

1 **Combining statistical and mechanistic models to identify the drivers of**
2 **mortality within a rear-edge beech population**

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4 **Authors:**

5 Cathleen Petit-Cailleux¹, Hendrik Davi¹, François Lefèvre¹, Joseph Garrigue², Jean-André Magdalou²,
6 Christophe Hurson^{2,3}, Elodie Magnanou^{2,4}, and Sylvie Oddou-Muratorio¹.

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8 **Adresses**

9 ¹INRAE, URFM, Avignon, France

10 ²Réserve Naturelle Nationale de la Forêt de la Massane, France

11 ³Fédération des Réserves Naturelles Catalanes, Prades, France

12 ⁴Sorbonne Université, CNRS, Biologie Intégrative des Organismes Marins, BIOM, F-66650 Banyuls-
13 sur-Mer, France

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15 **Keywords:** *Fagus sylvatica* L., logistic regression, process-based model, dynamic vegetation model,
16 CASTANEA, longitudinal analysis, defoliation.

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32 **Abstract**

33 Since several studies have been reporting an increase in the decline of forests, a major issue
34 in ecology is to better understand and predict tree mortality. The interactions between the different
35 factors and the physiological processes giving rise tree mortality, as well as the individual variability
36 in mortality risk, [still need to be better assessed](#).

37 This study investigates mortality in a rear-edge population of European beech (*Fagus sylvatica*
38 L.) using a combination of statistical and process-based modelling approaches. Based on a survey of
39 4323 adult beeches since 2002 within a natural reserve, we first used statistical models to quantify
40 the effects of competition, tree growth, size, [defoliation and fungi](#) presence on mortality. Secondly,
41 we used an ecophysiological process-based model (PBM) to separate out the different mechanisms
42 giving rise to temporal and inter-individual variations in mortality by simulating depletion of carbon
43 stocks, loss of hydraulic conductance and damage due to late frosts in response to climate.

44 The combination of all these simulated processes was associated with the temporal variations
45 in the population mortality rate. The individual probability of mortality decreased with increasing
46 mean growth, and increased with increasing crown defoliation, earliness of budburst, fungi
47 presence and increasing competition, in the statistical model. Moreover, the interaction between
48 tree size and defoliation was significant, indicating a stronger increase in mortality associated to
49 [defoliation in smaller than larger trees](#). Finally, the PBM predicted a higher conductance loss
50 together with a higher level of carbon reserves for trees with earlier budburst, while the ability to
51 defoliate the crown was found to limit the impact of hydraulic stress at the expense of the
52 accumulation of carbon reserves.

53 We discuss the convergences and divergences obtained between statistical and process-based
54 approaches and we highlight the importance of combining them to [characterize](#) the different
55 processes underlying mortality, and the factors modulating individual vulnerability to mortality.

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58 **Introduction**

59 Global changes have been repeatedly reported to be the cause of forest decline and tree
60 mortality, both in terms of background, non-catastrophic mortality (Van Mantgem et al. 2009,
61 Lorenz and Becher 2012) and of massive, catastrophic mortality due to extreme, ‘pulse’ events
62 (Allen et al. 2010; Lorenz and Becher 2012; Mueller et al. 2005). To predict how such a new regime
63 of trees mortality will impact upon forest structure, composition and ecosystem services (Anderegg
64 et al. 2015a; Choat et al. 2018), we need to better understand the respective roles of the various
65 drivers and mechanisms underlying tree mortality.

66 Studying mortality poses several challenges, in particular because it is triggered by several
67 factors and involves several interacting physiological processes. The factors triggering mortality
68 include extreme, pulse climatic events (i.e. repeated drought, storms, floods, heavy snow, late
69 frosts, wildfires) or sudden changes in biotic interactions (i.e. emerging pests, invasive species), but
70 also long-term climatic or biotic perturbations (i.e. recurrent water deficits, changes in competition
71 at the community level) (Maraun et al. 2003; McDowell et al. 2011). Moreover, these factors can
72 have interactive effects. For instance, drought may increase trees’ vulnerability to pests (Durand-
73 Gillmann et al. 2014; Anderegg et al. 2015b) or predispose them to wildfires (Brando et al. 2014).
74 Finally, a single factor triggering mortality may involve several underlying physiological processes,
75 with several thresholds leading to mortality and potential feedback between them (McDowell et al.
76 2011). This is exemplified by drought, which is usually considered to trigger mortality through the
77 combination of hydraulic failure and carbon starvation (Adams et al. 2017; Anderegg et al. 2012;
78 McDowell et al. 2011).

79 Another challenge when studying mortality is that the physiological processes governing tree
80 vulnerability may vary in space and time. For instance, vulnerability may vary among individual trees
81 within a population according to (i) the spatial heterogeneity in available resources, especially soil
82 water (Nourtier et al. 2014); (ii) the heterogeneity in an individual tree’s life history, and in particular
83 the effects of past stresses on tree morphology and anatomy (Vanoni et al. 2016); (iii) the inter-
84 individual variation of physiological responses to stresses, which depends on ontogenic, plastic, and
85 genetic effects controlling the expression of traits (Anderegg 2015a; Vitasse et al. 2009).
86 Vulnerability may also vary through time for a given individual/population, not only because of
87 temporal climatic variation but also through individual variations in phenological processes. This is
88 well illustrated by the risk of late frost damage, which is closely related to the coincidence between

89 temporal patterns of budburst phenology, and the climatic sequence of low temperatures. Although
90 relatively large safety margins were found regarding the risk of late frost damage during budburst
91 across many European temperate tree (Bigler and Bugmann 2018), these safety margins may reduce
92 with climate change, due to earlier budburst (Augspurger 2009). When young leaves have been
93 damaged, some species can reflush, i.e. produce another cohort of leaves (Augspurger 2009;
94 Menzel, Helm, and Zang 2015), but the time required to reflush may reduce the length of the
95 growing season (Lenz et al. 2013), and may lead to mortality if trees do not have enough reserves
96 to do this.

97 Available approaches to investigate the multiple drivers and processes underlying tree
98 mortality can be classified into two broad categories: statistical, phenomenological approaches
99 versus process-based, mechanistic approaches. Statistical approaches use forest inventory data to
100 test how tree characteristics (e.g. related to tree size and growth rate, biotic and abiotic
101 environment, including management) affect population- or individual-level mortality. By comparing
102 species or populations over areas with large climatic variations, such studies have demonstrated the
103 overall effect of drought severity on mortality, although usually explaining only a limited proportion
104 of the variance observed in mortality (Allen et al. 2010; Greenwood et al. 2017). Moreover,
105 probabilities of mortality have been predicted with a higher accuracy when individual covariates for
106 tree growth, size and/or competition were included in the statistical models, highlighting the
107 importance of inter-individual variability in the threshold for mortality (Hülsmann, Bugmann, and
108 Brang 2017; Monserud 1976). Recent statistical studies have attempted to include functional traits
109 involved in the response to stress as additional covariates to improve the accuracy of mortality
110 prediction, such as defoliation (Carnicer et al. 2011) or hydraulic safety margins (Benito-Garzón et
111 al. 2018). Overall, the main advantage of statistical approaches is their ability to account for a
112 potentially high number of factors and processes triggering mortality and for individual variability
113 in the threshold for mortality. However, these statistical models barely deal with the usually low
114 temporal resolution of mortality data, missing information on the cause of tree death, and non-
115 randomization inherent in natural population designs. In addition, the accuracy of statistical
116 predictions can decrease outside the studied area (Hülsmann, Bugmann, and Brang 2017).

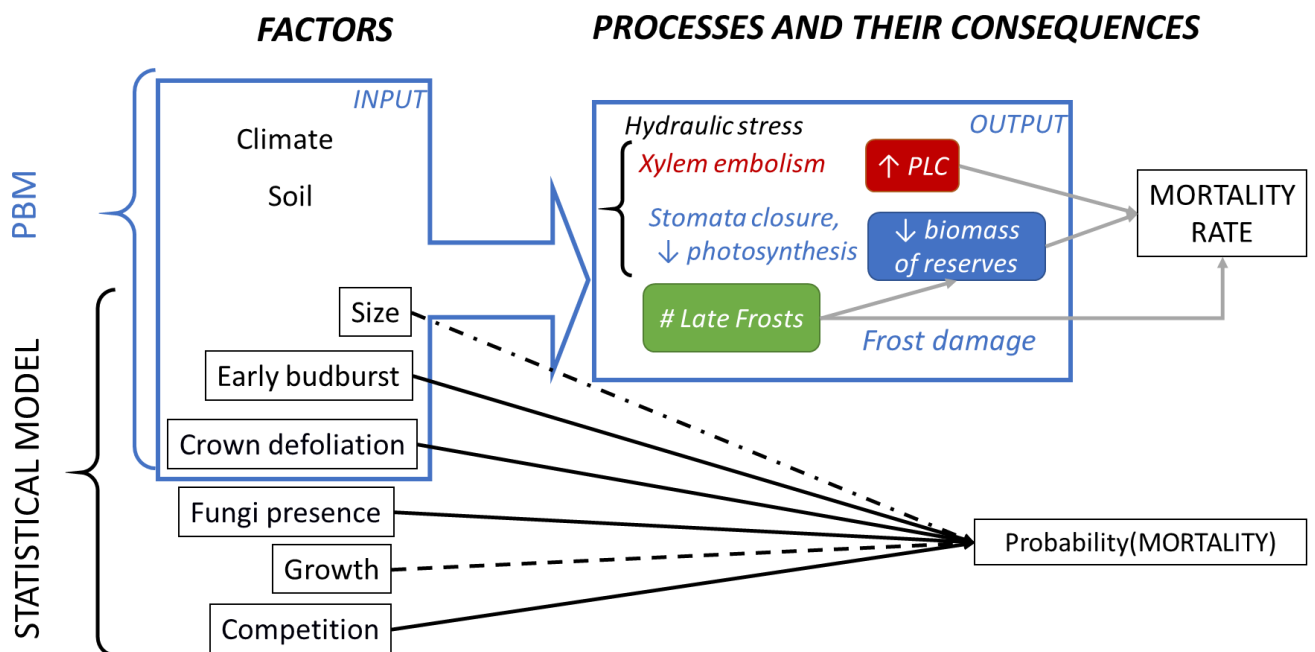
117 On the other hand, biophysical and ecophysiological process-based models (PBMs), initially
118 developed to simulate carbon and water fluxes in forest ecosystems, are also useful to investigate
119 the environmental drivers and physiological processes triggering tree mortality. For example, using

120 the PBM CASTANEA, Davi & Cailleret (2017) showed that mortality of silver fir in southern France
121 resulted from the combination of drought-related carbon depletion and pest attacks. Using six
122 different PBMs, Mc Dowell et al. (2013) found that mortality depended more on the duration of
123 hydraulic stress than on a specific physiological threshold. A main advantage of PBMs is their ability
124 to understand [how physiological processes drive mortality](#) and to predict mortality under new
125 combinations of forcing variables in a changing environment. However, they need a large number
126 of parameters to be calibrated. [Most often, calibration is made using the average parameter value
127 known at species level, and therefore does not account for possible inter-individual variability of
128 ecophysiological processes, and for its effect on response trajectory \(Berzaghi et al. 2019\).](#)
129 Moreover, biophysical and ecophysiological PBMs generally do not take into account individual tree
130 characteristics (i.e. related to ontogenic, plastic and/or genetic variation). Hence, statistical and
131 process-based approaches appear as complementary, and many authors have called for studies
132 comparing or combining them (Hawkes 2000; O'Brien et al. 2017; Seidl et al. 2011).

133 The European beech (*Fagus sylvatica* L.) combines a widespread distribution (from northern
134 Spain to southern Sweden and from England to Greece) and an [expected](#) high sensitivity to climate
135 change (Cheaib et al. 2012; Kramer et al. 2010). Bioclimatic niche models predict a future reduction
136 of this species at the rear edge of its range over the next few decades (Cheaib et al. 2012; Kramer
137 et al. 2010). [Its growth is highly sensitive to droughts](#) (Dittmar, Zech, and Elling 2003; Jump, Hunt,
138 and Penuelas 2006; Knutzen et al. 2017), which increase defoliation (Penuelas and Boada 2003).
139 However, the low mortality rate observed so far in beech has led some authors to propose that this
140 species presents a higher heat stress tolerance and metabolic plasticity when compared to other
141 tree species (García-Plazaola et al. 2008). This apparent paradox between a low mortality and a high
142 sensitivity to climate makes beech an interesting model species to study.

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147 In this study, we used a combination of statistical regression model and the PBM CASTANEA
 148 (Figure 1), to investigate the **drivers** of mortality within a population located at the warm and dry
 149 ecological margin for European beech (42° 28' 41" N, 3° 1' 26" E; Supplementary Figure S1).
 150 Mortality, decline (crown defoliation and fungi presence), size, growth, competition and budburst
 151 were characterised in a set of 4323 adult trees over a 15 year-period from 2002 to 2016. CASTANEA
 152 was used to simulate the number of late frost days, the percentage loss of conductance (PLC) and
 153 the biomass of carbon reserves in response to stress. Specifically, we addressed the following
 154 **questions**: (1) **How do climatic factors and physiological processes drive temporal variation in the**
 155 **mortality rate?** (2) How do factors varying at tree-level modulate the individual tree's probability of
 156 mortality? (3) How do physiological mechanisms modulate the vulnerability of individuals?



157
 158 **Figure 1: Combining process-based and statistical models to study variables and processes**
 159 **involved in tree mortality.** The square boxes indicate the measured factors and response variables
 160 considered in statistical models. Boxes with rounded corners indicate stress-related output variables
 161 simulated with the PBM CASTANEA. The blue box on the left delineates the input variables of
 162 CASTANEA. At the top, grey arrows indicate the relationships considered to link stress-related
 163 output variables simulated by CASTANEA with observed mortality rate at population level. At the
 164 bottom, the black arrows indicate the relationships considered in the statistical model for the
 165 probability of mortality at individual level (solid lines: expected positive effect; dashed lines:
 166 expected negative effect; non-linear effects were expected for size). Moreover, the effects of size,
 167 early budburst and defoliation on the individual probability of mortality were also investigated using
 168 the PBM. PLC – percentage loss of conductance.

171 **Materials and Methods**

172 **Study site**

173 La Massane is a forest of 336 ha located in the French eastern Pyrenees ranging from 600 to 1127
174 m.a.s.l. Located in the south of the beech range, the forest is at the junction of Mediterranean and
175 mountainous climates with a mean annual rainfall of 1260 mm (ranging from 440 to 2000 mm) and
176 mean annual temperature of 11°C (with daily temperature ranging from -10°C to 35°C)
177 (Supplementary Figure S2). No logging operations have been allowed since 1886 and the forest was
178 classified as a reserve in 1974. European beech is the dominant tree in the canopy representing
179 about 68% of basal area of the forest. Beech is in mixture with downy oak (*Quercus pubescens* Willd),
180 maple (*Acer opalus* Mill., *Acer campestre* L., *Acer monspessulanum* L.), and holly (*Ilex aquifolium* L.).
181 A 10 ha fenced plot has excluded grazing from cows since 1956. All trees from this protected plot
182 have been geo-referenced and individually monitored since 2002 (Supplementary Figure S3).

183 We estimated the soil water capacity (SWCa) through soil texture, soil depth and percentage of
184 coarse elements measured in two soil pits. Secondly, we estimated the mean Leaf Area Index (LAI)
185 by using hemispherical photographs (Canon 5D with Sigma 8mm EXDG fisheye). We computed the
186 LAI and clumping index following the methodology described by Davi et al. (2009). SWCa and LAI
187 were measured at population level.

188 **Individual tree measurements**

189 This study is based on the characterisation of twelve variables in 4323 beech trees in the
190 protected plot over the period from 2002 to 2016 (Table 1). Note that beech sometimes produces
191 stump shoots resulting in multiple stems from a single position (coppice), but that here, every stem
192 of all the coppices was individually monitored and subsequently referred to “tree”.

193

194 **Table 1: Quantitative (a) and categorical variables (b) measured at individual level.** All the variables
 195 were measured in 4323 trees, except for H₂₀₀₂ (1199 trees). The “Cat” column indicates the category
 196 (i.e. size, growth, competition, decline, phenology). The “YMeas.” column indicates the year of
 197 measurement; note that all the variables were measured only once, so when two dates are given
 198 they indicate the period over which the variable is computed.

199 (a)

Code	Variable	Cat	YMeas.	mean	min	max	unit
DBH ₂₀₀₂	Diameter at breast height measured in 2002	Size	2002	21.7	10.0	116.0	cm
DBH ₂₀₁₂	Diameter at breast height measured in 2012	Size	2012	22.8	10.0	116.0	cm
MBAI	Mean basal area increment between 2002 and 2012.	Growth	2002-2012	4.7	0.0	95.0	cm ² . year ⁻¹
H ₂₀₀₂	Height measured in 2002	Size	2002	8.8	2.0	26.0	m
DEFw	Cumulated and weighted defoliation score	Decline	2003-2016	0.1	0.0	1.0	-
Nstem	Number of stems observed in the coppice	Compet	2002	1.5	1.0	11.0	-
Compet _{intra}	Intra-specific competition index	Compet	2002	2.7	0.0	11.4	-
Compet _{intra+}	Intra-specific competition index accounting for within-coppice competition	Compet	2002	1.0	0.0	12.7	-
Compet _{tot}	Total competition index, accounting for within-coppice competition	Compet	2002	4.6	0.1	20.0	-

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202 (b)

Code	Variable	Cat	YMeas.	Level	Number of trees
Fungi	Presence (1) or absence (0) of the saproxylic fungus	Decline	2003-2016	1: 0:	414 3913
Budburst	Early (1) or late (0) budburst	Phenology	2002	1: 0:	237 4090

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204 Tree mortality was recorded every year from 2003 to 2016, based on two observations (in
 205 autumn, based on defoliation and in spring, based on budburst). A tree was considered to have died
 206 at year n when (1) budburst occurred in the spring of year n but (2) no leaves remained in the
 207 autumn of year n , and (3) no budburst occurred in year $n+1$. All the 4323 trees were alive in year
 208 2003 (Supplementary Figure S4). We computed the annual mortality rate (τ_n) for each year n as:

209
$$\tau_n = \frac{N_{dead,n}}{N_{alive,n-1}} \text{ (Equation 1),}$$

210 where $N_{dead,n}$ (respectively $N_{alive,n}$) is the number of dead (respectively alive) trees in year n .

211 Diameter at breast height (DBH) was measured 1.30 m above ground level in 2002 and 2012.

212 As we focused on the drivers of mature tree mortality, only trees with DBH₂₀₀₂ greater than 10 cm

213 were retained for analysis. Individual growth was measured by the mean increment in basal area
 214 (MBAI) between 2002 and 2012, estimated as:

$$215 \quad MBAI = (\pi(DBH_{2012} - DBH_{2002})^2/4)/NyearsAlive_i \quad (\text{Equation 2}),$$

216 where $NyearsAlive_i$ is the number of years where individual i was observed being alive. Height
 217 in 2002 was estimated for a subset of 1199 trees.

218 A bimodal pattern in budburst phenology had been previously reported in La Massane
 219 (Gausson 1958; Perci du Sert 1982). Some trees were observed to systematically initiate budburst
 220 about two weeks before all the others. Here, the monitoring allowed budburst phenology to be
 221 surveyed as a binary categorical variable, distinguishing trees with early budburst from the others.

222 The presence of defoliated major branches was recorded each year between 2003 and 2016
 223 (except 2010) as a categorical measure (DEF = 1 for presence; DEF = 0 for absence). These annual
 224 measures were cumulated and weighted over the observation period for each individual in the
 225 following quantitative variable:

$$226 \quad DEFw_i = \frac{\sum_{j=1}^{NyearsAlive_i} DEF_j}{NyearsAlive_i} \quad (\text{Equation 3}),$$

227 Year 2010 was not included in $NyearsAlive_i$. DEFw [integrates \(without disentangling\)](#) the
 228 recurrence of defoliation and the ability to recover from defoliation. The presence of fructification
 229 of the saproxylic fungus *Oudemansiella mucida* (Schrad.) was recorded as a categorical measure
 230 (Fungi = 1 for presence; Fungi = 0 for absence). Given that once observed, the fructification persists
 231 throughout the subsequent years, we analysed it as a binary variable.

232 Competition around each focal beech stem was estimated by the number of stems in the
 233 coppice ($Nstem$) as an indicator of within-coppice competition. We also computed competition
 234 indices accounting simultaneously for the diameter (DBH_{2002}) and the distance (d_{ij}) of each
 235 competitor j to the competed individual i , following Martin and Ek (1984):

$$236 \quad Compet_{i,dmax} = \frac{1}{DBH_{2002i}} \sum_{j=1}^{N_{compet}} DBH_{2002j} \exp \left[\frac{-16d_{ij}}{DBH_{2002i} + DBH_{2002j}} \right] \quad (\text{Equation 4}),$$

237 where N_{compet} is the total number of competitors in a given radius $dmax$ (in m) around each focal
 238 individual i . Only trees with $DBH_{2002j} > DBH_{2002i}$ are considered as competitors. Such indices were
 239 shown to describe more accurately the competition than indices relying on diameter only (Stadt et
 240 al. 2007). We computed this competition index in three ways. The intra-specific competition index
 241 $Compet_{intra}$ only accounts for the competition of beech stems not belonging to the coppice of the
 242 focal tree. The intra-specific competition index $Compet_{intra+}$ accounts for all beech stems belonging,

243 or not, to the coppice of the focal tree. The total competition index $Compet_{tot}$ accounts for all stems
244 and species. We considered that stems located less than 3 m away from the focal stem belonged to
245 the same coppice. The three indices were first computed at all distances from 1 m (or 3 m for
246 $Compet_{intra}$) to 50 m from the target tree, with 1 m steps. We retained $d_{max} = 15$ m in subsequent
247 analyses, because all indices [plateaued after this threshold value](#), suggesting that in a radius greater
248 than 15 m, the increasing number of competitors is compensated for by distance.

249 **Climate data**

250 Local climate has been daily monitored *in situ* since 1976 and 1960 for temperature and
251 precipitation/mean relative humidity, respectively. In order to obtain a complete climatic series
252 (from 1959 to 2016), we used the quantile mapping and anomaly method in the R package
253 “meteoland” (De Caceres et al. 2018), considering the 8-km-resolution-SAFRAN reanalysis (Vidal et
254 al. 2010) as reference.

255 From the corrected climate series, we derived the daily climatic input variables for CASTANEA,
256 which are the minimum, mean and maximum temperatures (in °C), the precipitation (mm), the wind
257 speed ($m.s^{-1}$), the mean relative humidity (%) and the global radiation ($MJ.m^{-2}$).

258 **Simulations with CASTANEA**

259 **Model overview:** CASTANEA is a PBM initially developed to simulate carbon and water fluxes in
260 forest ecosystems with no spatial-explicit representation of trees (Dufrêne et al. 2005). A tree is
261 abstracted as six functional elements: leaves, branches, stem, coarse roots, fine roots and reserves
262 (corresponding to non-structural carbohydrates). The canopy is divided into five layers of leaves.
263 Photosynthesis is half-hourly calculated for each canopy layer using the model of Farquhar et al.
264 (1980), analytically coupled to the stomatal conductance model proposed by Ball et al. (1987).
265 Maintenance respiration is calculated as proportional to the nitrogen content of the considered
266 organs (Ryan 1991). Growth respiration is calculated from growth increment combined with a
267 construction cost specific to the type of tissue (De Vries, Brunsting, and Van Laar 1974).
268 Transpiration is hourly calculated using the Monteith (1965) equations. The dynamics of soil water
269 content (SWCo; in mm) is calculated daily using a three-layer bucket model. Soil drought drives
270 stomata closure via a linear decrease in the slope of the Ball et al. (1987) relationship, when relative
271 SWCo is under 40% of field capacity (Granier, Biron, and Lemoine 2000; Sala and Tenhunen 1996).
272 In the carbon allocation sub-model (Davi et al., 2009; Davi & Cailleret 2017), the allocation
273 coefficients between compartments (fine roots, coarse roots, wood, leaf and reserves) are

274 calculated daily depending on the sink force and the phenological constraints. CASTANEA model was
275 originally developed and validated at stand-scale for beech (Davi et al. 2005).

276 **Focal processes and output variables:** In this study, we focussed on three response variables
277 simulated by CASTANEA: (1) the biomass of reserves (BoR) as an indicator of vulnerability to carbon
278 starvation; (2) the percentage loss of conductance (PLC) as an indicator of vulnerability to hydraulic
279 failure; and (3) the number of late frost days (NLF) as an indicator of vulnerability to frost damage.
280 Note that we did not simulate mortality with CASTANEA because the thresholds in PLC, NLF and BoR
281 triggering mortality are unknown. These variables were simulated using the CASTANEA version
282 described in Davi and Cailleret (2017) with two major modifications. First, for budburst, we used the
283 one-phase UniForc model, which describes the cumulative effect of forcing temperatures on bud
284 development during the ecodormancy phase (Chuine, Cour, and Rousseau 1999; Gauzere et al.
285 2017). We simulated damage due to late frosts (see details in Appendix 1) and considered that trees
286 were able to reflush after late frosts. We calculated NLF as the sum of late frost days experienced
287 after budburst initiation.

288 Second, we implemented a new option in CASTANEA to compute PLC following the formula of
289 Pammenter and Willigen (1998):

$$290 \quad \text{PLC} = \frac{1}{1 + e^{\text{slope}(\Psi_{\text{leaf}} - \Psi_{P50})}} \quad (\text{Equation 5}),$$

291 with Ψ_{leaf} (MPa) the simulated midday leaf water potential, Ψ_{50} (MPa) the species-specific
292 potential below which 50% of the vessels are embolized, and *slope* a constant fixed to 50.

293 The leaf water potential Ψ_{leaf} was calculated as:

$$294 \quad \Psi_{\text{leaf}}(t + 1) = \Psi_{\text{soil}}(t + 1) - \frac{\text{TR}}{3600} \times R_{\text{SoilToLeaves}} + \frac{\Psi_{\text{leaf}}(t)}{\Psi_{\text{soil}}(t + 1) + \text{TR} \times R_{\text{SoilToLeaves}}} \\ 295 \quad \times e^{\frac{\text{deltaT}}{R_{\text{SoilToLeaves}} \times \text{Cap}_{\text{SoilToLeaves}}}} \\ 296 \quad (\text{Equation 6}),$$

297 where the soil water potential (Ψ_{soil} MPa) was calculated from daily SWCo (Campbell 1974). Ψ_{leaf}
298 was calculated hourly (deltaT = 3600s) based on the sap flow (TR in $\text{mmol.m}^{-2}.\text{leaf}^{-1}$) simulated
299 following the soil-to-leaves hydraulic pathway model of Loustau et al. (1990). We used a single
300 resistance ($R_{\text{SoilToLeaves}}$ in $\text{MPa.m}^2.\text{s}^{-1}.\text{kg}^{-1}$, following Campbell 1974) and a single capacitance
301 ($\text{Cap}_{\text{SoilToLeaves}}$ in $\text{kg.m}^{-2}.\text{MPa}^{-1}$) along the pathway. $R_{\text{SoilToLeaves}}$ was assessed using midday and predawn
302 water potentials found in the literature.

303 We added a binary option in CASTANEA to simulate branch mortality and defoliation as a
304 function of PLC. If the PLC at year n was >0 , the LAI at year n was reduced by the PLC value for trees
305 able to defoliate (option “Defoli-able”). Otherwise, PLC has no consequences on LAI.

306

307 **Simulation design:** The aim of the first simulations was to investigate whether response variables
308 simulated by CASTANEA correlated with patterns of observed mortality at population scale. We
309 simulated a population of 100 trees representing the variability in individual characteristics
310 observed in La Massane in terms of height-diameter allometry, DBH, leaf area index and budburst
311 phenology (Appendix 1). We also simulated a range of environmental conditions representing the
312 observed variability in SWCa and tree density. We also used this first simulation to validate
313 CASTANEA based on the correlation between simulated and observed ring width (Appendix 1).
314 For this first simulation, the values of focal output variables (PLC, NLF and BoR) were averaged
315 across the 100 trees. We also computed a cumulated vulnerability index (CVI) for each year n
316 combining the simulated PLC, NLF and BoR as follows:

$$317 \quad \text{CVI}_n = \left(\frac{\text{PLC}_n}{\max(\text{PLC})} + \frac{\text{NLF}_n}{\max(\text{NLF})} \right) - \frac{\text{BoR}_n}{\max(\text{BoR})} \quad (\text{Equation 7}),$$

318 Note that each term is weighted by its maximal value across all years, so that the contribution of
319 the three drivers to vulnerability is balanced. The possible range of CVI is [-1; 2].

320 The second simulation aimed at investigating the differences in physiological responses
321 between individuals with different characteristics. We simulated eight individuals corresponding to
322 a complete cross design with two size categories (5 and 40 cm in DBH), two budburst types (early
323 and normal), and two defoliation levels (option “Defoli-able” activated or not).

324 **Statistical models of mortality to explore individual drivers of mortality**

325 We used logistic regression models to investigate how tree characteristics affect the individual
326 probability of mortality ($P_{\text{mortality}}$). This approach is appropriate for a binary response variable and a
327 mixture of categorical and quantitative explanatory variables, which are not necessarily normally
328 distributed (Hosmer and Lemeshow 2000). We considered the four following complete logistic
329 regression models:

$$330 \quad P_{\text{mortality}} = [\text{DEFw} + \text{Fungi} + \text{Budburst} + \text{MBAI} + (\text{Nstem OR Compet}_{\text{intra}} \text{ OR Compet}_{\text{intra+}} \text{ OR} \\ 331 \quad \text{Compet}_{\text{tot}})] \times (\text{DBH}_{2002} + \text{DBH}_{2002}^2) \quad (\text{Equation 8})$$

332

333 where the predictors defoliation (DEFw), growth (MBAI), size (DBH₂₀₀₂) and competition (Nstem or
 334 the Compet indices) were quantitative variables, and the presence of fungi (Fungi) and budburst
 335 phenology (Budburst) were categorical variables. We included both a linear and quadratic effect of
 336 DBH₂₀₀₂ by specifying this effect as a polynomial of second degree. Interaction effects of the previous
 337 predictors with this polynomial were included.

338 All variables were scaled before fitting the model. To select the best competition-related
 339 variables, we first fitted the model described by equation 8 with each competition term successively
 340 (Appendix 3). Then, we used [the R package “MuMin” to compare and](#) select the most parsimonious
 341 models based on AIC. When two models had similar AIC (delta < 2) (Arnold 2010), the one with
 342 fewer variables (most parsimonious) was selected. [With our model we seek to understand factors](#)
 343 [related to mortality and not to prediction, so we did not select a variable as recommended by Heinze](#)
 344 [et al. \(2018\) and Lederer et al. \(2019\). Model validity was checked based on the leverage points \(i.e.](#)
 345 [points having a greater weight than expected by chance\) with the Cook's distance \(Cook distance <](#)
 346 [0.5 indicate no leverage\). We evaluated the goodness-of-fit with the Brier test score \(Brier 1950\).](#)
 347 [We evaluated the sensitivity and specificity of the model using the receiver operating characteristic](#)
 348 [\(ROC\) curve.](#)

349 Collinearity resulting from correlations between predictor variables is expected to affect the
 350 statistical significance of correlated variables by increasing type II errors (Schielzeth 2010). To
 351 evaluate this risk, we first checked for correlation among predictors included in equation 9 (Figure
 352 S5). We also computed the variation inflation factor (VIF) with the R package “car”. A threshold of
 353 $GVIF^{1/2df} < 2$ is commonly accepted to show that variables are not excessively correlated and do not
 354 make the model unstable.

355 We expressed the results in terms of odds ratios, also called relative risk, indicating the degree
 356 of dependency between variables. For instance, the odds ratio for mortality as a function of
 357 budburst characteristics (early vs normal) is:

358
$$\text{OddsRatio}_{\text{Early.vs.Normal}} = \frac{\text{Odds}_{\text{Early}}}{\text{Odds}_{\text{Normal}}} \quad (\text{Equation 9}),$$

359
$$\text{With Odds}_{\text{Early}} = \frac{P_{\text{mortality(Early)}}}{1 - P_{\text{mortality(Early)}}} \quad \text{and} \quad \text{Odds}_{\text{Normal}} = \frac{P_{\text{mortality(Normal)}}}{1 - P_{\text{mortality(Normal)}}}.$$

360 We computed odds ratios with “questionr” the R package (Barnier, Briatte, and Larmarange 2018).
 361 The interactions were visualized with the package “jtools” (Long 2018).

362 **Results**

363 **Temporal variations in population mortality rate in relation to physiological vulnerability**
364 **simulated with CASTANEA.**

365 We found a significant positive correlation between observed and simulated ring widths (p-
366 value $\ll 0.01$). Although CASTANEA tended to overestimate growth at the beginning of the
367 simulated period, and simulated a decreasing trend in growth over time that was not visible in the
368 observed data. This is likely to be due to a bad estimation of population density prior to the
369 monitoring period (see details in Appendix 1).

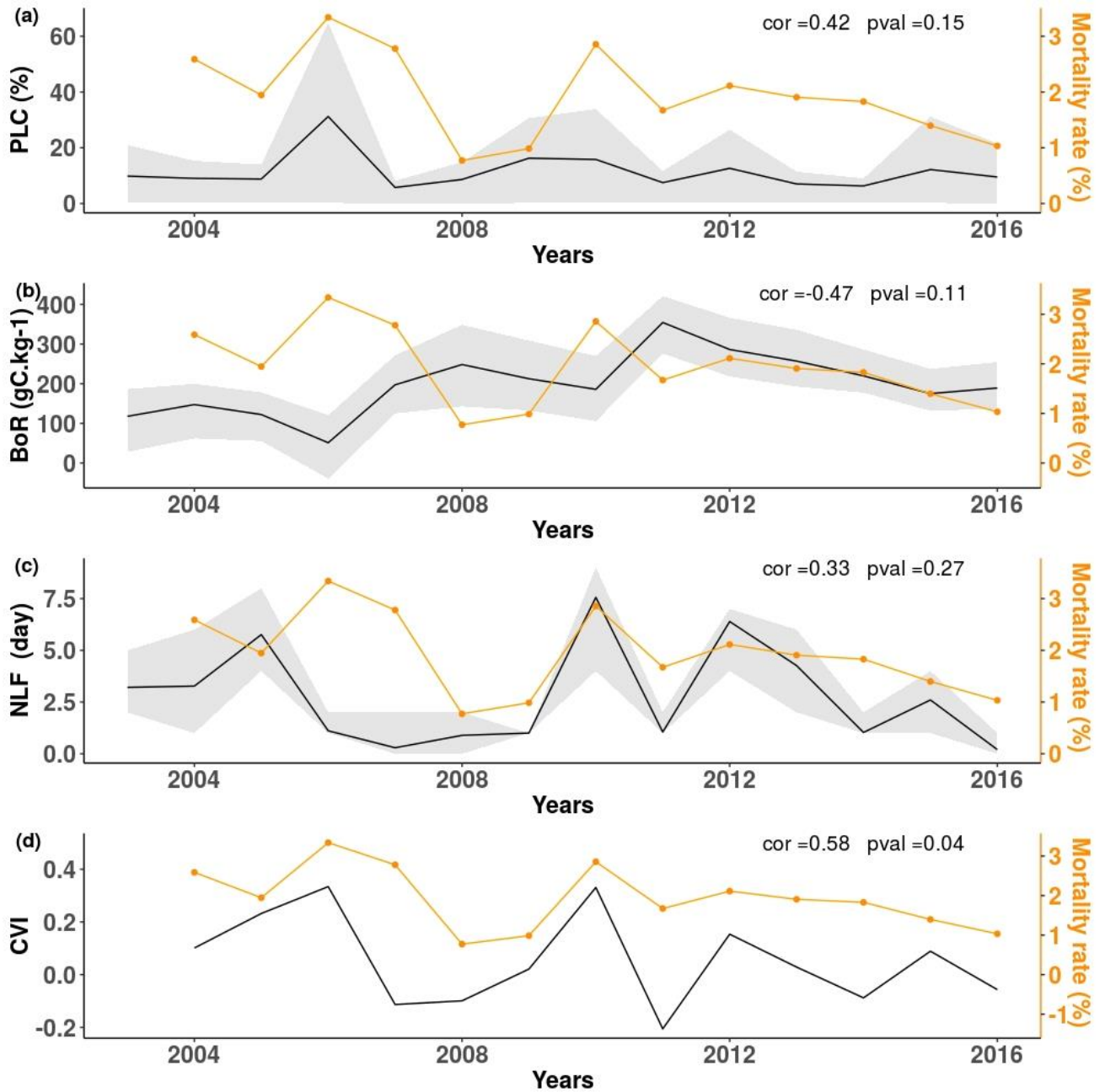
370 The total mortality rate between 2004 and 2016 was 23% (Figure 2; Table S1). After 2004
371 (2.6%), two peaks of high mortality were observed, in 2006-2007 (3.3% in 2006) and in 2010 (2.9%).
372 The lowest mortality rate was observed in 2008 (0.8%).

373 CASTANEA simulated inter-annual variations in the percent loss of conductance (PLC): the
374 mean PLC value varied among years, from 1% in 2004 and 2005 to 31% in 2006 (Figure 2a). The
375 mean simulated biomass of carbon reserves (BoR) varied among years, from 51 gC.m⁻² in 2006 to
376 354 gC.m⁻² in 2011. Finally, the number of late frost days (NLF) varied among years, from 0.2 in 2016
377 to 7.56 days in 2010 (Figure 2c). The variation in the cumulative vulnerability index (CVI) integrated
378 these different responses (Figure 2d), showed a peak in 2006 (drought), in 2010 (late frost) and in
379 2012 (combination of frost and drought).

380 None of the response variables simulated by CASTANEA (NLF, PLC, BoR) was significantly
381 correlated to annual variation in mortality rate. The only significant correlation was observed
382 between CVI and the annual mortality rate ($r = 0.58$, p-value = 0.04). Hence, inter-annual variations
383 in CVI were a good predictor of the mortality rate, except in year 2007. Besides the stress-related
384 variables simulated with CASTANEA, we also investigated the effects of climatic variables on inter-
385 annual variations in mortality rates using a beta-regression model (Appendix 2). We considered
386 drought indices computed from climatic series. This approach confirmed the effect of drought on
387 mortality.

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Figure 2: Stress-related output variable simulated with CASTANEA from 2004 to 2016: (a) percentage loss of conductance (PLC); (b) biomass of reserves in gC.kg^{-1} (BoR); (c) number of late frost days (NLF); (d) Cumulated vulnerability index (CVI) integrating a,b and c. The black line is the mean of simulation, and the grey area represents the inter-individual variation from the 1st to the 3rd quartile. The yellow line is the mortality rate observed in La Massane.



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399 **Inter-individual variation in the probability of mortality**

400 All the variables listed in equation 8 were retained in the best logistic regression model and
 401 had a significant main effect on the probability of mortality (Table 2). This model explained 49% of
 402 the observed mortality and had both a [good](#) validity and goodness-of-fit (Appendix 3). [However, the](#)
 403 [GVIF^{1/2df} score for DBH is superior to 2 meaning that the collinearity with other variables is high,](#)
 404 [which is certainly due to the high number of interaction tested and not significant.](#) Defoliation had
 405 the strongest linear effect on mortality: the [relative probability of mortality](#) increased by [1020](#) times
 406 for a one-unit increase in DEFw. Then, the [relative probability of mortality](#) was [2.28](#) higher for trees
 407 with earlier budburst as compared to others, and [1.88](#) higher for trees bearing fungi fructifications
 408 as compared to others. Among the competition-related variables, N_{stem} was selected as it was
 409 associated with the lowest AIC. The relative probability of mortality increased with increasing N_{stem},
 410 and decreased with increasing MBAI. Regarding the effect of tree size, the polynomial of degree 2
 411 corresponded to a U-shape and traduced a higher relative probability of mortality for both the
 412 smaller and the larger trees (In addition, this calibration is based on the mean of the individuals' 2,
 413 Appendix 3).

414
 415 **Table 2: Effects of tree characteristics on the individual tree's probability of mortality.** Variables
 416 are defined in Table 1. Effects were estimated with a logistic regression model (equation 8). β is the
 417 maximum likelihood estimate, with its estimated error (SE), z-value, and associated p-value. OR is
 418 the odds ratio.
 419

Variables	β	SE	z value	p-value	OR
DEFw	6.93	0.26	26.30	<0.0001	1.02 10 ³
Fungi	0.63	0.16	3.96	<0.0001	1.88
Budburst	0.82	0.17	4.71	<0.0001	2.26
MBAI	-0.45	0.08	-5.58	<0.0001	0.64
Nstem	0.13	0.04	3.44	<0.0001	1.14
DBH ₂₀₀₂	-9.19	8.16	-1.13	0.26	1.02 10 ⁻⁴
DBH ₂₀₀₂ ²	21.32	9.32	2.29	0.02	1.81 10 ⁹
DEFw:DBH ₂₀₀₂	-49.71	15.51	-3.20	5.91 10 ⁻⁴	2.57 10 ⁻²²
DEFw:DBH ₂₀₀₂ ²	32.97	17.08	1.93	0.05	2.08 10 ¹⁴
Fungi:DBH ₂₀₀₂	-11.33	8.69	-1.30	0.19	1.21 10 ⁻⁵
Fungi:DBH ₂₀₀₂ ²	-0.44	8.51	-0.05	0.96	0.65
Budburst:DBH ₂₀₀₂	0.27	10.41	0.03	0.98	1.31
Budburst:DBH ₂₀₀₂ ²	-3.11	12.19	-0.26	0.80	4.46 10 ⁻²
MBAI:DBH ₂₀₀₂	2.89	3.37	0.86	0.39	18.10
MBAI:DBH ₂₀₀₂ ²	-6.18	3.34	-1.85	0.06	2.07 10 ⁻³
Nstem:DBH ₂₀₀₂	1.32	4.12	0.32	0.75	3.76
Nstem:DBH ₂₀₀₂ ²	0.00	4.88	0.00	1.00	1.00

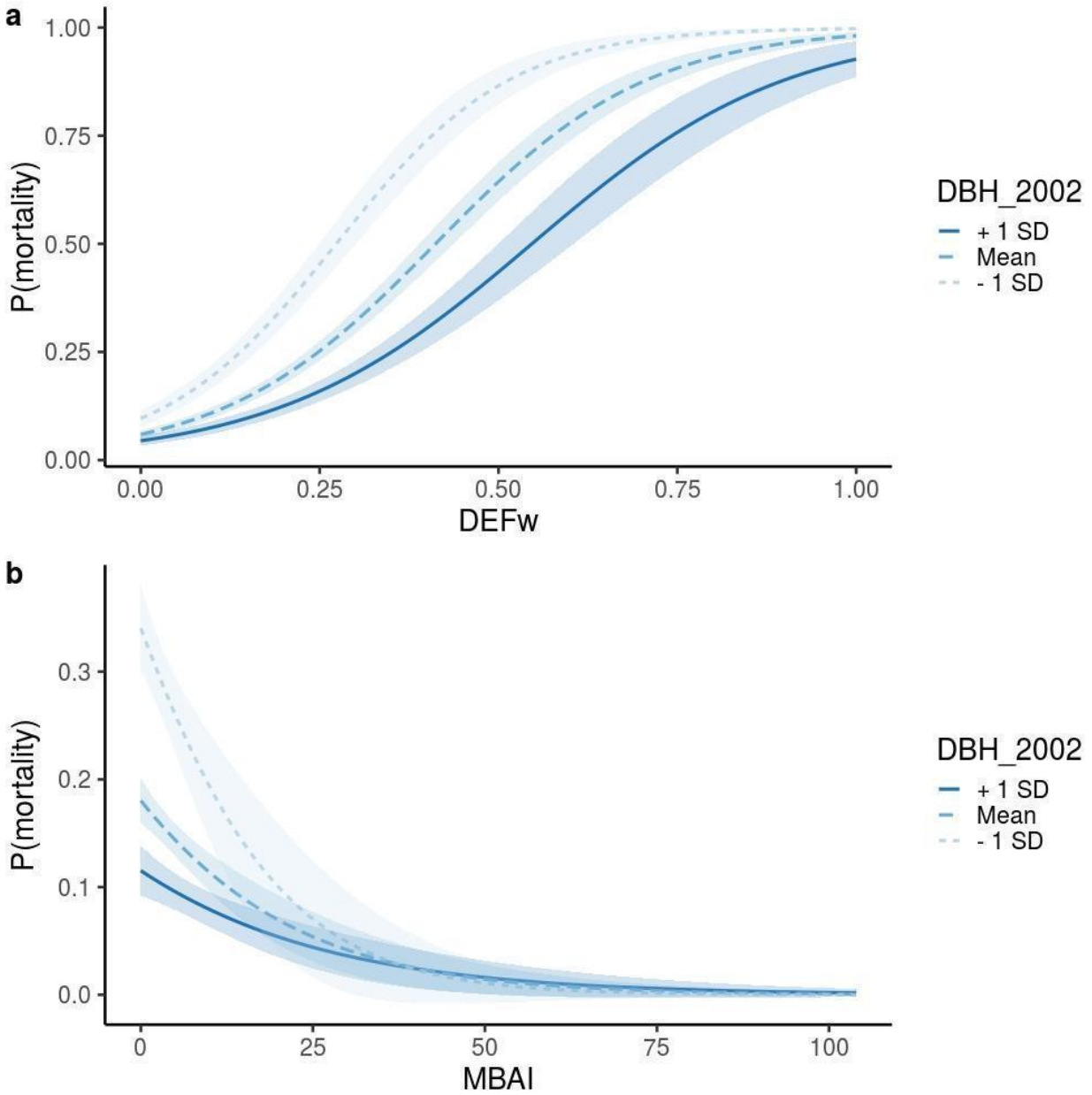
420 Interaction effects between size and defoliation on mortality were significant: the relative
421 probability of mortality increased more rapidly with DEFw for small rather than larger trees, and at
422 an equal level of defoliation, the probability of mortality was always higher for smaller trees (Figure
423 3a, Table 2). Interaction effects between size and growth on mortality were also significant: the
424 decrease in the relative probability of mortality with increasing mean growth was evident mostly
425 for small trees (Figure 3b). These results were robust for the choice of the competition variable
426 (N_{stem} versus competition indices), for the choice of the size variable (height instead of diameter)
427 and for the consideration of size (DBH_{2002}) as a quantitative versus categorical variable (Appendix
428 3). Finally, we obtained convergent results with an alternative approach (survival analysis) which
429 account simultaneously for both levels of variability (individual and temporal) in our data set
430 (Appendix 4).

431 **Individual variation in vulnerability simulated with CASTANEA**

432 Simulations with CASTANEA showed that inter-individual differences in tree size, phenology,
433 and defoliation, together with the intensity of climatic stress, affected the physiological responses
434 to stress. The magnitude of the individual effects on tree vulnerability differed during a drought year
435 (2006), a frost year (2010) and a good year (2008, 2014 or 2016; Figure 4). The loss of conductance
436 was higher for trees with early budburst and for larger trees, but this effect was only evident in
437 drought years (Figure 4a). Moreover, during drought, the ability to defoliate decreased the risk of
438 cavitation (Figure 4a) but increased the risk of carbon starvation (Figure 4b). By contrast, phenology
439 only poorly affected the biomass of reserve (BoR): even during a frost year, trees with earlier
440 budburst did not reduce their BoR, due to their ability to reflush (Figure 4b). BoR was always lower
441 for large tree, even without stress. This was expected, because there is no explicit competition for
442 light in CASTANEA. Hence large trees and small trees have a relatively similar photosynthesis when
443 it is scaled by soil surface (large trees photosynthesise slightly more because they have a stronger
444 LAI). Large trees, on the other hand, have a larger living biomass and thus a higher level of
445 respiration, which leads to lower reserves.

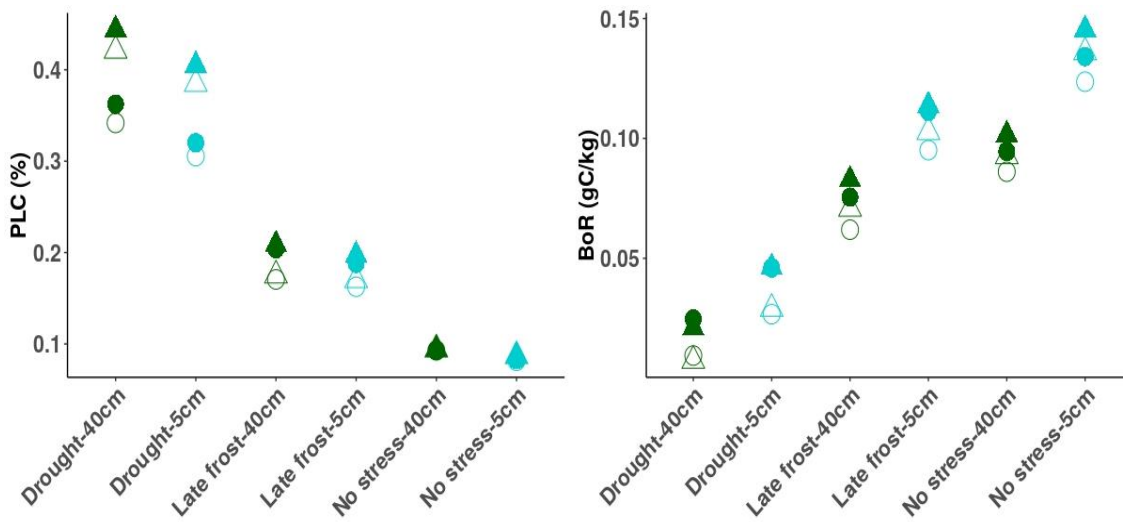
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453 **Figure 3: Interaction effects in the logistic regression model at individual-level** (a) between
 454 diameter (DBH₂₀₀₂) and weighted defoliation (DEFw). (b) between DBH₂₀₀₂ and the mean growth in
 455 basal area (MBAI). Regression lines are plotted for three values of DBH₂₀₀₂, corresponding to ± 1
 456 standard deviation (10.7 cm) from the mean (22 cm). Confidence intervals at 95% are shown around
 457 each regression line.



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461 **Figure 4: Physiological proxies of vulnerability simulated for eight trees differing in size,**
 462 **defoliation and budburst phenology.** We focus on three key years: 2006 (drought); 2008 (no stress);
 463 2010 (late frosts). Colours indicate the DBH at the beginning of the simulation: 5 cm (light blue)
 464 versus 40 cm (dark green). Triangles (respectively round) indicate individuals with early (respectively
 465 “normal”) budburst. Empty (respectively full) indicate individuals able (respectively not able)
 466 to defoliate.
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Table 3: Summary of the main effects of the studied variables on mortality.
NLF: number of late frost days; PLC= percentage of loss conductance; BoR: Biomass of reserve

<i>Temporal variations in the population mortality rate.</i>		
Simulated variables	Related climate stress	Process-based model
NLF	late frost	Not directly correlated with the observed mortality rate
PLC	drought	Not directly correlated with the observed mortality rate
BoR	late frost and drought	Not directly correlated with the observed mortality rate
CVI	PLC + NLF - BoR	Positively correlated with the observed mortality rate
<i>Inter-individual variations in tree's probability of mortality</i>		
Variables	Statistical model	Process-based model
Crown defoliation	Associated to a strong increase in mortality, especially for small trees	Associated to a lower BoR but also to a lower PLC
Size (DBH)	The smallest and the largest trees had a higher mortality	Large trees had always a lower BoR, and a higher PLC in drought year
Growth (MBAI)	Fast-growing trees had a lower mortality (evident only for small trees)	Not tested
Budburst phenology	Tree with earlier budburst had a higher mortality	Tree with earlier budburst had a lower PLC in drought year
Competition (Nstem)	Increasing competition was associated to a higher mortality	Not tested
Presence of fungi	Tree with fungi had a higher mortality	Not tested

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475 **Discussion**

476 By combining statistical and process-based models (Figure 1, Table 3), this study shed new
 477 light on the inter-annual and inter-individual variability of mortality in a drought- and frost-prone
 478 beech population. We showed that mortality in this marginal population is triggered by a
 479 combination of climatic factors, and that the vulnerability to drought and frost is modulated by
 480 several individual characteristics (defoliation, vegetative phenology, growth, size, competitors).

481 **The rate of mortality increased in response to drought and late frosts**

482 The annual mortality rates observed in this study ranged between 0.7 and 3.3% (mean value
 483 = 2%). This is at the upper range of the few mortality estimates available for beech. Hülsmann et al.
 484 (2016) reported annual mean rates of mortality of 1.4%, 0.7% and 1.5% in unmanaged forests of
 485 Switzerland, Germany and Ukraine, with a maximum mortality rate of 2.2%. Archambeau et al.

486 (2019) estimated even lower mortality rates (mean annual value = $3.8 \cdot 10^{-3}\%$, range = $3.7 \cdot 10^{-3}\%$ to
487 $3.8 \cdot 10^{-3}\%$) from European forest inventory data (including managed and unmanaged forests).
488 Overall, these mortality rates are low when compared to other tree species; for instance, according
489 to the French national forest inventory, the average mortality is 0.1% for beech against 0.3% on
490 average for other species and 0.4% for spruce or 0.2% for silver fir (IFN 2016). The relatively high
491 value observed here may result from the absence of management, combined with the population
492 location being at the dry, warm margin of species distribution (Figure S1), where most population
493 extinctions are expected in Europe (Thuiller et al. 2005). [However, we cannot rule out that the size
494 threshold in inventories, which differ between studies, also affects these different mortality
495 estimates \(e.g., a higher frequency of smaller trees increases the mortality rate\).](#)

496 We showed that inter-annual variations in the observed mortality rate at population-level
497 were significantly associated with variations in the [cumulative](#) vulnerability index (CVI) integrating
498 the number of late frost days (NLF), the percentage loss of conductance (PLC) and the biomass of
499 carbon reserves (BoR) simulated by CASTANEA. This association was not found when the three
500 response variables simulated by CASTANEA were considered separately, highlighting that patterns
501 of mortality in beech are driven by a combination [of drought and late-frost stresses](#). In particular,
502 simulations showed that in 2010 (a year without drought), the high mortality rate coincided with an
503 extreme late frost event. This is consistent with the study of Vanoni et al (2016), which showed that
504 both drought and frost could contribute to beech mortality. [Our results also support the emerging
505 consensus that mortality at dry, warm margins is not due either to carbon starvation or hydraulic
506 failure, but is rather the result of a balance of all these responses](#) (e.g. McDowell et al. 2011; Sevanto
507 et al. 2014).

508 In future developments, the CVI could be refined in several ways. Its different components
509 could be weighted based on ecophysiological knowledge. The CVI could also benefit from taking into
510 account the temporal dynamics of mortality, such as the existence of positive or negative post-
511 effects across years. The low number of observations in this study compelled us to ignore these
512 lagged effects, which probably explains why the CVI failed to predict the high mortality observed in
513 2007. Indeed, the high mortality [in 2007](#) is probably due to the lagged effect of the 2006 drought.
514 Such lags between the weakening of a tree and its final death were shown for beech in Vanoni
515 (2016) and silver fir in Davi & Cailleret (2017).

516 **The vulnerability to drought and frost varied among individuals**

517 The large number of trees individually monitored in this study provided us with an
518 exceptionally large sample size to test for the effects of [factors modulating individual vulnerability](#)
519 [to climatic hazards \(drought and late frost\)](#) and to [biotic pressures \(competition and the presence](#)
520 [of a fungus\)](#). Firstly, we found that a higher mean growth was associated with a lower probability of
521 mortality, as previously demonstrated (Cailleret and Davi 2011; Gao et al. 2018). This decrease in
522 mortality with increasing mean growth was evident mostly for small trees as already reported in
523 beech seedlings (Collet and Le Moguedec 2007) and other species (Kneeshaw et al. 2006; Lines,
524 Coomes, and Purves 2010), but not in adult beech trees to our knowledge.

525 Secondly, we found that increased defoliation was associated with increasing mortality. This
526 result was expected from previous studies (Dobbertin and Brang 2001, Carnicer et al. 2011),
527 although the consequences of defoliation are still being debated for beech. Senf et al. (2018)
528 showed that defoliation was associated with tree decline, while Bauch et al., (1996) and Pretzsch
529 (1996) found that the growth of highly defoliated beech trees did not decrease and could even
530 increase in some cases. Our simulations comparing trees able, or not able, to defoliate, shed light
531 on the multiple effects of defoliation on mortality. [These simulations showed](#) that defoliation indeed
532 decreased carbon reserves in good years but could also limit the loss of hydraulic conductance
533 during dry years. We also observed a significant interaction between defoliation and tree size on
534 mortality, showing that small trees were more vulnerable to mortality in response to defoliation
535 than large trees. However, we cannot rule out that this effect is due in part to the categorical
536 method used to survey defoliation, which does not take into account the percentage of crown loss.
537 Hence, defoliation may be biased with respect to size, such that small and defoliated trees will on
538 average have a higher proportion of canopy loss, and therefore be more impacted than large and
539 defoliated trees.

540 Thirdly, both statistical and process-based approaches found that trees with early budburst
541 were more prone to die. By contrast, Robson et al. (2013) showed that trees with early budburst
542 were not more vulnerable to mortality, but rather grew better, consistent with our simulations
543 where trees with early budburst accumulate more reserves during good years. This discrepancy may
544 be due to the location of our studied population at the rear-edge of beech distribution, where earlier
545 budburst dates are observed due to higher temperature and may expose trees to a higher risk of
546 late frost. It may be that the presence of trees with very early budburst in the studied population
547 makes it somewhat unusual, although similar cases have been observed elsewhere (Gausson 1958;

548 Perci du Sert 1982). In CASTANEA simulations, the higher vulnerability of early trees resulted rather
549 from a higher risk of hydraulic failure than from a higher impact of late frosts. This is because trees
550 with early budburst have a longer vegetation season and they develop their canopies faster, which
551 also increases their water needs [due to the increase of transpiration](#). Altogether, the relationships
552 between phenology and mortality deserve further investigation, especially since the spatio-
553 temporal variation of budburst patterns under climate change may produce complex spatio-
554 temporal patterns of stresses (Vanoni et al. 2016).

555 Regarding the effect of size, the results differed between the statistical approach, where large
556 trees died less than small ones, and the simulations, which predicted a greater vulnerability to
557 drought of large trees. There may be several explanations for this discrepancy. The first reason is
558 that CASTANEA simulates an average tree without explicit competition for light and water; hence
559 not accounting for the higher observed background mortality in small trees as compared to large
560 ones (Figure S7). In addition, CASTANEA also does not account for individual dominance status,
561 which can affect the current carbon balance of a tree and hence its capacity to mitigate stress. In
562 the studied population, large trees are more likely to be dominant, with better access to light
563 resources promoting carbon accumulation, as compared to small trees, which are more likely to be
564 suppressed. Another reason is that tree size may vary with environmental factors in the studied
565 population, such that large trees have a tendency to occur on better soils. Therefore, the size effect
566 observed through the statistical approach may reveal the confounding effect of spatial soil
567 heterogeneity, not taken into account in the PBM. A measurement of water availability at individual
568 tree level would be necessary to address this issue but was out of the scope of this study.

569 **Combining statistical and process-based approaches to identify the causes of tree** 570 **vulnerability**

571 These two approaches illustrate the classical compromise between a fine understanding of
572 physiological mechanisms driving mortality, with complex and expensive PBMs, versus [high](#)
573 [precision in local mortality predictions](#), with statistical models requiring less data, but having a
574 weaker ability to generalize proximal causes. Most often, studies adopt either of the two
575 approaches, and generally statistical approaches prevail (Hülsmann et al. 2016; Seidl et al. 2011).
576 However, the two approaches are highly complementary, and combining them allows the
577 deciphering of the respective roles of the drivers and mechanisms underlying tree mortality and
578 understanding their variability among individuals or years (Hawkes 2000; O'Brien et al. 2017; Seidl

579 et al. 2011). The two approaches can be compared as this study does at the individual level, or they
580 [can be combined](#) as when we analysed the correlation between the observed mortality rate and
581 simulated stress response variables. An upper level of integration would be inverse modelling,
582 where observed mortality rates could be used to infer the physiological thresholds (e.g. in BoR, PLC
583 and NLF) likely to trigger mortality (Davi & Cailleret 2017; [Cailleret et al., 2020](#)).

584 This study also illustrated a classical difficulty in combining statistical and process-based
585 approaches, related to the difference between observed variables and PBM parameters. For
586 instance, the comparison of defoliated and non-defoliated trees does not have exactly the same
587 meaning when using CASTANEA and the statistical approach. In CASTANEA, we compared trees, able
588 versus unable to defoliate, while these average trees shared on average the same edaphic
589 conditions. In the statistical approach, we compared trees with different levels of defoliation, but
590 which also probably did not share the same edaphic and biotic conditions. Defoliation was thus also
591 likely to be an indicator of the fertility of the environment, such that on shallow soils, defoliation
592 was stronger and the probability of mortality increased. Hence, the correlation does not necessarily
593 involve a causal relationship between defoliation and mortality.

594 The major benefits of our approach combining different approaches (statistical, process-
595 based) at different scales (population, individual) is that it [should ultimately allow to disentangle](#)
596 ecological patterns observed at an upper scale (population, multi-year period), and get back to
597 patterns observed at a lower scale where processes operate (individual, year). This ability to
598 aggregate/disaggregate patterns is acknowledged as a powerful approach to understand apparent
599 contradictions between patterns observed at different scales (Clark et al. 2011). There are however
600 some limitations to the approaches we used here. First, none of them could fully account for the
601 non-independence of climatic effects on mortality between years. Indeed, the effect of climatic
602 variables at a given year may depend on other variables expressed in previous years. This was
603 observed in beech, where several drought years finally led to a growth decline (Jump et al. 2006;
604 Knutzen et al. 2017; Vanoni et al. 2016) or a modification in sap flow (Hesse et al. 2019). Moreover,
605 the processes driving mortality may change through time as the most sensitive individuals are
606 progressively eliminated, and/or the surviving trees become less and less sensitive (i.e. acclimation
607 Niinemets 2010). Finally, the statistical model at the individual level could not fully make use of the
608 repeated measurements of mortality over the years, partly because other individual variables were
609 measured only once over the study period (except defoliation). Survival analyses could

610 unfortunately not fully address this limitation (Appendix 4), and the development of a finely tuned
611 Bayesian approach was out of the scope of this study. Besides methodological improvements,
612 another extension to the present study would be to combine statistical and process-based
613 approaches at a larger spatial scale, among populations across climatic gradients. This would allow
614 the investigation of whether the respective drought and late frost sensitivity differ between the
615 rear, core and leading edge of species distribution, as suggested by Cavin and Jump (2017).

616 ***Data accessibility***

617 The data set analysed in this preprint is available online under the zenodo repository
618 (<https://doi.org/10.5281/zenodo.3519315>). Raw data can be obtained from JG, JAM and CH.

619 ***Supplementary material***

620 The process-based model CASTANEA is an open-source software available on capsis website:
621 <http://capsis.cirad.fr/>
622 Supplementary materials (Figures and Tables) for this preprint are available on bioRxiv (XXX).

623 ***Author Contributions***

624 JAM, JG, CH and EM measured and mapped all the trees. CPC performed the wood core analyses.
625 CPC, FL and SOM designed and ran the statistical models. CPC and HD ran the PBM. CPC drafted the
626 manuscript, and all authors contributed to its improvement.

627 ***Acknowledgments***

628 We are grateful to M. Cailleret, B. Fady, and N. Martin Saint Paul for discussions and comments on
629 a previous version of this manuscript. We thank E.Walker and F.Bonneu for statistical discussions
630 and advices, N. Mariotte for wood core sampling, and F. Guibal for their analyses. SOM and HD were
631 funded by the EU ERA-NET BiodivERSa projects TIPTREE (BiodivERSa2-2012-15) and the ANR project
632 MeCC (ANR-13-ADAP-0006). CP received funding from the European Union's Horizon 2020 research
633 and innovation programme under grant agreement No. 676876 (GenTree).

634 ***Conflict of interest disclosure***

635 The authors of this preprint declare that they have no financial conflict of interest with the content
636 of this article. SOM is one of the PCIEcology recommenders.

637 ***References***

638 Adams, Henry D. et al. 2017. "A Multi-Species Synthesis of Physiological Mechanisms in Drought-
639 Induced Tree Mortality." *Nature Ecology and Evolution* 1(9):1285–91.

640 Akaike, Hirotugu. 1987. "Factor Analysis and AIC." Pp. 371–86 in. Springer, New York, NY.

641 Allen, Craig D. et al. 2010. "A Global Overview of Drought and Heat-Induced Tree Mortality Reveals

642 Emerging Climate Change Risks for Forests." *Forest Ecology and Management* 259(4):660–

643 84.

644 Anderegg, W. R. L. et al. 2012. "From the Cover: The Roles of Hydraulic and Carbon Stress in a

645 Widespread Climate-Induced Forest Die-Off." *Proceedings of the National Academy of*

646 *Sciences* 109(1):233–37.

647 Anderegg, William R. L. 2015a. "Spatial and Temporal Variation in Plant Hydraulic Traits and Their

648 Relevance for Climate Change Impacts on Vegetation." *New Phytologist* 205(3):1008–14.

649 Anderegg, William R. L. et al. 2015b. "Tree Mortality from Drought, Insects, and Their Interactions

650 in a Changing Climate." *New Phytologist* 208(3):674–83.

651 Archambeau, Juliette et al. 2019. "Similar Patterns of Background Mortality across Europe Are

652 Mostly Driven by Drought in European Beech and a Combination of Drought and

653 Competition in Scots Pine." *Agricultural and Forest Meteorology*, 2020, vol. 280, p. 107772.

654 Arnold, Todd W. 2010. "Uninformative Parameters and Model Selection Using Akaike's

655 Information Criterion." *Journal of Wildlife Management* 74(6):1175–78.

656 Augspurger, Carol K. 2009. "Spring 2007 Warmth and Frost: Phenology, Damage and Refoliation in

657 a Temperate Deciduous Forest." *Functional Ecology* 23(6):1031–39.

658 Ball, J. Timothy, Ian E. Woodrow, and Joseph A. Berry. 1987. "A Model Predicting Stomatal

659 Conductance and Its Contribution to the Control of Photosynthesis under Different

660 Environmental Conditions." Pp. 221–24 in *Progress in photosynthesis research*. Springer.

661 Barnier, Julien, François Briatte, and Joseph Larmarange. 2018. "Question: Functions to Make

662 Surveys Processing Easier."

663 Bauch, Josef. 1986. "Characteristics and Response of Wood in Declining Trees from Forests

664 Affected by Pollution." *IAWA Journal* 7(4):269–76.

665 Beguería, Santiago and Sergio M. Vicente-Serrano. 2017. "SPEI: Calculation of the Standardised

666 Precipitation-Evapotranspiration Index."

667 Benito Garzón, Marta et al. 2018. "The Legacy of Water Deficit on Populations Having Experienced

668 Negative Hydraulic Safety Margin." *Global Ecology and Biogeography* 27(3):346–56.

669 [Berzaghi, F., Wright, I. J., Kramer, K., Oddou-Muratorio, S., Bohn, F. J., Reyer, C. P., ... & Hartig, F. 2020. Towards a new generation of trait-flexible vegetation models. *Trends in Ecology & Evolution*, 35\(3\), 191-205.](#)

670

671

672 Bigler, Christof and Harald Bugmann. 2018. "Climate-Induced Shifts in Leaf Unfolding and Frost

673 Risk of European Trees and Shrubs." *Scientific Reports* 8(1):1–10.

674 Brando, Paulo Monteiro et al. 2014. "Abrupt Increases in Amazonian Tree Mortality Due to

675 Drought-Fire Interactions." *Proceedings of the National Academy of Sciences of the United*

676 *States of America* 111(17):6347–52.

677 Bréda, Nathalie, Roland Huc, André Granier, and Erwin Dreyer. 2006. "Temperate Forest Trees and

678 Stands under Severe Drought : A Review of Ecophysiological Responses , Adaptation

679 Processes and Long-Term Consequences." *Annals of Forest Science* 63(6):625–44.

680 Brier, Glenn W. 1950. "Verification of Forecasts Expressed in Terms of Probability." *Monthly*

681 *Weather Review* 78(1):1–3.

682 De Caceres, Miquel, Nicolas Martin-StPaul, Marco Turco, Antoine Cabon, and Victor Granda. 2018.

683 "Estimating Daily Meteorological Data and Downscaling Climate Models over Landscapes."

684 *Environmental Modelling and Software* 186–96.

685 Cailleret, Maxime et al. 2017. "A Synthesis of Radial Growth Patterns Preceding Tree Mortality."

686 *Global Change Biology* 23(4):1675–90.

687 Cailleret, Maxime and Hendrik Davi. 2011. "Effects of Climate on Diameter Growth of Co-Occurring
688 *Fagus Sylvatica* and *Abies Alba* along an Altitudinal Gradient." *Trees* 25(2):265–76.

689 [Cailleret, M., Bircher, N., Hartig, F., Hülsmann, L., & Bugmann, H. \(2020\). Bayesian calibration of a
690 growth dependent tree mortality model to simulate the dynamics of European temperate -
691 forests. *Ecological Applications*, 30\(1\), e02021](#)

692 Campbell, Gaylon S. 1974. "A Simple Method for Determining Unsaturated Conductivity from
693 Moisture Retention Data." *Soil Science* 117(6):311–14.

694 Carnicer, Jofre et al. 2011. "Widespread Crown Condition Decline, Food Web Disruption, and
695 Amplified Tree Mortality with Increased Climate Change-Type Drought." *Proceedings of the
696 National Academy of Sciences* 108(4):1474–78.

697 Cavin, Liam and Alistair S. Jump. 2017. "Highest Drought Sensitivity and Lowest Resistance to
698 Growth Suppression Are Found in the Range Core of the Tree *Fagus Sylvatica* L. Not the
699 Equatorial Range Edge." *Global Change Biology* 23(1):362–79.

700 Cheaib, Alissar et al. 2012. "Climate Change Impacts on Tree Ranges: Model Intercomparison
701 Facilitates Understanding and Quantification of Uncertainty." *Ecology Letters* 15(6):533–44.

702 Choat, Brendan et al. 2018. "Triggers of Tree Mortality under Drought." *Nature* 558(7711):531–39.

703 Chuine, Isabelle, P. Cour, and D. D. Rousseau. 1999. "Selecting Models to Predict the Timing of
704 Flowering of Temperate Trees: Implications for Tree Phenology Modelling." *Plant, Cell and
705 Environment* 22(1):1–13.

706 Clark, James S. et al. 2011. "Individual-Scale Variation, Species-Scale Differences: Inference
707 Needed to Understand Diversity." *Ecology Letters* 14(12):1273–87.

708 Collet, Catherine and Gilles Le Moguedec. 2007. "Individual Seedling Mortality as a Function of
709 Size, Growth and Competition in Naturally Regenerated Beech Seedlings." *Forestry*
710 80(4):359–70.

711 Cowan, I. R. and G. D. Farquhar. 1977. "Stomatal Function in Relation to Leaf Metabolism and
712 Environment." *Symposia of the Society for Experimental Biology* 31:471–505.

713 Cribari-Neto, Francisco and Achim Zeileis. 2010. "Beta Regression in R." *Journal of Statistical
714 Software* 34(2).

715 Davi, H. et al. 2005. "Modelling Carbon and Water Cycles in a Beech Forest. Part II.: Validation of
716 the Main Processes from Organ to Stand Scale." *Ecological Modelling* 185(2–4):387–405.

717 Davi, H., C. Barbaroux, C. Francois, and E. Dufrêne. 2009. "The Fundamental Role of Reserves and
718 Hydraulic Constraints in Predicting LAI and Carbon Allocation in Forests." *Agricultural and
719 Forest Meteorology* 149(2):349–61.

720 Davi, Hendrik and Maxime Cailleret. 2017. "Assessing Drought-Driven Mortality Trees with
721 Physiological Process-Based Models." *Agricultural and Forest Meteorology* 232:279–90.

722 Dittmar, Christoph, Wolfgang Zech, and Wolfram Elling. 2003. "Growth Variations of Common
723 Beech (*Fagus Sylvatica* L.) under Different Climatic and Environmental Conditions in
724 Europe—a Dendroecological Study." *Forest Ecology and Management* 173(1–3):63–78.

725 Dobbertin, Matthias and Peter Brang. 2001. "Crown Defoliation Improves Tree Mortality Models." *Forest Ecology and Management* 141(3):271–84.

726 Dufrêne et al. 2005. "Modelling Carbon and Water Cycles in a Beech Forest Part I : Model
727 Description and Uncertainty Analysis on Modelled NEE." *Ecological Modelling* 185:407–36.

728 Durand-Gillmann, Marion, Maxime Cailleret, Thomas Boivin, Louis Michel Nageleisen, and Hendrik
729 Davi. 2014. "Individual Vulnerability Factors of Silver Fir (*Abies Alba* Mill.) to Parasitism by
730 Two Contrasting Biotic Agents: Mistletoe (*Viscum Album* L. Ssp. *Abietis*) and Bark Beetles
731 (Coleoptera: Curculionidae: Scolytinae) during a Decline Process." *Annals of Forest Science*
732 71(6):659–73.

733

- 734 Farquhar, G. D., S. von Caemmerer, and J. A. Berry. 1980. "A Biochemical Model of Photosynthetic
735 CO₂ Assimilation in Leaves of C₃ Species." *Planta* 149(1):78–90.
- 736 Feng, Xue et al. 2018. "The Ecohydrological Context of Drought and Classification of Plant
737 Responses." *Ecology Letters*, November 1, 1723–36.
- 738 Gao, Shan et al. 2018. "Dynamic Responses of Tree-Ring Growth to Multiple Dimensions of
739 Drought." *Global Change Biology* 24(11):5380–90.
- 740 García-Plazaola, José Ignacio, Raquel Esteban, Koldobika Hormaetxe, Beatriz Fernández-Marín, and
741 José María Becerril. 2008. "Photoprotective Responses of Mediterranean and Atlantic Trees
742 to the Extreme Heat-Wave of Summer 2003 in Southwestern Europe." *Trees* 22(3):385–92.
- 743 Gausсен, H. 1958. "Le Hêtre Aux Pyrénées Espagnoles." Pp. 185–91 in *Actas del tercer congreso
744 internacional de estudios pirenaicos*, Gerona.
- 745 Gauzere, J. et al. 2017. "Integrating Interactive Effects of Chilling and Photoperiod in Phenological
746 Process-Based Models. A Case Study with Two European Tree Species: *Fagus Sylvatica* and
747 *Quercus Petraea*." *Agricultural and Forest Meteorology* 244–245:9–20.
- 748 Gillner, Sten, Nadja Rüger, Andreas Roloff, and Uta Berger. 2013. "Low Relative Growth Rates
749 Predict Future Mortality of Common Beech (*Fagus Sylvatica* L.)." *Forest Ecology and
750 Management* 302:372–78.
- 751 Granier, A., P. Biron, and D. Lemoine. 2000. "Water Balance, Transpiration and Canopy
752 Conductance in Two Beech Stands." *Agricultural and Forest Meteorology* 100(4):291–308.
- 753 Greenwood, Sarah et al. 2017. "Tree Mortality across Biomes Is Promoted by Drought Intensity,
754 Lower Wood Density and Higher Specific Leaf Area" edited by J. Chave. *ECOLOGY LETTERS*
755 20(4):539–53.
- 756 Heinze, Georg. Christine Wallisch et al., Variable selection – A review and recommendations for
757 the practicing statistician. *Biometrical Journal* 60 (2018), S. 431-449
- 758 Hawkes, Corinna. 2000. "Woody Plant Mortality Algorithms: Description, Problems and Progress." *Ecological Modelling* 126(2–3):225–48.
- 759 Hesse, Benjamin D., Michael Goisser, Henrik Hartmann, and Thorsten E. E. Grams. 2019.
760 "Repeated Summer Drought Delays Sugar Export from the Leaf and Impairs Phloem
761 Transport in Mature Beech" edited by M. Dannoura. *Tree Physiology* 39(2):192–200.
- 762 Hijmans, Robert J., Steven Phillips, John Leathwick, Jane Elith, and Maintainer Robert J. Hijmans.
763 2017. "Package 'Dismo.'" *Circles* 9(1):1–68.
- 764 Hosmer, David W. and Stanley Lemeshow. 2000. *Applied Logistic Regression*.
- 765 Hülsmann, Lisa et al. 2016. "Does One Model Fit All? Patterns of Beech Mortality in Natural Forests
766 of Three European Regions." *Ecological Applications* 26(8):2463–77.
- 767 Hülsmann, Lisa, Harald Bugmann, and Peter Brang. 2017. "How to Predict Tree Death from
768 Inventory Data – Lessons from a Systematic Assessment of European Tree Mortality Models -
769 SUPP." *Canadian Journal of Forest Research (April):cjfr-2016-0224*.
- 770 Hülsmann, Lisa, Harald Bugmann, Maxime Cailleret, and Peter Brang. 2018. "How to Kill a Tree:
771 Empirical Mortality Models for 18 Species and Their Performance in a Dynamic Forest
772 Model." *Ecological Applications* 28(2):522–40.
- 773 IGN. 2016. *La Mortalité*. France. https://inventaire-forestier.ign.fr/IMG/pdf/2018_mortalite.pdf
- 774 Jump, Alistair S., Jenny M. Hunt, and Josep Peñuelas. 2006. "Rapid Climate Change-Related
775 Growth Decline at the Southern Range Edge of *Fagus Sylvatica*." *Global Change Biology*
776 12(11):2163–74.
- 777 Kneeshaw, Daniel D., Richard K. Kobe, K. David Coates, and Christian Messier. 2006. "Sapling Size
778 Influences Shade Tolerance Ranking among Southern Boreal Tree Species." *Journal of
779 Ecology* 94(2):471–80.
- 780

- 781 Knutzen, Florian, Choimaa Dulamsuren, Ina Christin Meier, and Christoph Leuschner. 2017.
782 "Recent Climate Warming-Related Growth Decline Impairs European Beech in the Center of
783 Its Distribution Range." *Ecosystems* 20(8):1494–1511.
- 784 Kramer, Koen et al. 2010. "Modelling Exploration of the Future of European Beech (*Fagus Sylvatica*
785 L.) under Climate Change-Range, Abundance, Genetic Diversity and Adaptive Response."
786 *Forest Ecology and Management* 259(11):2213–22.
- 787 Lebourgeois, F., N. Bréda, E. Ulrich, and A. Granier. 2005. "Climate-Tree-Growth Relationships of
788 European Beech (*Fagus Sylvatica* L.) in the French Permanent Plot Network (RENECOFOR)."
789 *Trees* 19:385–401.
- 790 Lederer, D. J., S. C. Bell et al., Control of Confounding and Reporting of Results in Causal Inference
791 Studies. Guidance for Authors from Editors of Respiratory, Sleep, and Critical Care Journals.
792 *Ann Am Thorac Soc* 16 (2019), S. 22-28.
- 793 Lenz, Armando, Günter Hoch, Yann Vitasse, and Christian Körner. 2013. "European Deciduous
794 Trees Exhibit Similar Safety Margins against Damage by Spring Freeze Events along
795 Elevational Gradients." *New Phytologist* 200(4):1166–75.
- 796 Lines, Emily R., David A. Coomes, and Drew W. Purves. 2010. "Influences of Forest Structure,
797 Climate and Species Composition on Tree Mortality across the Eastern US" edited by A.
798 Hector. *PLoS ONE* 5(10):e13212.
- 799 Long, Jacob A. 2018. "Jtools: Analysis and Presentation of Social Scientific Data."
- 800 Lorenz, Martin and Georg Becher. 2012. *Forest Condition in Europe*.
- 801 Loustau, D., A. Granier, F. El Hadj Moussa, M. Sartore, and M. Guedon. 1990. "Evolution
802 Saisonnière Du Flux de Sève Dans Un Peuplement de Pins Maritimes." *Annales Des Sciences*
803 *Forestières* 47(6):599–618.
- 804 Van Mantgem, Phillip J. et al. 2009. "Widespread Increase of Tree Mortality Rates in the Western
805 United States." *Science* 323(5913):521–24.
- 806 Maraun, Mark, Jörg-Alfred Salamon, Katja Schneider, Matthias Schaefer, and Stefan Scheu. 2003.
807 "Oribatid Mite and Collembolan Diversity, Density and Community Structure in a Moder
808 Beech Forest (*Fagus Sylvatica*): Effects of Mechanical Perturbations." *Soil Biology and*
809 *Biochemistry* 35(10):1387–94.
- 810 Martin, George L. and Alan R. Ek. 1984. "A Comparison of Competition Measures and Growth
811 Models for Predicting Plantation Red Pine Diameter and Height Growth." *Forest Science*
812 30(3):731–43.
- 813 McDowell, Nate G. et al. 2013. "Evaluating Theories of Drought-Induced Vegetation Mortality
814 Using a Multimodel-Experiment Framework." *New Phytologist* 200(2):304–21.
- 815 McDowell, Nate G. et al. 2011. "The Interdependence of Mechanisms Underlying Climate-Driven
816 Vegetation Mortality." *Trends in Ecology & Evolution* 26(10):523–32.
- 817 Meir, Patrick, Maurizio Mencuccini, and Roderick C. Dewar. 2015. "Drought-Related Tree
818 Mortality: Addressing the Gaps in Understanding and Prediction." *New Phytologist*
819 207(1):1443–47.
- 820 Menzel, Annette, Raimund Helm, and Christian Zang. 2015. "Patterns of Late Spring Frost Leaf
821 Damage and Recovery in a European Beech (*Fagus Sylvatica* L.) Stand in South-Eastern
822 Germany Based on Repeated Digital Photographs." *Frontiers in Plant Science* 6:110.
- 823 Monserud, Robert A. 1976. "Simulation of Forest Tree Mortality." *Forest Science* 22(4):438–44.
- 824 Monteith, J. L. 1965. "Evaporation and Environment. The State and Movement of Water in Living
825 Organisms. Symposium of the Society of Experimental Biology, Vol. 19 (Pp. 205-234)."
- 826 Mueller, Rebecca C. et al. 2005. "Differential Tree Mortality in Response to Severe Drought:
827 Evidence for Long-Term Vegetation Shifts." *Journal of Ecology* 93(6):1085–93.

828 Niinemets, Ülo. 2010. "Responses of Forest Trees to Single and Multiple Environmental Stresses
829 from Seedlings to Mature Plants: Past Stress History, Stress Interactions, Tolerance and
830 Acclimation." *Forest Ecology and Management* 260(10):1623–39.

831 Nourtier, Marie et al. 2014. "Transpiration of Silver Fir (*Abies Alba* Mill.) during and after Drought
832 in Relation to Soil Properties in a Mediterranean Mountain Area." *Annals of Forest Science*
833 71(6):683–95.

834 O'Brien, Michael J. et al. 2017. "A Synthesis of Tree Functional Traits Related to Drought-Induced
835 Mortality in Forests across Climatic Zones." *Journal of Applied Ecology* 54(6):1669–86.

836 O'Brien, Michael J., Sebastian Leuzinger, Christopher D. Philipson, John Tay, and Andy Hector.
837 2014. "Drought Survival of Tropical Tree Seedlings Enhanced by Non-Structural Carbohydrate
838 Levels." *Nature Climate Change* 4(8):710–14.

839 Pammenter NW and Vander Willigen C. 1998. "A Mathematical and Statistical Analysis of the
840 Curves Illustrating Vulnerability of Xylem to Cavitation." *Tree Physiology* 18(Equation 1):589–
841 593.

842 Penuelas, Josep and Martí Boada. 2003. "A Global Change-Induced Biome Shift in the Montseny
843 Mountains (NE Spain)." *Global Change Biology* 9(2):131–40.

844 Perci du Sert, Th. 1982. *Relations Entre La Phenologie et La Morphologie Du Hêtre Dans Le Massif
845 Des Albères.*

846 Pretzsch, Hans. 1996. "Growth Trends of Forests in Southern Germany." Pp. 107–31 in *Growth
847 Trends in European Forests.* Berlin, Heidelberg: Springer Berlin Heidelberg.

848 Robson, T. Matthew, Erwin Rasztovits, Pedro J. Aphalo, Ricardo Alia, and Ismael Aranda. 2013.
849 "Flushing Phenology and Fitness of European Beech (*Fagus Sylvatica* L.) Provenances from a
850 Trial in La Rioja, Spain, Segregate According to Their Climate of Origin." *Agricultural and
851 Forest Meteorology* 180:76–85.

852 Ryan, Michael G. 1991. "Effects of Climate Change on Plant Respiration." *Ecological Applications*
853 1(2):157–67.

854 Sala, A. and J. D. Tenhunen. 1996. "Simulations of Canopy Net Photosynthesis and Transpiration in
855 *Quercus Ilex* L. under the Influence of Seasonal Drought." *Agricultural and Forest
856 Meteorology* 78(3–4):203–22.

857 Schielzeth, Holger. 2010. "Simple Means to Improve the Interpretability of Regression
858 Coefficients." *Methods in Ecology and Evolution* 1(2):103–13.

859 Seidl, Rupert et al. 2011. "Modelling Natural Disturbances in Forest Ecosystems: A Review." *Ecological Modelling* 222(4):903–24.

860 Senf, Cornelius et al. 2018. "Canopy Mortality Has Doubled in Europe's Temperate Forests over
861 the Last Three Decades." *Nature Communications* 9(1):4978.

862 Sevanto, Sanna, Nate G. McDowell, L. Turin Dickman, Robert Pangle, and William T. Pockman.
863 2014. "How Do Trees Die? A Test of the Hydraulic Failure and Carbon Starvation
864 Hypotheses." *Plant, Cell and Environment* 37(1):153–61.

865 Stadt, Kenneth J. et al. 2007. "Evaluation of Competition and Light Estimation Indices for
866 Predicting Diameter Growth in Mature Boreal Mixed Forests." *Annals of Forest Science*
867 64(64):477–90.

868 Thuiller, Wilfried, Sandra Lavorel, M. B. Araujo, Martin T. Sykes, and I. Colin Prentice. 2005.
869 "Climate Change Threats to Plant Diversity in Europe." *Proceedings of the National Academy
870 of Sciences* 102(23):8245–50.

871 Tyree, M. T. and J. S. Sperry. 1989. "Vulnerability of Xylem to Cavitation and Embolism." *Annual
872 Review of Plant Physiology and Plant Molecular Biology* 40(1):19–36.

873

- 874 Vanoni, Marco, Harald Bugmann, Magdalena Nötzli, and Christof Bigler. 2016. "Drought and Frost
875 Contribute to Abrupt Growth Decreases before Tree Mortality in Nine Temperate Tree
876 Species." *Forest Ecology and Management Journal* 382:51–63.
- 877 Vidal, Jean-Philippe, Eric Martin, Laurent Franchistéguy, Martine Baillon, and Jean-Michel
878 Soubeyroux. 2010. "A 50-Year High-Resolution Atmospheric Reanalysis over France with the
879 Safran System." *International Journal of Climatology* 30(11):1627–44.
- 880 Vitasse, Yann et al. 2009. "Leaf Phenology Sensitivity to Temperature in European Trees: Do
881 within-Species Populations Exhibit Similar Responses?" *Agricultural and Forest Meteorology*
882 149(5):735–44.
- 883 De Vries, F. W. T. Pennin., A. H. M. Brunsting, and H. H. Van Laar. 1974. "Products, Requirements
884 and Efficiency of Biosynthesis a Quantitative Approach." *Journal of Theoretical Biology*
885 45(2):339–77.
- 886

887 Appendices

888 Four supplementary appendices are available on bioRxiv (XXX):

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890 Appendix 1: CASTANEA model, calibration and simulation design

891 Appendix 2: Beta-regression model for the temporal variations in the rate of mortality at population
892 level

893 Appendix 3: Logistic regression models for the probability of mortality at tree-level

894 Appendix 4: Survival analysis the probability of mortality at tree- and year-levels

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