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1 Mining ecophysiological responses of European beech ecosystems to
2 drought

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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 CO₂ 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 CO₂; 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 20th
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) 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 CO₂ concentration in the future
149 was isolated by the production of MuSICA simulations at Hesse with both current and future CO₂ values.
150 Indeed, a 2.17-time increase in CO₂ 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/m³, 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/m³ 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 CO₂ 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/m³ 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 CO₂
223 concentration projected by RCP8.5 simulations at the 2080-2100 horizon (2.17 current CO₂). 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 CO₂ 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 CO₂, 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 CO₂ 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 21st 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 1st) to 48 °C (August 8th) 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 CO₂ 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 Asadiéh 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 CO₂ fertilization in the future
317 (+2.17-time increase of CO₂ 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 CO₂-enriched atmosphere
323 seem to show a more moderate CO₂ 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 CO₂ 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.

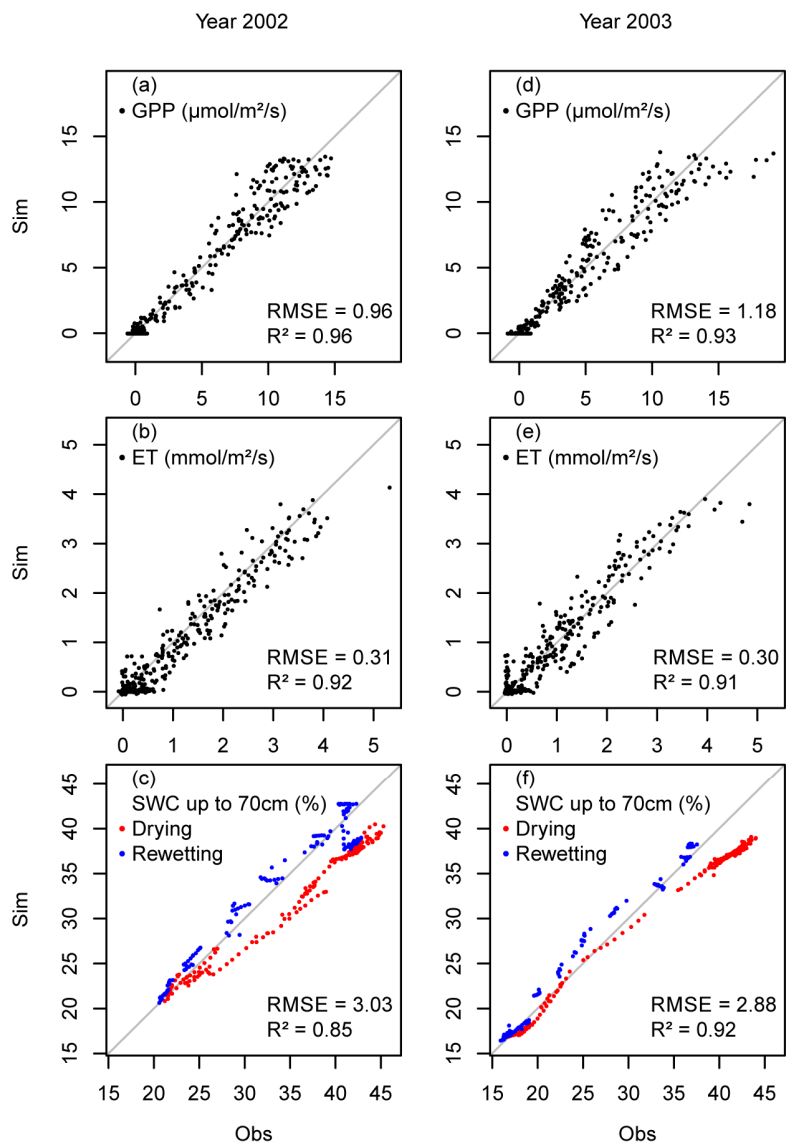
489

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

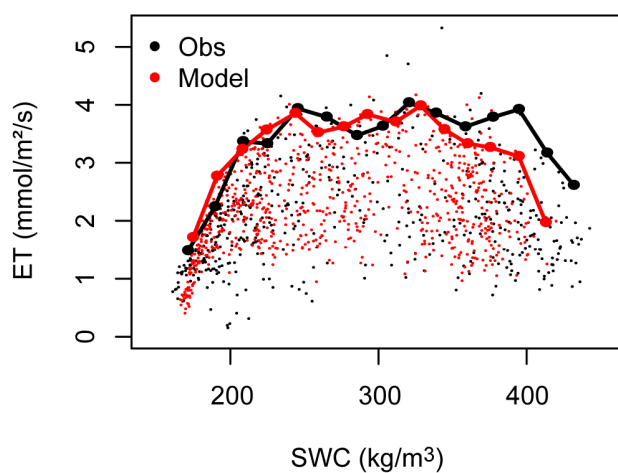
491 **Figures**

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.



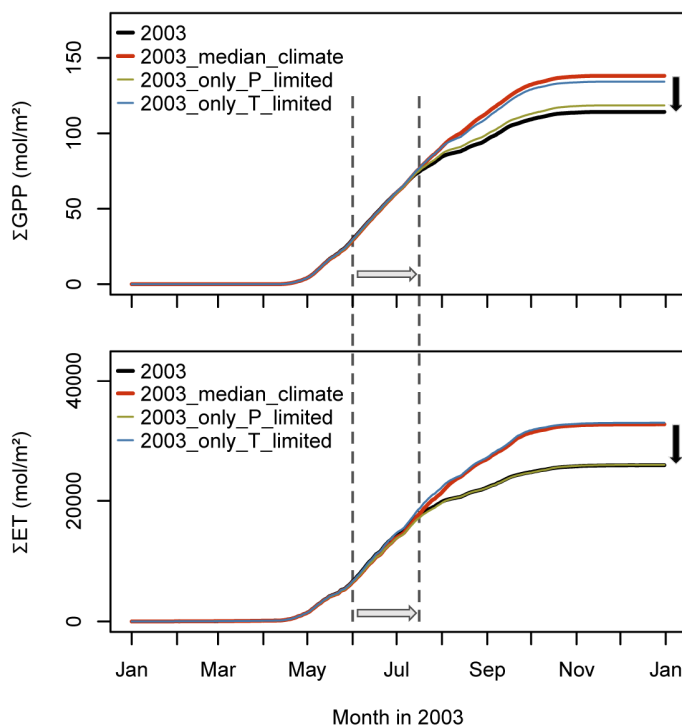
497

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 95th 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/m² were considered.



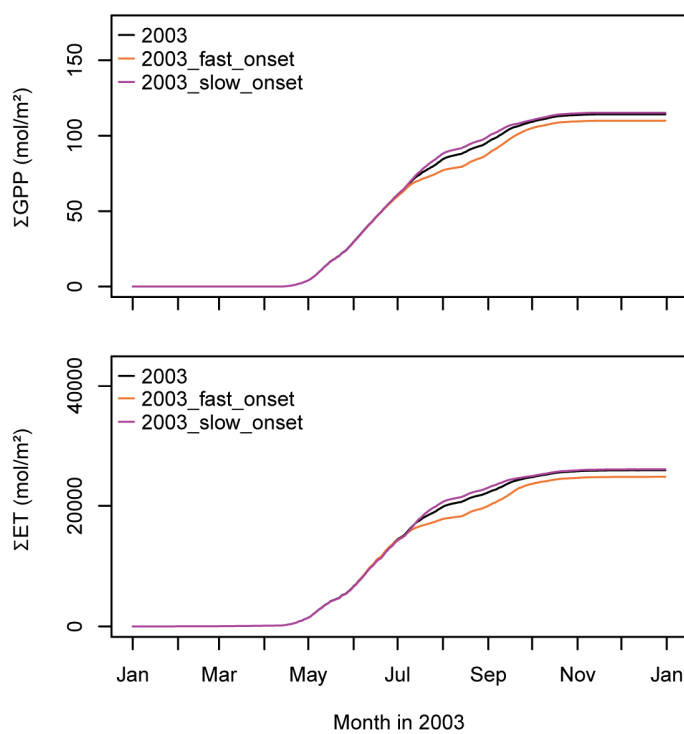
503

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.



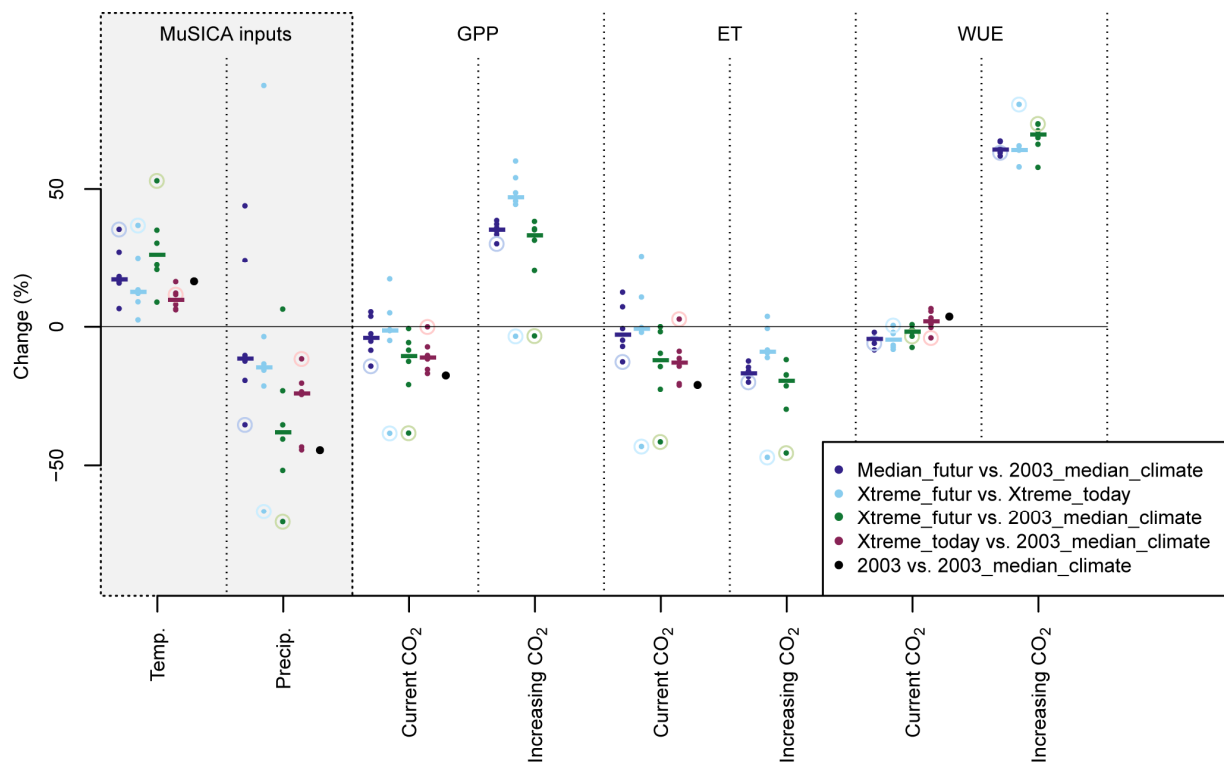
513

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).



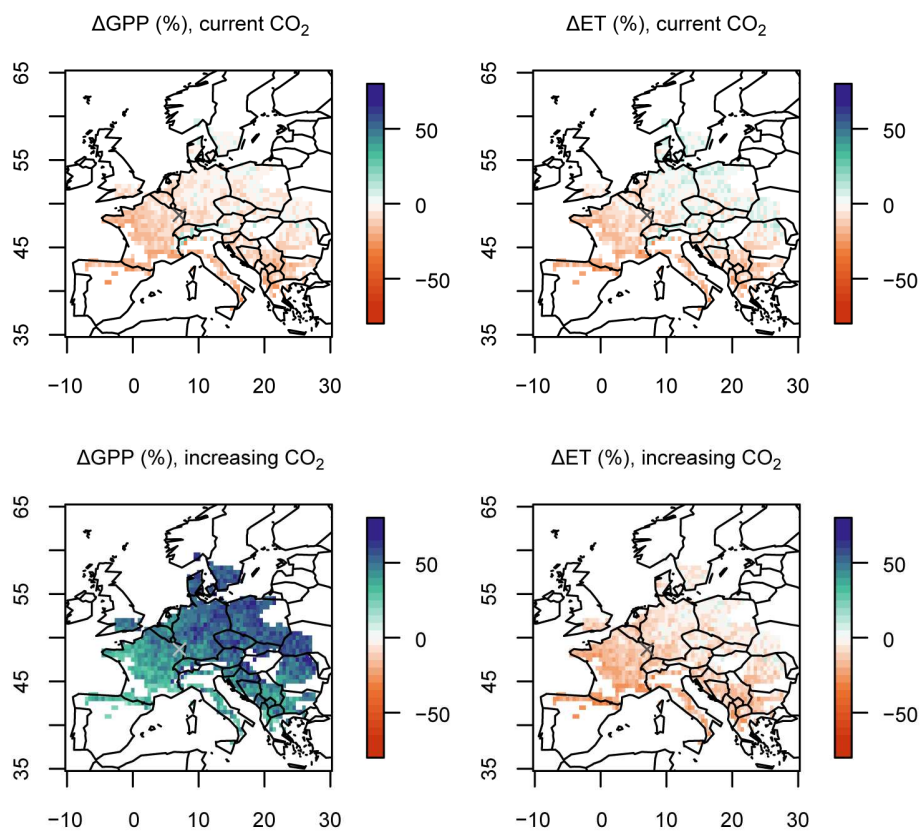
520

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 CO₂ levels or projected, increased atmospheric CO₂ 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 CO₂ concentration and the bottom row uses future CO₂
539 levels (2.17 current CO₂). The grey cross in Eastern France is the location of the Hesse forest
540 experimental station.



541