preferential and matrix flows, the latter ones being described by Richards'  
109 equations (Braud et al. 1995).

### 110 *2.3. Model calibration and validation*

111 MuSICA was optimized using as target half-hourly SWC, NEE and ET measurements of the year 2002,  
112 which had normal climate conditions. ET observations were corrected to ensure energy balance closure  
113 as proposed by Mauder et al. (2013). All MuSICA parameters were initialized according to our best  
114 knowledge of the ecophysiological traits of the Hesse experimental forest. Subsequently, we used  
115 Morris parameter screening (Morris 1991) to quantify the sensitivities of the target variables to the  
116 individual model parameters of MuSICA (Cuntz et al. 2015). The Morris parameter screening analyses  
117 the variations of the target variables with respect to variations in the model parameters (Saltelli et al.  
118 2004). The identified sensitive parameters were further optimized using a differential evolution  
119 algorithm (Abbass et al. 2001; Mier 2017). Finally, the 2003 dry year was used to verify that MuSICA  
120 realistically simulates drought-induced ecosystem limitations as well as daily variations of observed  
121 water-related variables during extreme dry periods. This calibration/validation scheme was specifically  
122 designed because drought severity is supposed to increase with future climate change and, therefore,  
123 plausible model extrapolations are crucial.

### 124 *2.4. Local simulation experiments*

125 Once MuSICA was optimized for Hesse, we performed several local simulations modifying the 2003  
126 temperature and precipitation input data. These simulations were grouped in four experiments (Table  
127 1). Experiment 1 quantifies the reduction of fluxes during the 2003 drought. Experiment 2 provides  
128 partitioning of heat stress and water limitations during drought. Experiment 3 studies the impact of

129 alternative drought trajectories having the same severity than the 2003 drought but different timing of  
130 occurrence over the growing season (i.e. faster or slower drought onset). Experiment 4 analyzes the  
131 impact of future climate change on the studied forest. All simulations use the 2003 half-hourly variability  
132 to avoid potential impacts of different structures of rainy/dry, warm/cold, sunny/cloudy days. Only the  
133 monthly temperature and precipitation mean values were modified and were specific to each  
134 simulation:

$$135 \quad T_{new_{i,y}} = T_{ref_i} + \Delta_{i,y} \quad (1)$$

$$136 \quad P_{new_{i,y}} = P_{ref_i} \cdot \lambda_{i,y} \quad (2)$$

137 where  $T_{new_{i,y}}$  ( $P_{new_{i,y}}$ ) is the new temperature (precipitation) mean value of the month  $i$  and the  
138 simulation  $y$ ,  $T_{ref_i}$  ( $P_{ref_i}$ ) is the reference temperature (precipitation) mean value of the month  $i$  of  
139 the median observed climate at Hesse (1997-2013),  $\Delta_{i,y}$  is the climate anomaly of temperature for the  
140 specific simulation  $y$ , and  $\lambda_{i,y}$  is the climate anomaly factor of precipitation for simulation  $y$ . Specific  
141 simulations and their climate anomalies are detailed in Table 1. Each simulation was preceded by a one  
142 year spin-up period, which was subsequently discarded from following analyses, where MuSICA was  
143 forced by the meteorology of an average year.

144 The impact of future climate change in experiment 4 was analyzed using an ensemble of six EURO-  
145 CORDEX simulations forced by an RCP8.5 (Table 2; Jacob et al. 2014; data downloaded from the Pierre  
146 Simon Laplace Institute node of the Earth System Grid Federation). This extreme RCP was selected to  
147 emphasize the potential impact of climate change on forest ecophysiology and analyze forest responses  
148 under extreme climate conditions. Furthermore, the role of increased CO<sub>2</sub> concentration in the future  
149 was isolated by the production of MuSICA simulations at Hesse with both current and future CO<sub>2</sub> values.  
150 Indeed, a 2.17-time increase in CO<sub>2</sub> concentration is forecast at the 2080-2100 horizon in RCP8.5  
151 scenarios. The annual ecosystem fluxes ( $F$ ) of the obtained MuSICA simulations  $y$  were compared



152 between each other by percent change (*PC*) computations relative to the fluxes of the reference  
153 simulation (median climate):

$$154 \quad PC = \frac{F_y - F_{Ref}}{F_{Ref}} 100 (\%) \quad (3)$$

### 155 *2.5. Regional simulation experiments*

156 Experiment 4 described in the previous section was extended to analyze the potential impact of  
157 projected climate change on European beech ecophysiology over the entire species distributional range  
158 as defined by Caudullo et al. (2017). The MuSICA temperature and precipitation input data were  
159 modified using the same EURO-CORDEX simulations (Table 2; all EURO-CORDEX data were extracted  
160 over a regular 0.5° grid) and the same equations described earlier (Eq. 1 and 2). This climate forcing was  
161 used to simulate European beech GPP and ET during extreme dry years at two time horizons (2006-2026  
162 and 2080-2100; an extreme year was defined with median monthly temperature and precipitation of six  
163 extreme dry years, one per simulation). We also took into account the impact of spatially different soil  
164 properties. We used USDA soil classification and soil texture data available at "soilgrids.org" to estimate  
165 MuSICA soil parameters, such as van Genuchten water retention parameters and saturated hydraulic  
166 conductivity, using the Rosetta computer program (Schaap et al. 2001).

## 167 **3. Results**

### 168 *3.1. Validation of MuSICA simulations during dry periods*

169 MuSICA accurately simulates daily variation of GPP, ET and SWC at the Hesse European beech forest  
170 (Figs. 1 and S1-S2). The typical annual cycle of drying and rewetting of the soil profile is well caught by  
171 the model (Fig. 1, red and blue points). Furthermore, MuSICA simulations show similar performance  
172 over both, the 2002 calibration year and the 2003 validation year (Fig. 1), the latter was characterized by  
173 reduced precipitation and a severe 4-month drought starting in June and ending in late September (Fig.

174 S3). Finally, observed drought-induced ecosystem limitations are well simulated, such as the limitation  
175 of evapotranspiration by soil water availability (Fig. 2). At Hesse, ecosystem fluxes begin to be limited by  
176 water availability once soil water in the top 70 cm drops below about 250 kg/m<sup>3</sup>, corresponding to  
177 values of relative extractable soil water (REW) lower than 0.3.

### 178 *3.2. Mining forest responses to drought with simulation experiments*

179 The first simulation experiment allowed a precise quantification of the reduction of ecosystem fluxes at  
180 Hesse during the 2003 drought. Comparison of the simulation with a median climate but diurnal  
181 variations of 2003 (2003\_median\_climate, red) and the full 2003 dry climate (2003, black) in Figure 3  
182 shows that there is a reduction of cumulated annual GPP by 17% and a reduction in total ET by 21% at  
183 Hesse due to higher temperatures and less precipitation. This suggests that such an important drought  
184 had only a slight impact on water use efficiency (evapotranspiration decreased slightly more than  
185 productivity). Interestingly, the divergence between the two simulations started only 1.5 months after  
186 the beginning of the 2003 heatwave in early June (Fig. S3). This is the time needed to dry out the soil  
187 profile to the threshold of about 250 kg/m<sup>3</sup> in the top 70 cm, or REW = 0.3, when plants start  
188 experiencing water stress (Fig. 2).

189 The second experiment allowed the partitioning of heat stress and water limitations at Hesse during  
190 drought. Comparing the simulation with a median climate but diurnal variations of 2003  
191 (2003\_median\_climate, red), the simulation with median climate and the 2003 temperature anomalies  
192 only (2003\_T\_limited, blue), the simulation with median climate and the 2003 precipitation anomalies  
193 only (2003\_P\_limited, green), and the simulation with full 2003 dry climate (2003, black) in Figure 3, we  
194 can observe that water limitations caused by low precipitations are responsible for most of the observed  
195 reductions in GPP and ET. Heat stress due to high temperature is instead very low for GPP and negligible  
196 for ET.

197 Subsequently, we show that droughts with same severity but diverse trajectories (i.e. timing of drought  
198 onset and recovery over the growing season) have different impacts on the ecosystem (Experiment 3;  
199 Table 1 and Fig. 4). The beech forest in Hesse shows very similar annual sums of GPP and ET if there is  
200 still some precipitation in June-July, which was the case in 2003 and is the case in the slow-onset  
201 scenario (black and purple lines). However, the forest is sensitive to fast drought onset. If there is a  
202 different precipitation timing with almost no precipitation in June-July, SWC decreases earlier than in  
203 2003, leading to a longer drought-limited period, which cannot be compensated during drought release  
204 later in the year (orange line). Note that all simulations in Fig. 4 have the same precipitation amount  
205 over the growing season (Table 1).

206 Our fourth experiments allowed an evaluation of the impact of projected climate change at the studied  
207 forest. Fig. 5 shows the expected changes between present and future forest performance over median  
208 climatological years (*Median\_futur vs. 2003\_median\_climate*; dark blue) and extreme dry years  
209 (*Xtreme\_futur vs. Xtreme\_today*; light blue). The same figure also allows the comparison of the expected  
210 impact of future extreme dry years (*Xtreme\_futur vs. 2003\_median\_climate*; green) and of present  
211 extreme dry years (*Xtreme\_today vs. 2003\_median\_climate*; red) relative to present median conditions.  
212 All CORDEX simulations used in Fig. 5 agree in projecting an important increase in temperature over the  
213 growing season (median increase of +3.0 °C; Fig. S4). Conversely, there is a large spread in the  
214 magnitude and sign of the precipitation change (Fig. 5; dark and light blue), which is the most influential  
215 parameter modifying ecosystem fluxes in MuSICA at Hesse. MuSICA, forced by these climate inputs and  
216 by stable, current CO<sub>2</sub> concentrations, projects only slight changes in GPP and ET during a median year  
217 (Fig. 5, dark blue) and an extreme year (Fig. 5, light blue) of 2080-2100. Although EURO-CORDEX climate  
218 simulations show hotter and drier extreme years in the future than today (Fig. 5, green and red), the  
219 reduction of the ecosystem fluxes relative to present median conditions remains very similar. Indeed,  
220 the simulated climate of extreme dry years in EURO-CORDEX is less severe than the observed extreme

221 year 2003, so that the soil water threshold of 250 kg/m<sup>3</sup> in the top 70 cm, or REW = 0.3, is rarely reached  
222 in the MuSICA simulations. The picture changes drastically if we include the future increase in CO<sub>2</sub>  
223 concentration projected by RCP8.5 simulations at the 2080-2100 horizon (2.17 current CO<sub>2</sub>). Over a  
224 median year (Fig. 5, dark blue), GPP increases by 36% in this case, ET decreases by 17%, leading to very  
225 high water use efficiency (+64%). We computed that a 1.22-time increase in CO<sub>2</sub> concentration (+89  
226 ppm) would be enough to counterbalance future negative drought impacts on carbon fluxes (i.e. the  
227 green horizontal bar in the fourth column of Fig. 5, showing the percent change in GPP with increased  
228 atmospheric CO<sub>2</sub>, which would then be located at the zero line).

229 We also compared the performance of potential European beech forests under current and future  
230 extreme dry years over the entire species distributional range (Fig. 6). The results show that the species  
231 is potentially vulnerable to climate change at its southern and western range, where projected  
232 precipitation changes are large (Fig. S4). European beech forests in the Alps and in the north-eastern  
233 part of the distribution range are insensitive to temperature and precipitation changes (Fig. 6, top row).  
234 Indeed, water availability over the growing season is not a limiting factor for European beech in the Alps,  
235 while CORDEX simulations project a precipitation increase in the north-eastern part of the species range  
236 (Fig. S4). As it was the case for the Hesse forest, beech productivity is highly enhanced (the first and the  
237 third quartiles of the GPP change are +40 and +55 %, respectively) if we include in our simulations the  
238 increase of future CO<sub>2</sub> concentrations, with a clear southwest-northeast gradient of increased forest  
239 productivity due to projected precipitation changes (Fig. 6, bottom row).

## 240 4. Discussion

241 Drought frequency over the 21<sup>st</sup> century will increase by more than 20% in Central and Southern Europe  
242 and the dynamic response of vegetation to these droughts is highly uncertain (Prudhomme et al. 2014).  
243 We thus need ecophysiological models able to capture key forest processes and to provide plausible

244 extrapolations over severe dry periods in order to assess the impact of increased drought frequency on  
245 forest functioning and carbon budgets (Clark et al. 2011; Williams et al. 2018). In our case, we used the  
246 MuSICA ecosystem model (Ogée et al. 2003) to analyze the ecophysiological responses of European  
247 beech to drought events. The model showed high skills in reproducing key variables and drought-  
248 induced ecosystem limitations over an independent verification year with severe drought (year 2003;  
249 Figs. 1-2). MuSICA thus seems an appropriate tool to extrapolate the ecosystem responses to future  
250 droughts.

251 Our work refines the results of previous studies and points out important forest processes and  
252 dynamical responses in a climate change context. Previous studies quantified a reduction of ecosystem  
253 fluxes (GPP and ET) of more than 30% at the Hesse beech forest in 2003 (Granier et al. 2007; Reichstein  
254 et al. 2007). Our results give instead a much more conservative estimate (-17% for GPP and -21% for  
255 ET). Previous studies used the preceding 2002 year as reference for their quantifications. We rather  
256 used a novel anomaly-based approach, attenuating the impact of specific years and of different climate  
257 structures such as of wet/dry, warm/cold, or sunny/cloudy days between the dry year 2003 and the  
258 reference.

259 We confirm here the key role of water limitations for reduced forest productivity during the 2003  
260 drought (Granier et al. 2007; Reichstein et al. 2007). Furthermore, we are able to disentangle the  
261 partitioning between heat stress and water limitations during drought. The results represented in Figure  
262 3 estimate that 82% of the reduced forest productivity in 2003 can be attributed directly to low  
263 precipitation. Only 16% of the reduced forest productivity comes from heat stress in the model, while  
264 only 2% comes from combined effect of heat stress and water limitations. This low impact of  
265 temperature is surprising because high temperatures influence plant biochemistry and increase vapor  
266 pressure deficit, dampening stomatal conductance and enhancing soil water evaporation. Granier et al.  
267 (2000) measured a difference of about 23% between ecosystem evapotranspiration and stand

268 transpiration at Hesse. They concluded that this difference could at least partly be due to soil  
269 evaporation. They argued, though, that measurement uncertainties in both, ecosystem  
270 evapotranspiration and stand transpiration, are so large that they cannot be proven to be significantly  
271 different. This led Betsch et al. (2011) to neglect soil evaporation in their analysis of drought effects on  
272 the Hesse beech forest. However, high temperatures should also affect plant biochemistry. Optimum  
273 temperatures for biochemical reactions, such a carboxylation, were found to be above 35 °C for *Fagus*  
274 *sylvatica* (Kattge and Knorr 2007), which are rarely reached in Hesse. However, maximum daily  
275 temperatures of the sunlit leaves increased from 39 (August 1<sup>st</sup>) to 48 °C (August 8<sup>th</sup>) during the hottest  
276 spell of summer 2003, inducing a progressive and almost complete cessation of photosynthesis and  
277 transpiration, especially in the upper canopy layer (Fig. S5). Such high temperatures have the potential  
278 to damage sun-exposed leaves (e.g. burned epidermis). Although these carry-over effects of heat stress  
279 are not accounted for in the model, the rather good agreement of MuSICA with ecosystem-scale water  
280 and CO<sub>2</sub> flux observations during and after the 2003 heat wave, indicates that these effects have only a  
281 minor influence at the ecosystem scale and that water limitations remain crucial.

282 An important point of our study is the demonstration that rain seasonality matters, i.e. specific drought  
283 trajectories over the growing season can potentially drive different impacts to ecosystem fluxes.  
284 European beech forests are more sensitive to fast drought onset in the early growing season (Fig. 4)  
285 because the soil profile dries out earlier, leading to water limitations during times of highest incoming  
286 radiation and hence highest ecosystem fluxes. This result is similar to what D'Orangeville et al. (2018)  
287 found for eastern North American forests using tree-ring data but partially contrasts with the findings of  
288 Granier et al. (2007) and Arend et al. (2016) pointing out that rainfall events during drought can rapidly  
289 restore ecosystem fluxes. Although fluxes increase after rainfall in the fast onset scenario, they cannot  
290 close the overall gap with the fluxes of alternative drought trajectories having the same severity but  
291 slower onset (i.e. the actual 2003 drought trajectory and the experiment 2003\_slow\_onset). For this

292 reason, a more in-depth analysis of the projected changes in drought seasonality should be sought (see  
293 Mo 2011). For example, do we have any indication that crucial months for beech forest productivity,  
294 such as June, are becoming drier relative to other months? How much precipitation deficit is needed  
295 during these crucial months to significantly reduce ecosystem fluxes and how long does it take to the  
296 soil profile to dry (e.g. 1.5 months in 2003 at Hesse; Fig. 3)? Such drought analysis should not be  
297 performed with simplistic drought indices, which respond mainly to temperature changes and result in  
298 biased interpretations (e.g. Thornwaite equation for potential ET; see Sheffield et al. 2012).

299 Our comparison of the impact of current and future extreme dry years on European beech forests  
300 reveals important key findings. First, the large uncertainties in the future trends of precipitation limit the  
301 predictability of forest responses at specific sites and at European scale (see Fig. 5). This known issue  
302 cannot fully be resolved due to the impact of high internal climate variability on precipitation (Knutti and  
303 Sedláček 2013). Furthermore, we confirmed that caution should be paid when using climate model  
304 simulations to analyze extreme years (see Asadih and Krakauer 2015); climate models are constructed  
305 to simulate climate and hence dampen interannual variations of meteorology. Observed severe  
306 droughts at specific sites are more extreme than those simulated at the corresponding grid cells (see red  
307 and black dots in Fig. 5). Consequently, drastic reductions of ecosystem fluxes at the Hesse forest (a  
308 humid site only sensitive to extreme dry years) are only projected for those simulations with lower  
309 precipitation amounts at the 2080-2100 horizon compared to today (Fig. 5; see points surrounded by  
310 circles). This is consistent with the important role of critical thresholds in relative extractable water  
311 determining forest responses to drought (Granier et al. 2007). These thresholds are clearly reached  
312 more often over the southern and the western part of the beech distributional range (Fig. 6), where the  
313 species has already shown its vulnerability to climate change (Hacket-Pain et al. 2016; Peñuelas et al.  
314 2007). Although our analysis of the potential impact of future droughts on beech forests relies on  
315 MuSICA's performance for Hesse, drought response traits of beech trees only show small differences

316 according to tree provenance (Aranda et al. 2014). In all cases, increased CO<sub>2</sub> fertilization in the future  
317 (+2.17-time increase of CO<sub>2</sub> concentrations in the RCP8.5 scenarios at the 2080-2100 horizon) will  
318 compensate negative drought impacts (Fig. 6). This response is consistent with retrospective studies  
319 based on tree-ring  $\delta^{13}\text{C}$  data, which show important increases in water use efficiency of beech trees over  
320 the past century (up to 44%; Duquesnay et al. 1998). This response is also consistent with the increased  
321 productivity of European forests projected by other modelling studies over the next century (Davi et al.  
322 2006; Gea-Izquierdo et al. 2017). However, controlled experiments under a CO<sub>2</sub>-enriched atmosphere  
323 seem to show a more moderate CO<sub>2</sub> fertilization effect with almost no changes in productivity (Bader et  
324 al. 2013). The effects of nutrient limitations should hence be included in future studies (see Luo et al.  
325 2004; Norby et al. 2010).

## 326 5. Conclusion

327 In this study, we used the MuSICA ecosystem model (Ogée et al. 2003) to analyze the potential impact  
328 of present and future droughts on fluxes and processes of European beech forests. Using MuSICA, we  
329 were able to simulate realistic carbon and water fluxes at the leaf- and soil-level, and to quantify  
330 precisely the impact of drought. Severe droughts may reduce European beech GPP and ET annual fluxes  
331 by 20%. We demonstrated that low precipitation limits beech forest productivity much more than heat  
332 stress. Beech forest ecosystems are also sensitive to the timing of drought onset over the growing  
333 season. Finally, our results show a good adaptation of European beech ecosystems to projected climate  
334 change because increased CO<sub>2</sub> concentration in the future will enhance plant water use efficiency  
335 counterbalancing negative drought impacts. However, large uncertainties exist as simulated trends in  
336 ecosystem fluxes depend mainly on projected trends and anomalies of precipitation, which are both  
337 largely uncertain in climate model projections. This study represents a step forward to a more complete  
338 ecophysiological understanding of the potential impact of drought on the productivity and seasonal



339 dynamics of European beech forests, which should be enhanced in the future by the inclusion of  
340 additional processes such as nitrogen limitations, legacy/carry-over effects after extreme events, or  
341 growing season and phenological changes.

342

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352

## 353 Competing interests

354 Declarations of interest: none.

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488 *Table 1. Local MuSICA simulations at Hesse used in the four experiments.*

Experiments*	Simulation name	Monthly temperature	Monthly precipitation	Daily/hourly variability	Temperature/precipitation annual anomalies
1, 2, 3	2003	2003	2003	2003	2003
1, 2	2003_median_climate	Median climate (1997-2013)	Median climate (1997-2013)	2003	Median climate
2	2003_only_P_limited	Median climate (1997-2013)	2003	2003	Median climate/2003
2	2003_only_T_limited	2003	Median climate (1997-2013)	2003	2003/Median climate
3	2003_fast_onset	Anomalies added to June-September: +2, +1, -1, -2 (°C)	Anomalies of June-September: 10%, 20%, 30%, 40% of total precipitation over the period	2003	2003
3	2003_slow_onset	Anomalies added to June-September: -2, -1, +1, +2 (°C)	Anomalies of June-September: 40%, 30%, 20%, 10% of total precipitation over the period	2003	2003
4	Xtreme_today	Modified by deltas relative to extreme dry years in CORDEX simulations at the 2006-2026 horizon	Modified by change factors relative to extreme dry years in CORDEX simulations at the 2006-2026 horizon	2003	Extreme simulated years at the 2006-2026 horizon
4	Median_futur	Modified by deltas relative to median years in CORDEX simulations at the 2080-2100 horizon	Modified by change factors relative to median years in CORDEX simulations at the 2080-2100 horizon	2003	Median simulated years at the 2080-2100 horizon
4	Xtreme_futur	Modified by deltas relative to extreme dry years in CORDEX simulations at the 2080-2100 horizon	Modified by change factors relative to extreme dry years in CORDEX simulations at the 2080-2100 horizon	2003	Extreme simulated years at the 2080-2100 horizon

\* Experiments are defined in the section "Local simulation experiments". The same simulation can be used in more than one experiment.

489

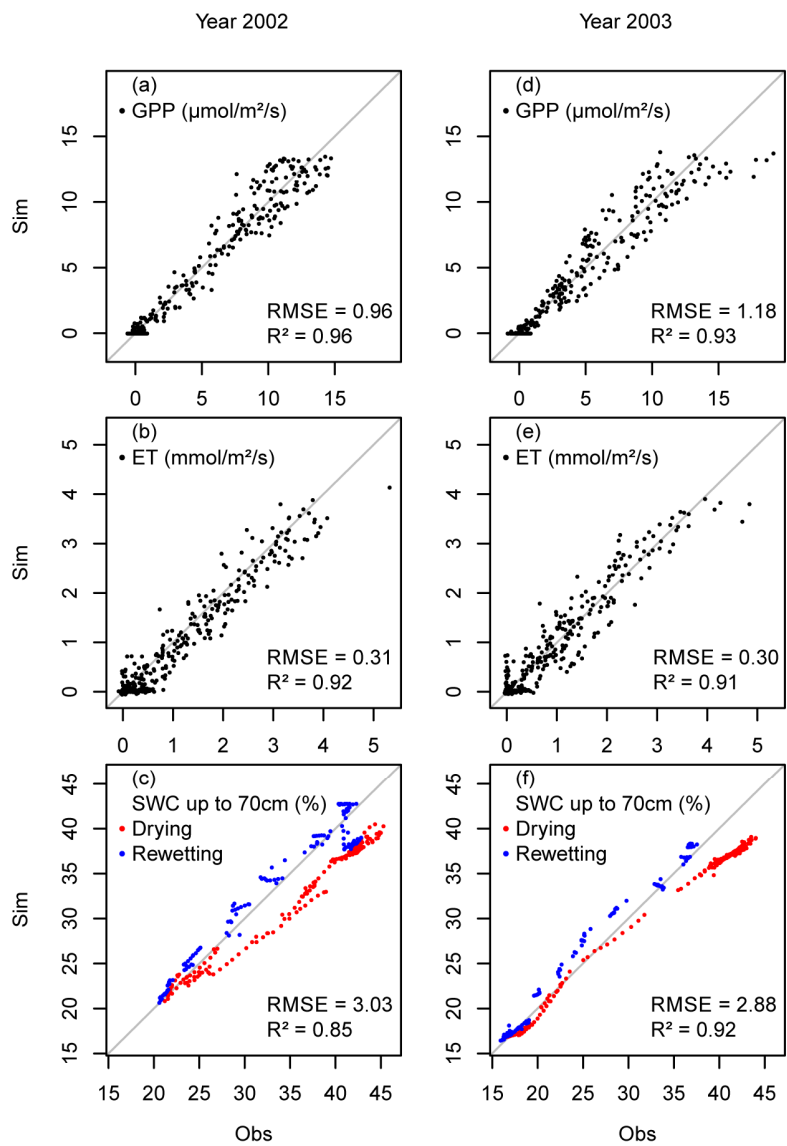
490 *Table 2. EURO-CORDEX RCP8.5 simulations used to define the projected climate change.*

Regional climate model	Driving global climate model	Member
ALADIN53	CNRM-CERFACS-CNRM-CM5	r1i1p1
RCA4	ICHEC-EC-EARTH	r12i1p1
WRF331F	IPSL-IPSL-CM5A-MR	r1i1p1
CCLM4-8-17	MOHC-HadGEM2-ES	r1i1p1
REMO2009	MPI-M-MPI-ESM-LR	r1i1p1
REMO2015	NCC-NorESM1-M	r1i1p1



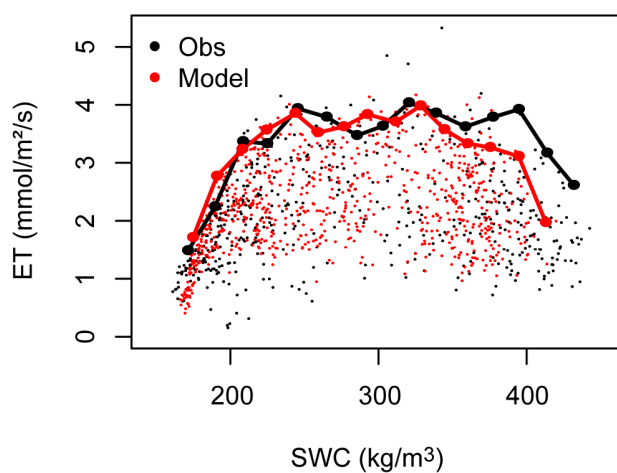
491 **Figures**

492 Figure 1. Simulated versus observed daily values of water-related variables and forest productivity at  
493 Hesse during the 2002 calibration year and the 2003 dry validation year. From top to bottom: gross  
494 primary productivity, evapotranspiration, soil water content in the top 70 cm. For soil water content, red  
495 (blue) points correspond to daily values before (after) August 15, which is in the middle of the yearly dry  
496 period at Hesse. Grey lines are the one-to-one lines.



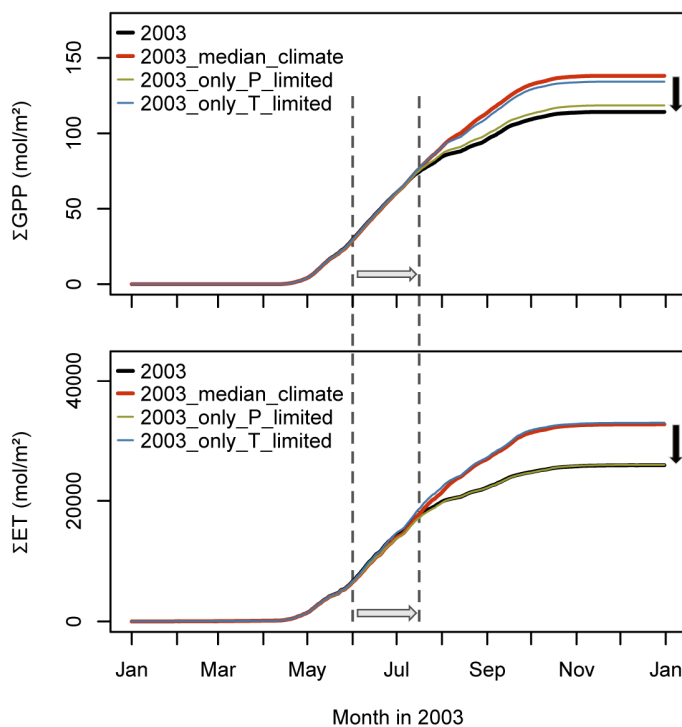
497

498 Figure 2. Impact of soil water availability on evapotranspiration (2001-2008): daily mean observed  
499 (black) and simulated (red) evapotranspiration versus soil water content in the top 70 cm for May to  
500 September. The upper envelope lines with larger circles show the 95<sup>th</sup> percentiles of the  
501 evapotranspiration data divided in 15 equally spaced bins of soil water content. Only sunny days with  
502 mean daily net radiation greater than 100 W/m<sup>2</sup> were considered.



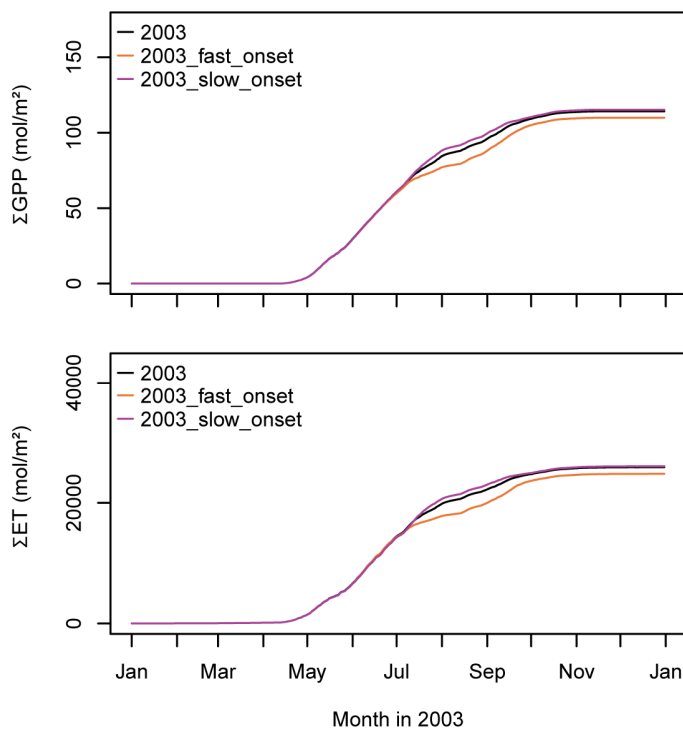
503

504 Figure 3. Quantification of the reduction of gross primary production and evapotranspiration due to  
 505 heat stress, water limitations and combined effects during the 2003 drought. Lines are cumulative sums  
 506 of daily gross primary productivity and evapotranspiration in 2003, simulated with the full 2003 dry  
 507 climate (2003, black), simulated with a median climate but diurnal variations of 2003  
 508 (2003\_median\_climate, red), simulated with median climate and the 2003 precipitation anomalies only  
 509 (2003\_P\_limited, green), simulated with median climate and the 2003 temperature anomalies only  
 510 (2003\_T\_limited, blue). Horizontal grey arrows show the time lapse between the start of the drought  
 511 and the divergence among simulations. Vertical black arrows indicate the 2003 reductions of fluxes  
 512 between simulations with a median climate and the full 2003 dry climate.



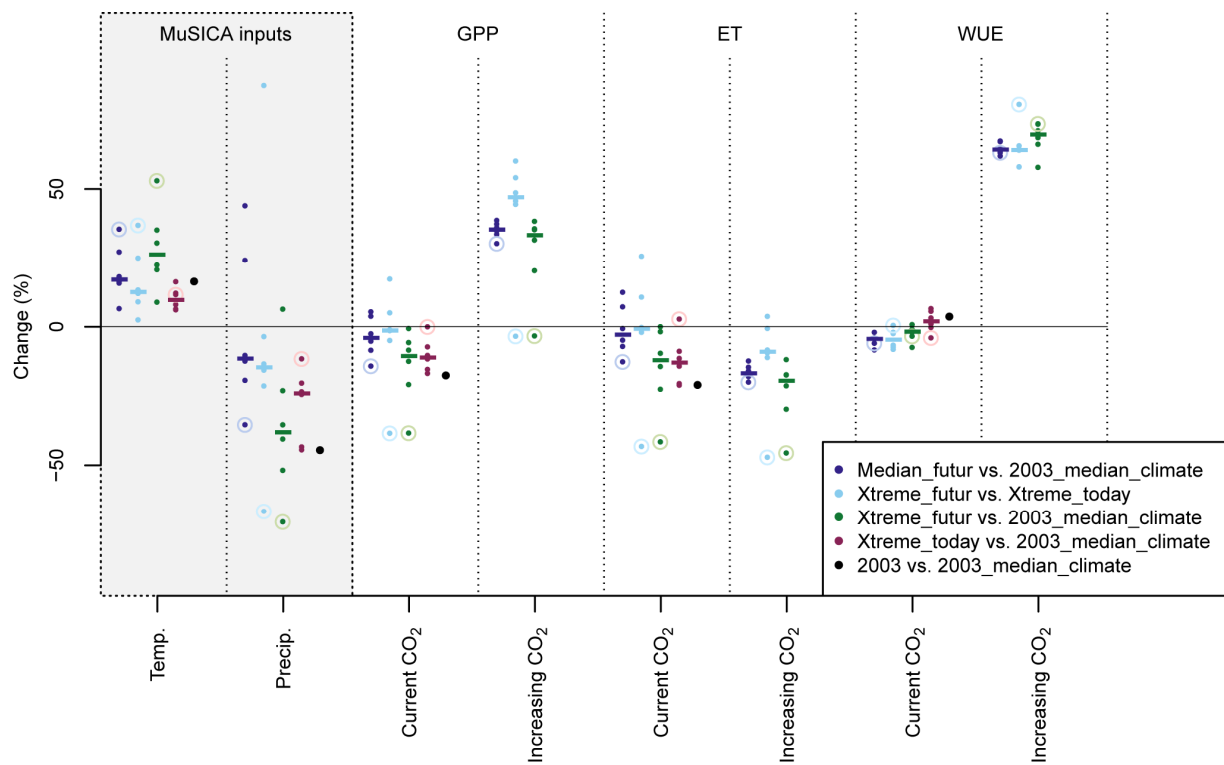
513

514 Figure 4. Quantification of the impact of different hypothetical drought trajectories. Lines are cumulative  
515 sums of daily gross primary productivity and evapotranspiration in 2003, simulated with the full 2003  
516 dry climate (2003, black) and with modified versions of the 2003 climate. In the simulations  
517 "2003\_fast\_onset" and "2003\_slow\_onset", the 2003 temperature and precipitation values were  
518 modified to have a faster or slower drought onset but same overall anomalies over the growing season  
519 (see Table 1).



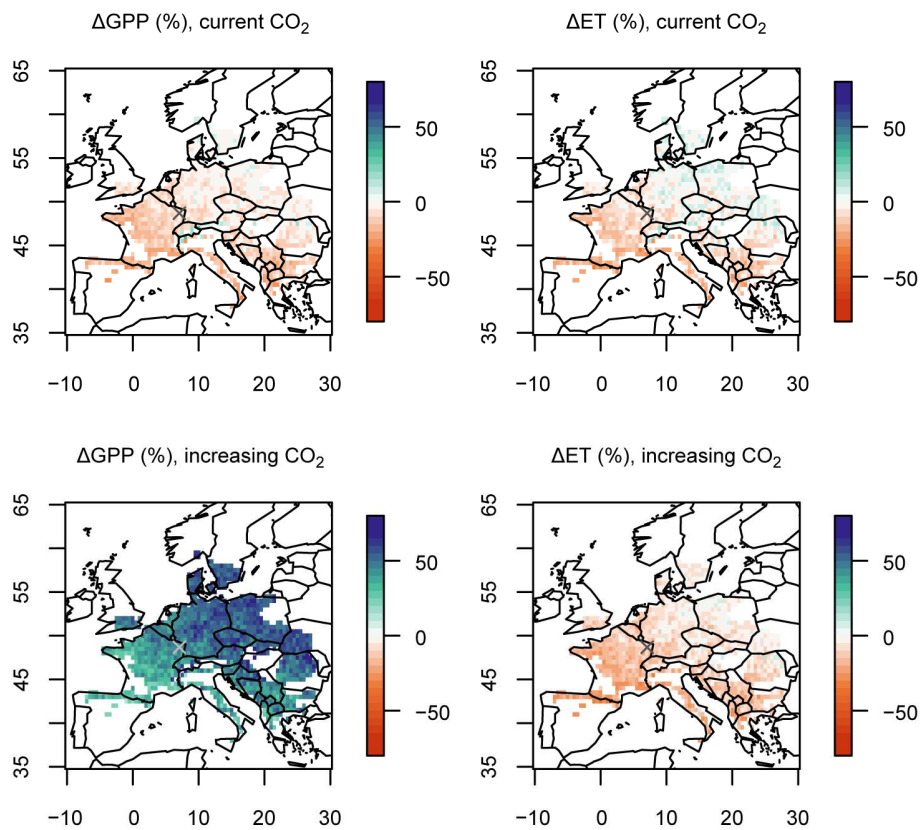
520

521 Figure 5. Comparison of annual gross primary productivity, evapotranspiration and water use efficiency  
 522 (net assimilation divided by transpiration) at the Hesse beech forest under current and future (2080-  
 523 2100) climate from six EURO-CORDEX simulations; future MuSICA simulations use either current  
 524 atmospheric CO<sub>2</sub> levels or projected, increased atmospheric CO<sub>2</sub> concentrations (2.17-time increase).  
 525 Each point represents the percent change (Eq. 3) of MuSICA input climate (May-September mean  
 526 temperature and precipitation) from Regional Climate Models (Table 2) and of MuSICA simulated fluxes.  
 527 The points for the simulation with driest projected climate are surrounded by circles. Horizontal bars  
 528 represent the median of the six simulations. The specific MuSICA simulations are given in Table 1.  
 529 *Xtreme\_future vs. 2003\_median\_climate*, for example, means the percent change in the annual sum if  
 530 MuSICA is driven by the most extreme year of specific CORDEX simulations over 2080-2100 compared to  
 531 MuSICA driven by the median climate of 1997-2013. Black dots, showing the estimated impact of the  
 532 observed 2003 drought at Hesse, are given for comparison.



533

534 Figure 6. Comparison of gross primary productivity and evapotranspiration of potential European beech  
 535 forests under current and future (2080-2100) extreme dry years over the species distributional range.  
 536 Forcing temperature and precipitation used to drive MuSICA simulations are derived from the median of  
 537 six extreme years, one year each EURO-CORDEX simulation. Percent changes are computed as described  
 538 in Eq. 3. The top row uses current atmospheric CO<sub>2</sub> concentration and the bottom row uses future CO<sub>2</sub>  
 539 levels (2.17 current CO<sub>2</sub>). The grey cross in Eastern France is the location of the Hesse forest  
 540 experimental station.



541