Title:

Combining statistical and mechanistic models to unravel the drivers of mortality within a rear-edge beech population

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Abstract

As several studies report an increasing decline of forests, a major issue in ecology is to better understand and predict tree mortality. The interactions between the different factors and physiological processes driving tree mortality, as well as the individual between-trees variability of mortality risk remain to be characterised.

This study is based on an exceptional yearly individual monitoring of 4327 European beeches (*Fagus sylvatica*) since 2002 in a rear-edge population within a natural reserve. We combined two types of approaches. Statistical models were used to quantify the effects of climate, competition, tree size and health on mortality. Carbon reserves, hydraulic conductance and late frosts were simulated using a process-based model to disentangle the mechanisms driving temporal and inter-individual variations in mortality.

The mortality rate at population level was associated to drought indices in statistical models, and driven by a combination of conductance loss, carbon reserve depletion and late frost damages in the process-based simulations. In statistical models, the individual probability of mortality decreased with mean growth, and increased with crown defoliation, budburst earliness, fungi presence and competition. Interaction effects between tree size and defoliation were significant, the probability of mortality being higher for a small-defoliated tree than for a tall one. Finally, the process-based model predicted a higher conductance loss and a higher frequency of late frosts for earlier trees together with a higher level of carbon reserve, while the ability to defoliate crown was found to limit the impact of hydraulic stress and allow carbon reserve accumulation.

We discuss the convergences and divergences obtained between statistical and process-based approaches and we highlight the importance of combining them to disentangle the processes underlying mortality, and to account for individual variability in vulnerability.

Keywords: *Fagus sylvatica*, logistic regression, process-based model, CASTANEA, Longitudinal analysis, defoliation.

Introduction

Global change has been repeatedly reported to generate forest decline and tree mortality, both in terms of background, non-catastrophic mortality(Van Mantgem et al. 2009, Lorenz and Becher 2012) and of massive, catastrophic mortality due to extreme, pulse events (Allen et al. 2010; Lorenz and Becher 2012; Mueller et al. 2005). To predict how such new regime of tree mortality will impact forest structure, composition and ecosystem services (Anderegg et al. 2015; Choat et al. 2018), we need to better decipher the respective roles of the various drivers and mechanisms underlying tree mortality.

Studying mortality poses several well-recognized challenges. It is triggered by several factors and involves several underlying and interacting physiological processes. The factors triggering mortality include extreme, pulse climatic events (i.e. repeated drought, storm, flood, heavy snow, late frost, wildfire) or sudden changes in biotic interactions (i.e. emerging pests, invasive species), but also long-term climatic or biotic perturbations (i.e. recurrent water deficits, changes in competition at the community level) (Maraun et al. 2003; McDowell et al. 2011). Moreover, these factors can have interactive effects: for instance, drought may increase tree vulnerability to pests (Durand-Gillmann et al. 2014; Anderegg et al. 2015) or stand vulnerability to fire (Brando et al. 2014). Finally, a single factor triggering mortality may involve several underlying physiological processes, with several thresholds leading to mortality and potentially feedbacks between them (McDowell et al. 2011). This is exemplified by drought, which is usually considered to trigger mortality through the combination of hydraulic failure and carbon starvation (Adams et al. 2017; Anderegg et al. 2012; McDowell et al. 2011). Hydraulic failure is the loss of conductance resulting from major xylem embolism, i.e. the formation of water vapour or air bubbles within the conductive vessels due to high water tension from soil to canopy (Tyree and Sperry 1989). To avoid hydraulic failure, trees can close their stomata before reaching the vessel species-specific embolism point (Cowan and Farquhar 1977). However, stomata closure mechanically reduces photosynthetic activity, forcing the tree to ensure basal metabolism using carbon reserves, which can eventually deplete them particularly during long drought, leading to mortality through carbon starvation. Many experimental studies on drought suggest that hydraulic failure is the most frequent cause of tree mortality, and at least, often the initial step towards cascading processes leading to mortality (Choat et al. 2018). Nevertheless, the relationship between carbon and water fluxes and the role of biotic factors during and after drought are far from being resolved (Adams et al. 2017; Feng et al. 2018; McDowell et al. 2011; Meir, Mencuccini, and Dewar 2015; O'Brien et al. 2014).

Another challenge when studying mortality is that the physiological processes governing tree vulnerability may vary in space and time. For instance, vulnerability may vary among individual trees within a population according to (i) the local spatial heterogeneity of resources availability,

especially soil water (Nourtier et al. 2014); (ii) the heterogeneity in individual life history, and in particular the legacies of past stresses on tree morphology and anatomy (Vanoni et al. 2016); (iii) the inter-individual variation of physiological response to stresses, which depends on ontogenic, plastic, and genetic effects controlling the expression of traits (Anderegg 2015; Vitasse et al. 2009). Vulnerability may also vary through time during the year for a given individual/population, not only because of temporal climatic variation but also through individual variation in phenological processes. This is well illustrated by the risk of late frost damages, which tightly depend on the coincidence between temporal patterns of budburst phenology, and the climatic sequence of low temperatures. Although relatively large safety margins were found regarding the risk of late frost damages during budburst across many European temperate tree and shrub species (Bigler and Bugmann 2018), these safety margins may reduce with climate change, due to the advance in the budburst date of trees (Augspurger 2009). When young leaves have been damaged, some species can reflush, i.e. produce another cohort of leaves (reflush, Augspurger 2009; Menzel, Helm, and Zang 2015), but the time required to reflush leads to a shorter growing season (Lenz et al. 2013), and eventually to mortality if trees do not have enough reserves to reflush.

Available approaches to investigate the multiple drivers and processes underlying tree mortality can be classified into two broad categories: statistical, phenomenological approaches vs process-based, mechanistic approaches. Statistical approaches use forest inventory data to test how endogenous factors (e.g. related to tree/stand size and growth rate) and exogenous factors (the biotic and abiotic environment, including management) affect stand- or individual- mortality rates. In the last decades, many statistical studies compared mortality rates among species or populations over large climatic gradients and demonstrated the overall positive effect of drought severity on mortality, although usually explaining only a limited proportion of the variance in mortality rates (Allen et al. 2010; Greenwood et al. 2017). Moreover, mortality rates were predicted with a higher accuracy when individual covariates for tree growth, size and/or competition were included in the statistical models, highlighting the importance of inter-individual variability in the threshold to mortality (Hülsmann, Bugmann, and Brang 2017; Monserud 1976). Recent statistical studies attempted to include functional traits involved in the response to stress as additional covariates to improve the accuracy of mortality prediction. For instance, Carnicer et al. (2011) showed that defoliation trends are consistent with mortality trends in southern European forests. Benito Garzón et al. (2018) found that mortality increased in populations with negative hydraulic safety margins for 15 species out of the 25 studied. Overall, the main advantage of statistical approaches is their ability to account for a potentially high number of factors and processes triggering mortality, and for individual variability in the threshold to mortality. However, one should keep in mind that statistical models hardly handle co-linearity and non-linearity of effects and non-randomization inherent to

natural population designs. In addition, the accuracy of statistical predictions dramatically decreases outside the studied area (Hülsmann , Bugmann, and Brang 2017).

On the other hand, biophysical and ecophysiological process-based models initially developed to simulate carbon and water fluxes in forest ecosystems can also be used to investigate the environmental drivers and physiological processes triggering tree mortality. For example, using the model CASTANEA, Davi & Cailleret (2017) showed that mortality of *Abies alba* in southern France resulted from the combination of drought-related carbon depletion and pest attacks. Using six different models, Mcdowell et al. (2013) found that mortality depended more on the duration of hydraulic stress rather than on a specific physiological threshold. A main advantage of process-based models is their ability to predict mortality outside the study area (i.e. under new combinations of forcing variables in a changing environment). Their main limitation is their large number of parameters, which makes it difficult to use them in populations where the model has not been precisely calibrated and validated. Moreover, biophysical and ecophysiological process-based models generally do not well take into account individual effects at tree level. Hence, statistical and process-based approaches appear as complementary, and many authors call for studies comparing or combining them (Hawkes 2000; O'Brien et al. 2017; Seidl et al. 2011).

An iconic tree of pan-European forests, the European beech (*Fagus sylvatica* L Crantz) combines a widespread distribution and a high-predicted sensitivity to climate change (Cheaib et al. 2012; Kramer et al. 2010). In particular, bioclimatic niche models predict a future reduction of this species at the rear-edge of its distribution over the next few decades, in response to reduced precipitations (Cheaib et al. 2012; Kramer et al. 2010). This prediction is consistent with this species' well-known sensitivity to summer droughts. For instance, more frequent extreme drought events have been associated in beech to decreased growth (Dittmar, Zech, and Elling 2003; Jump, Hunt, and Penuelas 2006; Knutzen et al. 2017), altered physiological performances (Bréda et al. 2006) and increased defoliation (Penuelas and Boada 2003). However, the low mortality rate observed so far in beech has led some authors to propose that this species presents a higher heat stress tolerance and metabolic plasticity as compared to other tree species (García-Plazaola et al. 2008). This apparent paradox between a low mortality and a high sensitivity to climate makes of beech an interesting model species to study mortality.

In this study, we used a combination of statistical regression models, and the process-based model CASTANEA to investigate patterns of mortality within a population located at the warm and dry ecological margin of European beech (Supplementary Fig. S1). Growth, decline, mortality and budburst characteristics have been monitored for 14 years in a set of 4327 adult trees. First, we tested the impact of climatic variables on population-level mortality rate with a beta-regression model, simultaneously using CASTANEA to investigate which physiological mechanisms drove

mortality at population scale. Then, we used logistic regression to characterise the respective effects of exogenous (competition) and endogenous factors (size, growth, crown defoliation, fungi presence) on the individual probability of mortality, simultaneously using CASTANEA to simulate trees with different endogenous characteristics and to investigate differences of physiological responses between individuals.

Materials and Methods

Study site

La Massane (42° 28' 41" N, 3° 1' 26" E) is a forest of 336 ha located in the French eastern Pyrenees; its elevation ranges from 600 m to 1127 m above sea level. Located at the South of beech distribution area, the forest is at the junction of Mediterranean and mountainous climate with mean annual rainfall of 1260 mm (ranging from 440 to 2000 mm) and mean annual temperature of 11°C (with temperature from -10°C to 35°C) (Supplementary Fig. S2). No logging operation was allowed since 1886 and the forest was classified as a reserve in 1974. European beech is the dominant tree in the canopy representing about 68% of basal area of the forest. Beech is in mixture with downy oak (*Quercus pubescens* Wild), maples (*Acer opalus Mill., Acer campestris L., Acer monspessulanum L.*), and holly (*Ilex aquifolium L.)*. A 10-ha fenced plot was remoted from cow grazing since 1956. All trees from this protected plot were geo-referenced and individually monitored since 2002 (Supplementary Fig. S3).

We estimated the soil water content (SWC) through soil texture, soil depth and percentage of coarse elements measured in two soil pits. Secondly, we estimated the mean Leaf Area Index (LAI) by using hemispherical photographs (Canon 5D with Sigma 8mm EXDG fisheye). We computed the LAI and clumping index following the methodology described in (Davi et al. 2009).

Monitoring of tree characteristics

This study is based on the monitoring of 4327 beech trees in the protected plot from 2002 to 2016. Beech sometimes produces stump shoots resulting in multiple stems at a single position (coppice). Here, every stem of all coppices was individually monitored and called “tree” in the following.

Tree mortality was recorded twice a year, in spring and autumn, from 2003 to 2016. We considered that a tree died at year n-1 when its buds failed to burst at spring of year n, and that a tree died at year n when budburst occurred at spring but no leaves were remaining at autumn of year n, and no budburst occurred at year n+1. All the 4327 trees were alive at year 2003 (Supplementary Fig. S4). We computed the annual mortality rate (τ) for each year *n* as:

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

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

Several variables where measured or computed at tree level (Table 1). Diameter at breast height (i.e. 1.30 m above ground) was measured in 2002 and 2012 (respectively DBH and DBH2012). Here we focus on the impact of climate change on mature trees, hence only trees with DBH greater than 10 cm in 2002 were retained for the analysis. Individual growth was measured by the relative increment in basal area (MBAI) between 2002 and 2012, estimated as: $MBAI_i = (\pi(DBH2012_i - DBH_i)/4)/N_{yearsAlive,\,i}$., where $N_{yearsAlive,\,i}$ is the number of year where individual i was observed being alive. For a subset of 1199 trees, height in 2002 was estimated.

A strong individual variation in budburst phenology is documented in La Massane (Gaussen 1958; Perci du Sert 1982), with ~10% beeches initiating budburst about 2 weeks before all the others. Here, budburst was thus treated as a binary qualitative variable, and our sample included 237 such “early” beeches.

The presence of major defoliated branches and leaves was recorded each year between 2003 and 2016 (except 2010) as a qualitative measure (DEF=1 for presence; DEF=0 for absence). These annual measures were cumulated and weighted over the observed period as:

$$DEFw = \frac{\sum_{i=1}^{Nalive}(\mathrm{DEF}_i)}{N_{alive}} \text{ (eq 2)},$$

where Nalive is the number of years where a tree was observed as alive (year 2010 was not taken into account). DEFw is an integrative, ratio ordered variable combining the recurrence of defoliation, and the ability to recover from defoliation.

The presence of fructification of the saproxylic fungus *Oudemansiella mucida* was recorded as a qualitative measure (Fungi = 1 for presence; Fungi = 0 for absence). Because once observed, the fructification persists all the subsequent years, we analysed it as a binary variable.

Competition around each focal beech stem was estimated by four variables. Firstly, we used the number of stems in the coppice as an indicator of within-coppice competition (Nstem). Secondly, we used the competition index introduced by Martin and Ek (1984), which accounts simultaneously for the diameter (DBH) and the distance (d_{ij}) of each competitor *j* to the competed individual *i*:

$$\mathrm{Compet}_{i,dmax} = \frac{1}{\mathrm{DBH}_i}\sum_{j=1}^{n} \mathrm{DBH}_j \exp\left[\frac{-16d_{ij}}{\mathrm{DBH}_i + \mathrm{DBH}_j}\right] \text{ (eq 3)},$$

where, *n* is the total number of competitors in a given radius dmax (in m) around each focal individual i. Only trees j with $DBH_j > DBH_i$ are considered as competitors. This index was previously shown to describe more accurately the competition than indices relying on diameter only (Stadt et al. 2007). We computed three competition indices: the intra-specific competition index

($Compet_{intra}$) which only accounts for the competition of beech stems not belonging to the coppice of the focal tree; the intra-specific competition index ($Compet_{intra+}$) which accounts for all beech stems belonging or not to the coppice of the focal tree; and the total competition index ($Compet_{tot}$), which accounts for all stems and species. We considered that stems located less than 3 m away from the focal stem belonged to the same coppice. All the indices were computed at all distances from 1m (or 3m for $Compet_{intra+}$) to 50 m from the target tree, with 1m step. We retained d_{max}= 15m, because all indices reached a plateau after this value, suggesting that in a radius greater than 15m, the increasing number of competitors is compensated by the distance.

Table 1: Quantitative (A) and qualitative (B) variables monitored at individual level. All the variables were measured in 4327 trees, except for H_2002 (1199 trees).

Code	Quantitative variable	mean	min	max	unit
DBH	Diameter at breast height measured in 2002	21.65	10	116	cm
DBH_2012	Diameter at breast height measured in 2012	22.84	10	116	cm
MBAI	Mean basal area increment between 2002 and 2012.	0.13	0	2.8	$cm^{-2}.year^{-1}$
H_2002	Height measured in 2002	8.8	2	26	m
DEFw	Defoliation mark cumulated and weighted by the number of living year over the period	0.14	0	1	
Nstem	Number of stems observed in the coppice	1.54	1	11	
Compet intra	Intra-specific competition index	2.74	0	11.44	
Compet intra+	Intra-specific competition index accounting also for competition within the coppice	2.35	0	10.052	
$Compet_{tot}$	Total competition index, where we accounted for all stems from every speciesB	4.63	0.12	19.98	

Code	Qualitative variable	Level	Number of trees
Fungi	Presence (1) or absence (0) of the saproxylic fungus	1	414
		0	3913
Budburst	Beeches initiating budburst about 2 weeks before all the others (1) or not (0)	1	237
		0	4090

Climate data

Local climate was daily monitored on site since respectively 1976 for temperature and 1960 for precipitation and mean relative humidity. In order to obtain a complete climatic series, we used the quantile mapping and anomaly method in the R package “meteoland” (De Caceres et al. 2018), considering the 8-km-resolution-SAFRAN reanalysis (Vidal et al. 2010) as reference. From the corrected climate series, 14 bioclimatic variables were computed using the "dismo" R package (Hijmans et al. 2017) (Online Appendix 1). We also derived several drought-related variables from the standardised precipitation-evapotranspiration index (SPEI) using the R package “SPEI” (Beguería and Vicente-Serrano 2017). We modified the calibration of evapotranspiration (ETP), adapted to crop in SPEI package, and used the ETP estimation provided by CASTANEA. The SPEI

variables were the maximum, minimum, mean and the cumulated SPEI from June to August, computed over one, three and twelve months. The number of late frost days (i.e. the number of days with negative temperature occurring after beech budburst) and a late frost index (the cumulative amount of negative temperatures occurring after beech budburst) were also computed. In total, 28 climatic variables were considered (Online Appendix 1).

Statistical model of annual mortality rate at population level

We used beta-regression models to investigate the effect of climatic variables on the annual mortality rate at population-level. Beta-regression models predict a response variable varying between [0,1], and account as for features like heteroscedasticity or asymmetry, which are commonly obtained in time-series of annual mortality rates. To face the problem of explaining 14 observations with 28 climatic variables highly correlated among each other's, we first grouped them by category (precipitation, temperature, frost, SPEI) and selected between one and four variable per category (Online Appendix 1). We ended-up with the following complete model for mortality at year n (with n varying from 2004 to 2016):

$$\tau_n = \mathrm{MeanTColdestQ}_n + \mathrm{MeanTWarmestQ}_n + \mathrm{PDriestM}_n + \mathrm{PWettestM}_n + \mathrm{NLF}_n + \mathrm{SPEI12_mean}_n + \mathrm{SPEI1_min}_n + \mathrm{SPEI3_JJA}_n \text{ (model I)},$$

where MeanTDriestQ is the mean temperature of the driest quarter; PDriestM and PColdestQ are the mean precipitation of the driest and coldest quarter respectively; NLF is the number of late frost days; SPEI12_meann and SPEI1_minn, SPEI_maxn are the mean and minimum SPEI values computed over respectively 12 and 1 month-references; and SPEI3_JJA is is the mean SPEI computed over June, July and August (Online Appendix 1).

Then, we used a stepwise, backwards procedure to select the best model based on Akaike's Information Criterion (AIC, Akaike 1987), and to test for interactions between factors (Online Appendix 1). Beta-regression was fitted with the R package betareg (Cribari-Neto and Zeileis 2010). We investigated model validity by checking the leverage points (i.e. points having a greater weight than expected randomly) with the Cooks distance (Cook distance < 0.5 indicate not leverage). We tested the goodness-of-fit with the Brier test score (Brier 1950). To explore the sensitivity and specificity of the model, we use also the receiver operating characteristic (ROC) curve.

Statistical model of mortality at individual level

We used logistic regression models to investigate how tree characteristics affect the individual probability of mortality ($P_{mortality}$). This approach is appropriate for a binary response variable, and a mixture of qualitative and quantitative explanatory variables not necessarily normally distributed

(Hosmer and Lemeshow 2000). We considered the following complete logistic regression models for $P_{mortality}$:

$$P_{mortality} = [DEFcum + Fungi + Budburst + MBAI + (Nstem \textbf{ OR } Compet_{intra} \textbf{ OR } Compet_{intra+} \textbf{ OR } Compet_{inter})] \times (DBH+DBH^2) \text{ (model II)}$$

where defoliation (DEFcum), growth (MBAI), size (DBH) and competition (Nstem and the Compet indices) factors were quantitative variables, while fungus presence (Fungi) and budburst phenology were qualitative variables. We included both a linear and quadratic effect of DBH by specifying this factor as a polynomial of degree 2. Interaction effects of each factors with this polynomial were included.

To select the best competition-related variables, we first ran model II with each competition term successively (Online Appendix 3). Then, we used a stepwise procedure to select the most parsimonious model based on AIC. When two models had similar AIC (delta < 2) (Arnold 2010), the one with less variable (most parsimonious) was selected.

Collinearity resulting from correlations between predictor variables is expected to affect statistical significance of correlated variables by increasing type II errors (Schielzeth 2010). To evaluate this risk, we first checked for correlation among factors included in model II (Fig. S5). We also computed the generalized variation inflation factor (GVIF) with the R package “car” (Fox and Weisberg 2011). A threshold of $GVIF^{1/2dof} < 2$ is commonly accepted to considers that variables are not too much correlated and do not make the model unstable. Note that here, we aim at identifying the climatic factors and the tree characteristics involved in mortality and not to maximize the prediction of mortality.

As classically done in logistic regression, results were expressed in terms of odd ratios, also called relative risk. The odd ratio, is a statistical measure, expressing the degree of dependency between variables (eq: 4 a,b). For instance, the odds-ratio for mortality as a function of Budburst are:

$$Oddsratio_{earlysvsnormal} = \frac{Odds_{early}}{Odds_{normal}} \qquad \text{(eq 4,a)},$$

$$\text{With } Odds_{early} = \frac{P_{mortality}(early)}{1-P_{mortality}(early)} \text{ (eq 4,b)},$$

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

Simulations with CASTANEA process-based model

CASTANEA model: CASTANEA is a process-based model used to simulate carbon and water fluxes in forest ecosystems with no spatial-explicit representation of trees (Dufrêne et al. 2005). A tree is abstracted as six functional elements: leaves, branches, stem, coarse, fine roots and reserve

(corresponding to non-structural carbohydrates). The canopy is divided into five layers of leaves. Photosynthesis is half-hourly estimated for each canopy layer using the Farquhar et al. (1980) model analytically coupled to the stomatal conductance model proposed by Ballet al. (1987). Maintenance respiration is estimated as proportional to the nitrogen content of the considered organs (Ryan 1991). Growth respiration is estimated from growth increment combined with a construction cost specific to the type of tissue (De Vries, Brunsting, and Van Laar 1974). Transpiration is also hourly calculated using the Monteith (1965) equations. The dynamics of soil water content (SWC; in mm) is estimated daily using a three-layers bucket model. Soil drought drives stomata closure via a linear decrease in the slope of the Ball et al. (1987) relationship, when relative SWC is under 40% of field capacity (Granier, Biron, and Lemoine 2000; Sala and Tenhunen 1996). In the carbon allocation sub-model (Davi et al., 2009; Davi & Cailleret 2017), the allocation coefficients between compartments (fine roots, coarse roots, wood, leaf and reserves) are estimated daily depending on the sink force and the phenology constraints. More details are provided in Dufrêne et al. (2005). CASTANEA model was originally developed and validated at stand-scale for beech (Davi et al. 2005).

In this study, we used the CASTANEA version described in Davi and Cailleret (2017) with two major modifications. First, for budburst, we used the one-phase UniForc model, which described the cumulative effect of forcing temperatures on bud development during the ecodormancy phase (Chuine, Cour, and Rousseau 1999; Gauzere et al. 2017). We computed the number of late frost days (NLF) as the sum of late frost days experimented after budburst initiates.

Second, from the calculation of daily midday water potential and beech vulnerability curve to embolism (eq5), we estimated the Percentage of Loss of Conductance (PLC) (eq:6) and simulated the defoliation by a loss of LAI. The leaf water potential Ψ_{leaf} was computed as:

$$\Psi_{leaf}(t+1) = \Psi_{soil}(t+1) - \frac{TR}{3600} \times R_{SoilToLeaves} + \frac{\Psi_{leaf}(t)}{\Psi_{soil}(t+1) + TR \times R_{SoilToLeaves}} \times e^{\frac{deltaT}{R_{SoilToLeaves} \times Cap_{SoilToLeaves}}} \text{ (eq: 5)},$$

where soil water potential (Ψ_{soil} MPa) was calculated from daily soil water content (Campbell 1974); leaf water potential was estimated hourly (deltaT=3600s) from simulated sapflow (TR in $mmol.m^{-2}.leaf^{-1}$). We simulated TR following the soil-to-leaves hydraulic pathway model used in (Loustau et al. 1990). We used one resistance (RsoilToleaves in $MPa.m^{-2}.s^{-1}.Kg^{-1}$) and one capacitance (CapSoilToleaves in $kg.m^{-2}.Mpa^{-1}$) along the pathway. The Campbell (1974) resistance ($R_{soilToleaves}$) was assessed using midday and predawn water potentials found in the literature.

PLC computation was adapted from Pammenter and Willigen (1998) formula:

$$PLC = \frac{1}{1+e^{slope(\Psi_{minSoil} - \Psi_{P50})}} \text{ (eq:6)},$$

with $\Psi_{min\ soil}$ (MPa) the simulated midday water potential in the soil and Ψ_{50} (MPa) the species-specific potential below which 50% of the vessels are embolized, slope is a constant fixed to 50. We have added an option in the model that allows to simulate branch mortality. We simulate branch mortality and defoliation induced by this mortality from the emboli level of xylem vessels, assuming that branch mortality is proportional to PLC. The LAI is thus reduced during the season by this process. To qualify the effect of this process, we compared simulations with branch mortality modelling and simulations without.

We used PLC, NLF and carbon reserves as proxies of tree responses to drought and late frost stresses. In addition to investigate the interaction between these stresses without a priori, we computed a compound vulnerability index (CVI) combining PLC, NLF and carbon reserve with an identical weight:

$$CVI_n = \left(\frac{PLC_n}{max(PLC_{period})} + \frac{NLF_n}{max(NLF_{period})}\right) - \frac{Reserve_n}{max(Reserve_{period})} \qquad \text{(eq:7)},$$

with n, the focal year. The composite index could vary between two and minus one.

Simulation design: First, we simulated a population of 100 trees representing the variability in individual characteristics observed in La Massane (height-diameter allometry, DBH, leaf area index and early/late budburst). The values of these individual characteristics were randomly drawn in a Gaussian law with mean and standard deviation measured in the whole population (Online appendix 3). We also simulated a range of environmental conditions representing the variability: in SWC and tree density randomly drawn in uniform law (Online appendix 3).

Second, we simulated 16 individuals corresponding to a complete cross design with four size categories (5, 15, 30, 40 cm in DBH), two budburst type (about 10 % early and about 90% 2 weeks later), and two defoliation level (Defoliated or Non-defoliated).

Results

Statistical model at population level

The total mortality rate reached 23% of the monitored trees between 2004 and 2016. The highest annual mortality rates were observed in 2006 (3.3%) and 2010 (2.9%); the lowest in 2008 (0.7%) and 2009 (0.9%).

The best beta-regression model for annual population-level mortality rate explained 74% of its variation among years (Table 2). The best model had both a high validity and goodness-of-fit (online appendix A1). It included spring and summer SPEI (SPEI_JJA), the precipitation of the driest month (PdriestM) and the interaction between them (Table 1). SPEI_JJA and PdriestM decreased the relative mortality rate by 1.15 and 3.03 times (p-value < 0.01), respectively, while

their interaction increased the relative mortality rate by 5.37 times (p-value < 0.01). The effect of PdriestM corresponded to an effect of summer droughts for the first part of the studied period (2004-2010) and to an effect of winter drought in the most recent years (2009, 2011-2016) (online appendix A1). The three highest observed annual mortality rates (>2%) coincide with the driest month of the year being in summer.

Table 2: Parameter estimates and related statistics for the best model I (beta regression at population level). β is the maximum likelihood estimate, with its estimated error (SE), z-value, and associated p-value (Pr(>|z|). OR is the odds ratio. This table shows only the factors with significant effects (see Appendix A1 for complete results).

Variables	β	SE	z value	Pr(>|z|)	OR
SPEI3_JJA	-0.15	0.054	-2.71	8.10e-03	0.87
PDriestM	-1.10	0.28	-3.89	1.10e-04	0.33
SPEI3_JJA : PdriestM	1.69	0.31	5.37	1.15e-07	5.37

Process based model at population scale

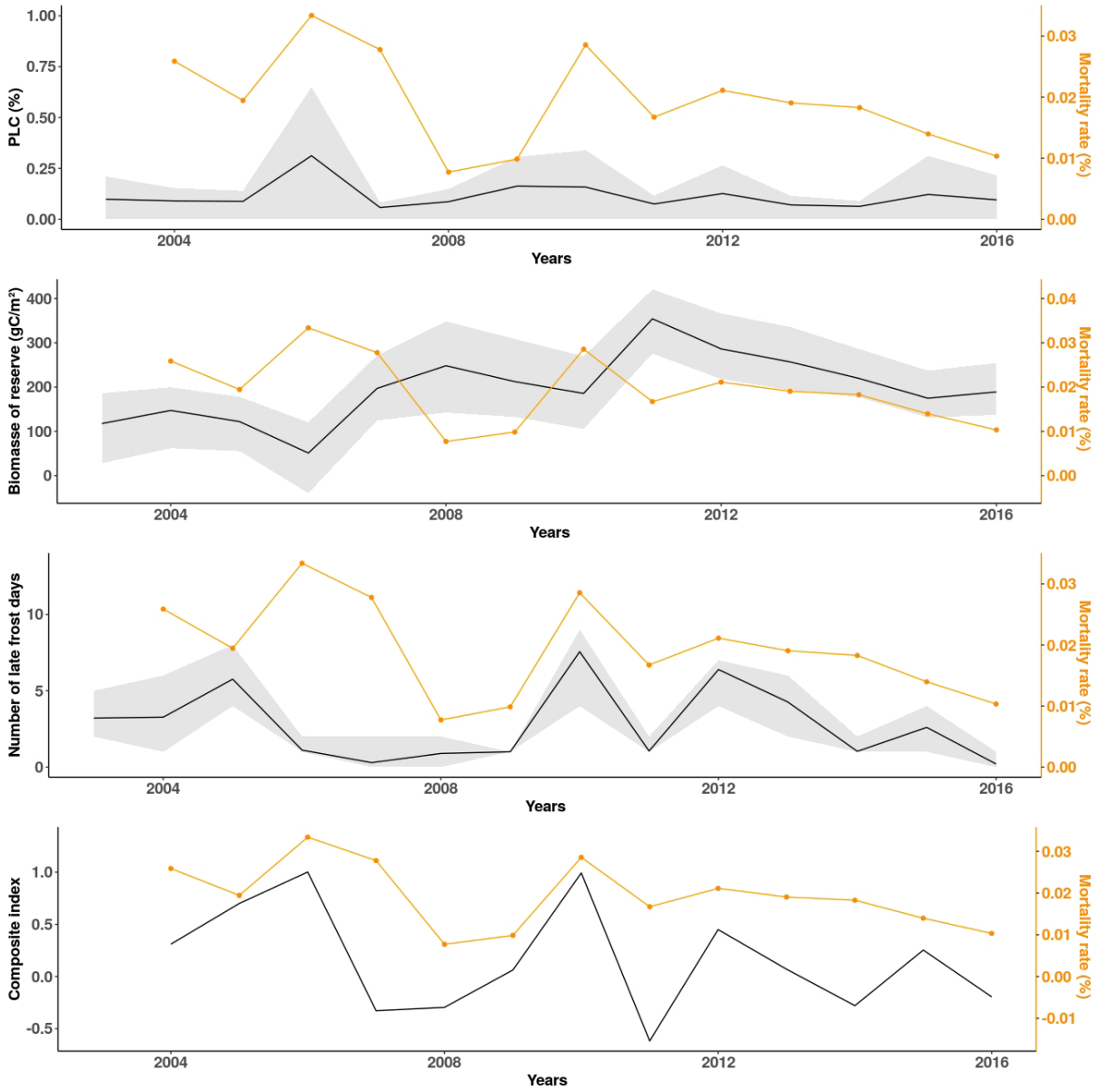
CASTANEA simulated in 2006 an important increase in PLC, with a population mean of 31% and a range from 14% to 64% among individuals (Fig. 1a). Four other years had a high mean PLC (>10%): 2009, 2010, 2012 and 2015, with respective PLC of 18%, 18%, 14% and 14%.

Simulated carbon reserves decreased in years 2006 (51 gC.m²), 2010 (186 gC.m²) and 2015 (175 gC.m²). After a peak in 2011, with 354 gC.m², carbon reserves continuously decreased until 2015 (Fig. 1b).

Finally, simulated trees suffered seven years of late frost during the period, with a peak in 2005 where individuals suffered from 4 to 8 days of late frost depending on individual phenology. Two other years of high late frost occurred in 2010 and 2012, with respectively from 5 to 9 days and from 5 to 7 days of late frost (Fig. 1c).

None of these indicators was significantly correlated to annual variation of ring width or mortality rate. But, the composite vulnerability index was significantly correlated to the annual mortality rate observed between 2004 and 2016 (r= 0.58, p-value 0.04) (Fig. 1d).

Figure 1: Proxies of physiological stresses simulated by CASTANEA at population-level from 2004 to 2016: (a) percentage of loss of conductance (PLC); (b) biomass of reserve; (c) number of late frost day;. (d) Composite vulnerability index integrating a+b+c. The black line is the mean of simulation, and the grey envelope represent the variation from the 1st to the 3rd quartile. The yellow line is the mortality rate observed in La Massane.



Statistical model of mortality at individual level

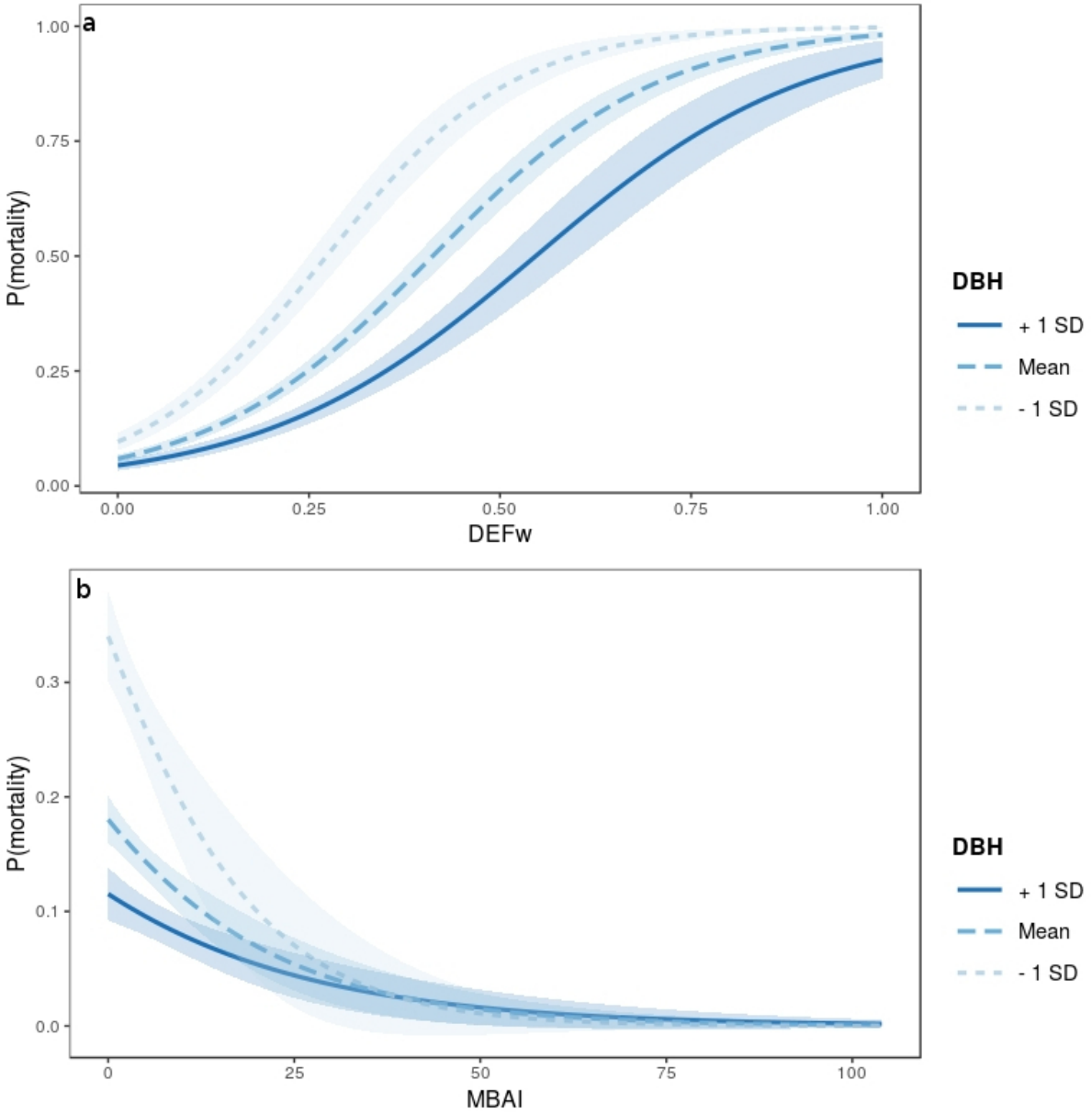
All the variables listed in model II had a significant main effect on the probability of mortality (Table 3) and were retained in the best model. This model explained 49 % of the observed mortality (i.e. dead individuals truly observed dead) and had both a high validity and goodness-of-fit (Online appendix 3 for details). Among the competition indices, N_{stem} was selected as it led to the fit with the lower AIC (Online Appendix 3). The relative probability of mortality increased by 1000, 1.13, 2.25 and 1.75 times, respectively for trees with a high defoliation, a higher density of coppice stems, an earlier budburst and the presence of fungi (Table 3). By contrast, trees with high mean growth had 1.06 times lower probability of mortality. The polynomial of degree 2 correspond to a U-shape and traduced a higher relative probability of mortality for both the smaller and the bigger trees (Table 3, Online appendix 3).

Table 3: Parameter estimates and related statistics for the model II (logistic regression at individual level). β is the maximum likelihood estimate, with its estimated error (SE), z-value, and associated p-value (Pr(>|z|)). OR is the odds ratio.

Variables	β	SE	z value	Pr(>|z|)	OR
DEFw	6.91	0.26	26.29	< 2.2 e-16	1.0 e03
DBH	-11.59	5.15	-2.25	2.42 e-02	9.22 e-06
DBH²	22.25	4.95	4.50	6.86 e-06	4.60 e09
MBAI	-5.91e-02	1.06 e-02	-5.55	2.80 e-08	0.94
Budburst (Early)	0.81	0.17	4.69	2.69 e-06	2.25
Nstem	0.12	3.60 e-02	3.42	6.24 e-04	1.13
Fungi (Presence)	0.56	0.14	3.94	8.10 e-05	1.75
DEFw:poly(DBH)1	-55.17	14.81	-3.73	1.95 e-04	1.10 e-24
DEFw:poly(DBH)2	32.09	16.81	1.91	5.63 e-02	8.64 e13
poly(DBH)1:MBAI	0.37	0.45	0.83	0.41	1.45
poly(DBH)2:MBAI	-0.83	0.44	-1.89	5.90 e-02	0.43

Interactions effects on mortality between size and defoliation were significant (Fig. 2a). At equal level of defoliation, the probability of mortality increased significantly more for smaller trees (Fig. 2a, Table 3). At equal mean growth, the relative probability of mortality for smaller trees was lower than for bigger trees. This interaction is only true for lower mean growth (MBAI <25 $cm^2.y^{-1}$) (Fig. 2b). Only the strength of the effects changed for alternative models considering the stem not belonging to a coppice and the model with DBH as qualitative variable (Online appendix 3).

Figure 2: Interaction effects in model II (a) between dimeter (DBH) and weighted defoliation (DEFw). (b) between DBH and the mean growth in basal area (MBAI). Regression lines are plotted for three values of DBH, corresponding to +/- 1 standard deviation (10.7cm) from the mean (22 cm). Confidence interval at 95% are shown around each regression line.

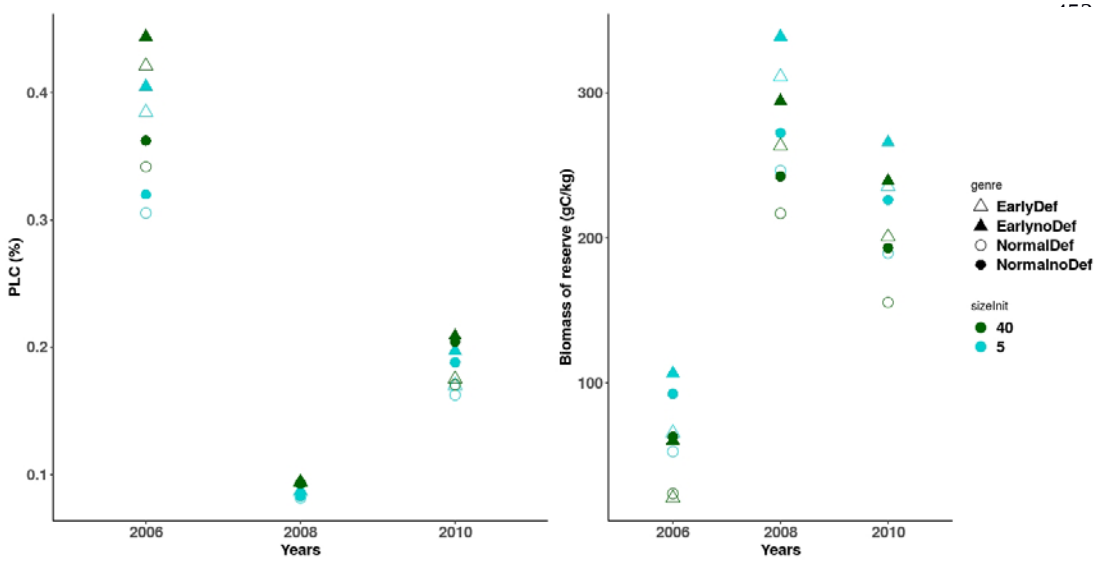


Process based model at individual scale

Simulations for the different individuals showed that tree vulnerability was driven by the intensity of climatic stress and by tree individual characteristics. The process-based model allowed to identify the factors that increased individual tree vulnerability during a drought year (2006) and a frost year (2010) and those that enhance their efficiency during a good year (2008). Drought-induced embolism was higher for early budburst trees and for bigger trees. The ability to defoliate

was limiting the risk of cavitation (Fig. 3a), but The ability to defoliate increased the risk of carbon starvation (Fig. 3b). The drought induced risk of carbon starvation (i.e. low reserve) was also higher for bigger trees and early trees. The resilience measured by carbon reserve in 2008 is higher for smaller, early, and non-defoliated trees (Fig. 3b). The positive effect of earlier budburst remains high even a year of frost in 2010 (Fig. 3b).

Figure 3: Physiological proxies of vulnerability simulated for eight trees differing in size, defoliation and budburst phenology. We focus on three key years: 2006 (severe drought); 2008 (no stress); 2010 (late frosts). Colours indicate the initial DBH at the beginning of the simulation: 5cm (light blue) versus 40 cm (dark green). Triangle (respectively round) symbols indicate individuals with early (respectively "normal") budburst. Empty (respectively full) symbols indicate individuals able (respectively not able) to defoliate.



Discussion

A relatively high population-level rate of mortality in response to drought and frost

The annual mortality rates observed in this study ranged between 0.7 and 3.3%. The statistical model explained 74% of its variation among years, which is higher than usually observed (30-40%) (Greenwood et al. 2017). Their best abiotic predictors were the mid-term drought from June to August (SPEI_JJA) and the amount of precipitations in the driest month (PdriestMonth). Meanwhile, simulations suggested that a combination of late frost sensitivity, loss of hydraulic conductance and reduction of carbon reserve drove population-level mortality rate.

The annual mean rate of mortality estimated here (2%) is in the upper range of the (few) mortality estimates available for beech. Hülsmann et al. (2016) reported annual mean rates of mortality of 1.4%, 0.7% and 1.5% in unmanaged forests of Switzerland, Germany and Ukraine,

with a maximum of mortality rate of 2.2%. Archambeau et al. (2019) estimated even lower mortality rates (mean annual value=0.0038%, range = 0.00374% to 0.00382%) from European forest inventory data (including managed and unmanaged forests). Overall, these mortality rates are low as compared to other tree species; for instance, according to the French national forest inventory, the average mortality is 0.1% for Beech against 0.3% in average and 0.4% for spruce or 0.2% for silver fir (IFN 2016). The relatively high value observed here may result from the absence of management, combined with the population location at the dry, warm species margin (Fig. S1), where most population extinctions are expected in Europe (Thuiller et al. 2005).

Moreover, our results suggest that the high observed mortality is primarily driven by summer droughts, including both the pulse effects of severe drought (PdriestMonth) but also long-term effects of repeated droughts (through SPEI_JJA). The major role of SPEI on beech mortality was also found of Archambeau et al. (2019), while Hülsmann et al. (2016) found a major role of competition (except for stroms in Ukraine). A long-term effect of drought was also found by Davi and Cailleret (2017) in *Abies alba Mill.*, or by Carnicer et al., (2011) in 12 European tree species, but our results additionally suggest positive interaction of long-term and pulse effects of drought on increasing risk of mortality.

Another major result from this study is that besides drought, other sources of stresses such as late frosts cannot be neglected to predict patterns of mortality in beech. The benefit of integrating drought- and frost-related stresses was particularly clear when we combined the number of late frost days, the percentage of loss of conductance and the level of carbon reserves into a composite vulnerability index. Indeed, this composite vulnerability index yielded a good correlation between predicted and observed mortality at population level. In particular, simulations showed that in 2010 (a year without drought), the high-observed mortality rate coincides with an extreme late frost event. This is consistent with the emerging consensus that mortality at dry, warm margins is not due either to carbon starvation or to hydraulic failure, but rather results from a balance between stresses vulnerability and carbon assimilation (e.g. McDowell et al. 2011; Sevanto et al. 2014). These results are also consistent with study of Vanoni et al (2016), which showed that both drought and frost could contribute to beech mortality.

In future developments, the composite vulnerability index could be refined by weighting its different components. In addition, in this study, we could not account for the temporal dynamics of mortality, such as the existence of positive or negative post-effects across years. But whenever possible(for instance in dendrochronological studies), such effects could be included, especially since there may be a lag between the weakening of a tree and its final death as already shown for beech tree in Vanoni (2016) and silver fir in Davi & Cailleret (2017).

Inter-individual variation in the vulnerability to drought and frost

The main strength of this study is the large number of trees individually monitored, which provided us with unusual large sample size to test for the effects of factors modulating individual vulnerability to mortality in beech. Firstly, we confirmed that mean growth has a positive effect on survival, as previously shown (Cailleret and Davi 2011; Gao et al. 2018). Moreover, interaction effects between growth and size were detected, such that for weak mean growth, bigger trees were less vulnerable to mortality than smaller trees. The probability of mortality also decreased faster with increasing mean growth for small than big trees. The variation of the relationship between mean growth and mortality according to tree size was already reported in beech seedlings (Collet and Le Moguedec 2007) and other species (Kneeshaw et al. 2006; Lines, Coomes, and Purves 2010).

Secondly, we found that defoliation increased the risk of mortality. This result was expected from previous studies (Dobbertin and Brang 2001, Carnicer et al. 2011), although the consequences of defoliation are still debated for beech. Senf et al. (2018) showed that defoliation was associated to tree decline, while Bauch et al., (1996) and Pretzsch (1996) found that the growth of highly defoliated beech trees did not decrease and could even increase in some cases. Such a positive effect of defoliation is not trivial, as drought-driven defoliation, occurring typically during summer due to vessels embolism in some branches, is expected to mechanically decrease carbon reserves during the current year. Our simulations comparing trees able or not to defoliate shed light on the multiple effects of defoliation, by showing that defoliation indeed decreased carbon reserves in good years but could also limit the embolism and the decrease of reserves during very dry years. We also observed significant interaction between defoliation and trees size on defoliation, suggesting that small trees were more vulnerable to defoliation than big trees. However, we cannot rule out this this effect is due in part to the qualitative method used to survey defoliation, which does not take into account the percentage of the crown loss. Hence, defoliation may be biased with respect to size, such that small defoliated trees will on average have a higher proportion of canopy loss, and therefore be more impacted than big tree.

Thirdly, both statistical and process-based approaches found that early individuals were more vulnerable. By contrast, (Robson et al. 2013) report no evidence of higher vulnerability of early trees, but a higher growth of early individuals, as also found in our simulation where early trees accumulate more reserves during good years. This discrepancy may be due to the fact that our studied population is at the rear-edge of beech distribution, where earliest budburst dates are observed due to higher temperature and may expose trees to a higher risk of late frost. Moreover, the presence of very early trees in the studied population makes it somehow peculiar, although

similar cases were observed (Gaussen 1958; Perci du Sert 1982). The higher vulnerability of early trees could also result from a faster depletion of their carbon reserve (Fig. S6), probably because they develop faster their canopy, which also mechanically increase their water needs, and the risk of embolism. Hence, the relationships between phenology and mortality deserve further investigation, especially since the spatio-temporal variation of budburst patterns under climate change may combine into complex spatio-temporal patterns of stresses (Vanoni et al. 2016).

Regarding the effect of size, the results differed between the statistical approach, where large trees died less than small ones, and the simulations, which predicted a greater vulnerability of larger trees. There may be several explanations to this discrepancy. The first reason is that CASTANEA model simulates an average individual, without effect of competition for light and water, and may thus underestimate the background mortality due to competition (which is higher, although weak, in small trees). In addition, CASTANEA also does not account for individual dominance status, which can affect the current carbon balance of a tree and hence the capacity to mitigate the stress. Indeed, in the observed populations, big trees are more likely to be dominant, with a better access to light resources promoting carbon accumulation, as compared to small trees, which are more likely to be suppressed. A second reason is that tree size may covary in environment quality in the studied population, such that big trees have more chance to occur on better soils, while environment do not covary with tree size in the simulations. Therefore, the size effect observed through the statistical approach may reveal a confounding effect of spatial soil heterogeneity, not taken into account in the process-based model. A measurement of water availability at individual tree level would be necessary but was out of the scope of this study.

Combining statistical and process-based approaches to disentangle the drivers of tree vulnerability

This study highlighted the interest of combining statistical and process-based approaches of mortality. These two approaches illustrate the classical compromise between fine understanding of physiological mechanisms driving mortality with complex and expensive process-based models, versus high precision in local mortality predictions with statistical models requiring less data but having also a weaker ability of generalization. Most often, studies adopt either of the two approaches, and generally statistical approaches prevails (Hülsmann et al. 2016; Seidl et al. 2011). However, the two approaches are tightly complementary, and combining them is a powerful approach to decipher the respective roles of the drivers and mechanisms underlying tree mortality and understand their variability among individuals or years (Hawkes 2000; O’Brien et al. 2017; Seidl et al. 2011).

In this study, the statistical model at individual scale, which aggregates the defoliation effect over the whole period including dry and good years, showed a predominant negative effect of defoliation, while the process-based model showed that during a severe drought, defoliation somehow limits the risk of hydraulic failure. These results overall suggest that the studied period may include so many recurrent dry years that the benefit of defoliation becomes negligible. Another contradiction was the higher vulnerability of early individuals to late frost demonstrated by the process-based model, while no effect of late frost was detected using the statistical approach at population level. However, the low proportion of early individuals in the studied population (~10 %) can explain this apparent contradiction. The major benefits of our approach combining different approaches (statistical, process-based) at different scales (population, individual) is that it allows to disaggregate ecological patterns observed at an upper scale (population, multi-year period), and to get back to patterns observed at a lower scale where processes operate (individual, year). This ability to aggregate/disaggregate patterns is acknowledged as a powerful approach to understand apparent contradictions between patterns observed at different scales (Clark et al. 2011) .

There are however some limitations to the approaches that were used here. First, none of them could fully account for the non-independence of climatic effects on mortality between years. Indeed, the effect of a climatic event at year n may depends on the effects of previous years, as already observed for beech, where successive drought lead to a growth decline (Jump et al. 2006; Knutzen et al. 2017; Vanoni et al. 2016) or even a modification in sap flow (Hesse et al. 2019). Moreover, the processes driving mortality may change through time as the most sensitive individuals are progressively eliminated, and/or the surviving trees become less and less sensitive (i.e. acclimation Niinemets 2010). Besides accounting for these limitations, another extension of the present study would be to combine statistical and process-based approaches at a larger spatial scale. This would allow investigating whether the respective drought and late frost sensitivity differ among the rear, core and leading edge of species distribution, as suggested by Cavin and Jump (2017).

Author Contributions

JAM, JG, CH and EM provided the data. CP performed the wood core analyses. CP, FL and SOM designed and ran the statistical models. CP and HD ran the process-based model. CP drafted the manuscript, and all the authors contributed to improve it.

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