



**HAL**  
open science

## Occurrence but not intensity of mortality rises towards the climatic trailing edge of tree species ranges in European forests

Alexandre Changenet, Paloma Ruiz-benito, Sophia Ratcliffe, Thibaut Fréjaville, Juliette Archambeau, Annabel Porte, Miguel Zavala, Jonas Dahlgren, Aleksi Lehtonen, Marta Benito-Garzón

### ► To cite this version:

Alexandre Changenet, Paloma Ruiz-benito, Sophia Ratcliffe, Thibaut Fréjaville, Juliette Archambeau, et al.. Occurrence but not intensity of mortality rises towards the climatic trailing edge of tree species ranges in European forests. *Global Ecology and Biogeography*, 2021, 30 (7), pp.1356-1374. 10.1111/geb.13301 . hal-03277653

**HAL Id: hal-03277653**

**<https://hal.inrae.fr/hal-03277653v1>**

Submitted on 3 Jun 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# **1 Occurrence but not intensity of mortality rises towards the climatic 2 trailing edge of tree species ranges in European forests.**

3

4 **Running title:** European forests mortality

5

6 **Corresponding author:** Marta Benito Garzón

7

8 **Authors:** Alexandre Chagnenet<sup>1</sup>, Paloma Ruiz-Benito<sup>2</sup>, Sophia Ratcliffe<sup>3,4</sup>, Thibaut Fréjaville<sup>1</sup>, Juliette

9 Archambeau<sup>1</sup>, Annabel J. Porte<sup>1</sup>, Miguel A. Zavala<sup>5</sup>, Jonas Dahlgren<sup>6</sup>, Alekski Lehtonen<sup>7</sup>, Marta

10 Benito Garzón<sup>1</sup>.

11

12 **Laboratory origins:**

13 <sup>1</sup>BIOGECO INRAE UMR 1202 University of Bordeaux, Pessac, 33400, France

14 <sup>2</sup>Departamento de Geología, Geografía y Medio Ambiente, Universidad de Alcala, Spain; and Forest

15 Ecology and Restoration Group, Departamento de Ciencias de la Vida, Universidad de Alcala, Spain

16 <sup>3</sup>National Biodiversity Network Trust, Nottingham, UK

17 <sup>4</sup>Department of Systematic Botany and Functional Biodiversity, University of Leipzig, Johannisallee

18 21-23, 04103 Leipzig, Germany.

19 <sup>5</sup>Forest Ecology and Restoration Group, Department of Life Sciences, Universidad de Alcalá (UAH).

20 Edificio Ciencias, Campus Universitario, 28871 Alcalá de Henares, Madrid, Spain.

21 <sup>6</sup>Swedish University of Agricultural Sciences, 90183 Umeå, Sweden

22 <sup>7</sup>Natural Resources Institute Finland (Luke), FI-00710 Helsinki, Finland

23 **Keywords:** background mortality, die-off mortality, European trees, biogeography, modeling,

24 National Forest Inventories, range margins, FunDivEUROPE

25

26

27

## 28Abstract

29

30**Aim:** Tree mortality is increasing worldwide, leading to changes in forest composition and altering  
31global biodiversity. Yet, due to the multi-faceted stochastic nature of tree mortality, large-scale spatial  
32patterns of mortality across species ranges and their underlying drivers remain difficult to understand.  
33Our main goal is to describe the geographical patterns and drivers of the occurrence and intensity of  
34tree mortality in Europe. We hypothesize that the occurrence of mortality represents background  
35mortality and is higher in the margin than the core populations, whereas the intensity of mortality  
36could have a more even distribution according to the spatial and temporal stochasticity of die-off  
37events.

38

39**Location:** Europe (Spain, France, Germany, Belgium, Sweden and Finland)

40

41**Time period:** 1981 to 2014.

42

43**Major taxa studied:** More than 1.5 million trees belonging to 20 major forest tree species

44

45**Methods:** We develop hurdle models to tease apart the occurrence and intensity of tree mortality in  
46National Forest Inventory plots at range-wide scale. The occurrence of mortality indicates that at least  
47one tree has died in the plot and the intensity of mortality refers to the number of trees dead per plot.

48

49**Results:** The highest mortality occurrence was found in peripheral regions and the climatic trailing  
50edge linked with drought, whereas the intensity of mortality was driven by competition, drought and  
51high temperatures and was uniformly scattered across species ranges.

52

53**Main conclusions:** Our findings provide a new perspective in our understanding of tree mortality  
54across species ranges. We show that tree background mortality but not die-off is generally higher in  
55the trailing edge populations, but whether other demographic traits such as growth, reproduction and  
56regeneration would also decrease at the trailing edge of European tree populations needs to be  
57explored.

58

59**Keywords:** Tree mortality, National Forest Inventory, drought, climatic edges, European forests,  
60hurdle models, background mortality, die-off mortality

61

## 621 INTRODUCTION

63 Tree mortality is occurring worldwide (Allen, Breshears, & McDowell, 2015; IPCC, 2014; McDowell  
64 et al., 2018). Tree mortality can change forest community, ecosystem dynamics and function, and  
65 hence alter biodiversity (McDowell et al., 2008). Yet, tree mortality remains difficult to predict at  
66 large spatial scales (Hartmann et al., 2018) because it is a multi-faceted, stochastic process (Franklin,  
67 Shugart, & Harmon, 1987). Background tree mortality is a phenomenon that generally occurs in  
68 individual trees (Hartmann et al., 2018) and is defined as the local mortality rate in the absence of  
69 catastrophic events (Csilléry, Seignobosc, Lafond, Kunstler, & Courbaud, 2013; Franklin et al., 1987;  
70 McDowell et al., 2018). It is a complex process driven by the combination of climate, forest  
71 composition, trees interactions and age (Cailleret et al., 2017; Hülsmann, Bugmann, & Brang, 2017;  
72 Ruiz-Benito, Lines, Gómez-Aparicio, Zavala, & Coomes, 2013). In contrast, die-off mortality is a  
73 local phenomenon where many trees die together in the same environment (Bugmann et al., 2019;  
74 Mueller-Dombois, 1987). Die-off mortality has been related to heatwaves and climate warming  
75 including extreme localized events, disturbances or environmental conditions such as intense drought,  
76 storms or fire (Allen et al., 2010; Breshears et al., 2005; McDowell, 2008), and is exacerbated by pest  
77 and disease outbreaks (Anderegg et al., 2015; Kurz et al., 2008).

78

79 Climate change, especially increases in the number and duration of drought events, has been linked to  
80 increases in both background mortality rates and the extent of die-off events (Allen et al., 2015; Allen  
81 et al., 2010; Benito Garzón, Ruiz-Benito, & Zavala, 2013). However, identifying the drivers of die-  
82 off and background mortality along large environmental gradients remains challenging because tree  
83 sensitivity to biotic and abiotic factors depends on the species identity (Ruiz-Benito et al., 2013), their  
84 age (Hülsmann et al., 2017) and their ecological strategies (Benito Garzón et al., 2018; Ruiz-Benito et  
85 al., 2017; Archambeau et al., 2020).

86

87In the context of climate change, we could expect an increase of mortality in trailing edge populations  
88due to increased drought and rising temperatures (Benito Garzón et al., 2013; Carnicer et al., 2011;  
89Purves, 2009; Young et al., 2017). However, very little is known about the differential drivers of  
90background tree mortality and die-off events at large geographical scales, and both processes can  
91occur throughout the species ranges, in the leading edge, the trailing edge and the core of the species  
92ranges (e.g. Jump, Mátyás, & Peñuelas, 2009; Allen et al. 2010; Greenwood et al. 2017). Although,  
93we could expect higher background mortality at the margins than at the core of the distribution  
94(Neumann, Mues, Moreno, Hasenauer, & Seidl, 2017), and most intense events of mortality evenly  
95distributed across species ranges (Allen et al., 2015; Allen et al., 2010; Jump et al., 2009; Jump et al.,  
962017).

97  
98Here, we analyze tree mortality of 20 major forest tree species from more than 1.5 million trees  
99recorded in the National Forest Inventories from Spain, France, Germany, Belgium (Wallonia),  
100Sweden and Finland to understand their patterns along species distribution ranges. We assume that  
101the occurrence of mortality found in a plot reflects background mortality whereas the intensity of tree  
102mortality found in a plot reflects die-off events. We develop hurdle models of mortality occurrence  
103and intensity to understand the effect of climatic marginality defined as areas exhibiting the highest or  
104the lowest values of several climatic variables and its interaction with drought. The aims of our study  
105are to i) identify the underlying drivers of mortality occurrence and intensity and how they are  
106influenced by the marginality of the population, and ii) to evaluate tree mortality occurrence and  
107intensity patterns across species distribution ranges. We hypothesize that marginal populations will  
108have higher occurrence of mortality than core populations, and that the intensity of mortality will  
109show a patchy distribution over spatial range reflecting the stochastic nature of die-off events.

110

111

## 1122 MATERIAL & METHODS

## 113 **2.1 National Forest Inventory harmonization**

114 We used mortality records and stand variables from National Forest Inventories (NFIs) of five  
115 countries (Spain, Germany, Finland, Sweden, Wallonia (Belgium)) (harmonized in FunDivEUROPE;  
116 (Baeten et al., 2013)) and the French National Forest Inventory (harmonized in Archambeau et al.,  
117 2020). The French NFI has temporary plots recorded between 2005 and 2014 whereas the other  
118 countries have permanent plots sampled several years apart, ranging from 1981 to 2011 (Supporting  
119 Information Table S1). Data from the six NFIs together cover a latitudinal gradient from 36° N  
120 (Spain) to 70.05° N (Finland).

121

## 122 **2.2 Plot-level tree mortality recorded from NFI**

123 We used individual tree mortality data for 20 major forest tree species, gathering a total of 1,649,850  
124 trees and 235,394 plots (Supporting Information Table S2) varying from 10 to 263 cm (mean = 28)  
125 diameter at breast height (DBH; cm) and with a mean census intervals of 10.7 years ranging from 2  
126 (29 plots) to 20 years (46 plots). Mortality occurrence was calculated as a binary variable, with zero  
127 when all trees were alive in the plot and one when at least one tree died in the plot during the census  
128 interval. Mortality intensity was calculated in each plot as the percentage of trees that died between  
129 the first and second inventory in the NFIs with permanent plots, divided by the number of years  
130 between census and calculated at the hectare level. In the French NFI tree mortality per plot was  
131 calculated as the percentage of trees that died within the five years before sampling in the temporary  
132 plot. We removed plots with trees recently recorded as harvested or managed between consecutive  
133 inventories and individual trees under 100 mm DBH to make the tree measurements consistent across  
134 country with different DBH thresholds (Table S1).

135

136 To avoid the potential bias caused by the different years of NFIs campaigns and the different size of  
137 the plots between the NFIs (Table S1), we upscaled tree mortality from plot to hectare per year using  
138 a weighted index provided by each NFI and dividing this value by the number of years between

139 campaigns for NFI with repetitive measurements or by five for the French NFI, where mortality was  
140 estimated for five years (Supporting Information Table S3). The weighted index reflected the size of  
141 the plot or the density of the grid or both depending on the country (Table S1 and  
142 <http://project.fundiveurope.eu/>).

143

## 144 **2.3 Model predictors**

### 145 **2.3.1 Indexes of climatic marginality and climatic areas**

146 We determined the distribution range of each species using information available from Caudullo,  
147 Welk, & San-Miguel-Ayanz (2017) or EUFORGEN (<http://www.euforgen.org/>). Within each range  
148 we characterised the climate using a Weighted Principal Component Analysis (WPCA, Benito-  
149 Garzón, Leadley, & Fernández-Manjarrés, 2014) based on 21 climatic variables averaged over the  
150 2000-2014 time period at each point in a 1 x 1 km pixel size grid (Supporting Information Table S4).  
151 The WPCA was calculated using 10,000 randomly selected points within each species ranges. The  
152 variance explained by the two first axis of the WPCA ranged from 71.53% to 87.42% for *Fagus*  
153 *sylvatica* and *Larix decidua*, respectively, Supporting Information Table S8). Based on the weighted  
154 scores of the two first WPCA axis we defined three climatic groups: core, transition and marginal  
155 regions (Supporting Information Figure S1 and Table S5). Species-specific thresholds for attributing  
156 the core (C), climatic marginal (M) and transition (T) areas were calculated based on the WPCA  
157 scores (Table S2): values from 0 to 60% were attributed to core areas, values between 60 and 80 %  
158 are transition areas and values higher than 80% are marginal areas.

159 To further separate climatic marginal areas (M) into climatic trailing edge (TE) for the southernmost  
160 one and climatic leading edge (LE) for the northernmost, we used a Discriminant Principal  
161 Component Analysis (DPCA) and an attribution test to check whether individual points were  
162 successfully reassigned in their attributed group based on the discriminant functions (Jombart, 2008;  
163 Figure S1).

164Finally, NFI plots were linked with the WPCA scores and classified as core (C), leading or trailing  
165edge (LE and TE) accordingly. Plots lying in the transition region (T) were not used in the analysis  
166(Supporting Information Table S2 and Figures S1,S2).

167

### 168**2.3.2 Climatic data**

169We characterised the long-term climate of each plot with eight climate variables. To make the  
170variables comparable between different survey dates and countries, we averaged them over the last 30  
171years prior to the first survey (hereafter climatic variables; Table S4) (Fréjaville & Benito Garzón,  
1722018). The eight variables included four temperature-related variables and four precipitation-related  
173variables that were uncorrelated and that have been shown to have an effect on tree mortality  
174(Archambeau et al., 2020; Benito Garzón et al., 2018; Ruiz-Benito et al., 2017): annual mean  
175temperature (bio1), maximal temperature of the warmest month (bio5), winter mean temperature  
176(tmean.djf), autumn mean temperature (tmean.son) (temperature variables) & annual precipitation  
177(bio12), precipitation of the wettest month (bio13), precipitation of the driest month (bio14), annual  
178water balance (precipitation minus potential evapotranspiration (ppet.mean) (Table S4).

179

180 In addition, we used the Standardized Precipitation Evapotranspiration Index (SPEI v.2.5 (2017)  
181(<http://hdl.handle.net/10261/104742>). SPEI is a multi-scalar drought index where negative values  
182indicate drier conditions over the timescale considered (from 3 to 48 months), relative to median  
183values for a long-term reference period (from 1901 to 2015) (Vicente-Serrano, Beguería, & López-  
184Moreno, 2010). For each month during the time interval between inventory campaigns, we used 1901  
185to 2015 as a reference period and calculated SPEI monthly index considering a period of 12 months  
186relative to our reference period. For each plot and based on these monthly data, we calculated the  
187annual means and extracted the minimum and mean values for this time period (hereafter SPEI  
188variables; Table S4).

189



### 1902.3.3 Stand and competition variables

191All stand variables were calculated using NFI data, transformed where necessary to meet the model  
192assumptions of normality (Supporting Information Table S6): total basal area increment ( $BAI_j$ ,  $m^2 ha$   
193 $yr^{-1}$ ), calculated as the difference in basal area between two inventory periods for all NFIs except  
194France where five years cores were used; mean basal area increment ( $meanBAI_j$ ,  $m^2 ha yr^{-1}$ ); mean  
195diameter at breast height (DBH, mm), tree density calculated as the number of trees per hectare  
196( $treenumber$ , No. trees  $ha^{-1}$ ); total (BA,  $m^2 ha^{-1}$ ) conspecific stand basal area (estimated as the basal  
197area of all individuals of the species in the plot,  $BA_{con}$ ,  $m^2 ha^{-1}$ ) and heterospecific stand basal area  
198(estimated as basal area of all individuals excluding the studied species) ( $BA_{hetero}$ ,  $m^2 ha^{-1}$ ).

199The DBH,  $BAI_j$ ,  $meanBAI_j$  and  $treenumber$  were included in the model as proxies of the average age  
200(DBH), growth and tree density in the plot because they are known to influence tree mortality  
201(Hülsmann et al., 2017; Vanoni, Cailleret, Hülsmann, Bugmann, & Bigler, 2019). The number of  
202years between surveys ( $yearsbetweensurvey$ ) was also included in the model to account for mortality  
203probability increases with elapsed time. We used BA,  $BA_{con}$  and  $BA_{hetero}$  as proxies of total  
204competition, intraspecific and interspecific competition (Kunstler et al., 2016).

205

### 2062.4 Statistical analyses

#### 2072.4.1 Selection of climatic and competition covariates in the mortality models

208For each species, we ran 48 competing occurrence of mortality models. In each model we included  
209the climatic marginality as a qualitative variable (i.e. the core, leading or trailing edge of each plot),  
210the five stand covariates, and the minimum and mean SPEI indexes. We added all the possible  
211combinations of one precipitation-related, one temperature-related and two competition variables. We  
212included all interactions between marginality, the two SPEI indexes, the two competition-related  
213variable and the two climate variables (Table S7).

214We included both precipitation- and temperature-related variables to the models, in addition to  
215marginality, because they could vary within the species margins and thus capture variations not

216accounted by marginality variable. The collinearity between precipitation- and temperature-related  
217variables and marginality were assessed using variation inflation factors (Supporting Information  
218Table S8a,b).

219

#### 2202.4.2 Statistical models of mortality

221We used species-specific hurdle models to handle the zero-inflated distribution of tree mortality  
222(Ruiz-Benito et al. 2017; Benito Garzón et al. 2018; Archambeau et al. 2020). Consequently, we  
223analyzed separately the mortality occurrence between two census (0/1 = at least one tree is dead in the  
224plot/ all trees are alive in the plot) and the intensity of mortality in plots where mortality occurs (the  
225proportion of trees dead in the plot, Young et al., 2017). Firstly, mortality occurrence was analyzed  
226with the binomial part of the hurdle model ( $Y_{1i}=1$ , table S3) where  $p_i$  is the probability of  
227occurrence of a mortality event in an individual plot  $i$  during the census interval. We used a binomial  
228GLMM with a *logit* link (BIN model) to estimate the parameters of the species-specific linear  
229function  $\eta_{1i,sp}$  (Hülsmann et al., 2017):

$$230 Y_{1i}=1 \sim Bin(n, p_i)$$

$$231 \text{logit}(p_i) = \eta_{1i,sp}$$

232Secondly, we analyzed the intensity of mortality as the annual rate of mortality in plots where at least  
233one tree was recorded as dead ( $Y_{2i}$ , Table S3) with zero truncated negative binomial mixed-effect  
234models in the second part of the hurdle model (NB model),  $Y_{2i}$  where  $\mu_i$  is the mean number of  
235mortality events per year per hectare and  $k$  is the inverse of the dispersion ( $Y_{2i} \sim NB(\mu_i, k)$ ). We used  
236NB models with a *log* link to estimate the parameters of the species-specific linear function  $\eta_{2i,sp}$ :

$$237 Y_{2i} \sim NB(\mu_i, k)$$

$$238 \log(\mu_i) = \eta_{2i}$$

239

240 Functions  $\eta_{1i,sp}$  and  $\eta_{2i,sp}$  take the same general form:

241

$$242 \eta_{i,sp} = \alpha_0 + \sum_{h=1}^{16} \beta_h x_{hi,sp} + \sum_{n=1}^{21} \gamma_n x_{n,sp} z_{n,sp} + \alpha_{country,sp} + \varepsilon_{i,sp} + b_{sp}$$

243 Where  $\alpha_0$  is an intercept term,  $\alpha_{country,sp}$  is the random country intercept to account for sampling

244 differences between each NFI and follows a Gaussian distribution  $\alpha_{country,sp} \sim N(0, \sigma_{\alpha_{country,sp}}^2)$ ;  $\varepsilon_{i,sp}$  is the

245 residual error following a Gaussian distribution ( $\varepsilon_{i,sp} \sim N(0, \sigma_{\varepsilon}^2)$

246);  $b_{sp}$  is an autocorrelation spatial effect that follows a Matérn distribution ( $b_{sp} \sim Mat \acute{e} rn(v_{sp}, \rho_{sp})$

247, where  $v_{sp}$  is the smoothness and  $\rho_{sp}$  the shape, Supporting Information Figure S3).  $\beta_h$  is the regression

248 coefficient for the  $h$ th of 16 fixed effect predictors  $x_{sp}$  (including 5 stand covariates, 2 climatic

249 variables and their respective quadratic effect, 2 drought-related (SPEI) variables and their respective

250 quadratic effect, 2 competition variables and marginality, see details below and in Supporting

251 Information Tables S4, S6 and S7) and  $\gamma_n$  the regression coefficient of the  $n$ th interaction between

252 fixed effect predictors  $x_{sp}$  and  $z_{sp}$  (including all interactions between climatic variables, drought-

253 related variables, competition variables and marginality).

254

$$255 \alpha_{country,sp} \sim N(0, \sigma_{\alpha_{country,sp}}^2)$$

$$256 \varepsilon_{i,sp} \sim N(0, \sigma_{\varepsilon}^2)$$

257

$$258 b_{sp} \sim Mat \acute{e} rn(v_{sp}, \rho_{sp})$$

259

#### 260 2.4.5 Model selection

261 To select the most parsimonious model, we applied the following procedure for each species:

262 (1) We calculated the Variance Inflation Factor (VIF) for all 48 possible combinations of variables

263 and removed combinations with  $VIF > 10$  (Dormann et al., 2013; Table S8a,b); (2) We ran BIN

264 models including each remaining combinations of variables and selected the combination with the

265best predictive ability using the AIC ( $AIC < 2$ ) and the log H-likelihood (largest values; Lee & Nelder,  
2662018); (3) We fitted an NB model including the same variables as those in the BIN model with the  
267best predictive ability. (4) We used a stepwise approach for both the BIN and NB models (i.e. we  
268removed the least significant variable to fit a new model) to obtain the most parsimonious models.  
269All models were fitted with the SpaMM package (Rousset, Ferdy & Courtiol, 2016; Table S6) under  
270the R version 3.6.1.

271

#### 272**2.4.6 Model validation**

273The goodness-of-fit was evaluated with the area under the curve (AUC) for BIN models (Hurst,  
274Allen, Coomes, & Duncan, 2011) and with cross-validation for the NB models (models were fitted on  
27566% of the data while the remaining 33% were used to validate the predictions, Table 1).

276The percentage of the variance explained by BIN and NB models was estimated by the marginal and  
277conditional R-squared including fixed-effect and fixed plus random effects, respectively (Nakagawa  
278& Schielzeth, 2013). The proportion of change in explained variance between full and null model  
279(PCV) indicates the variance retained by the selected model. All these metrics were calculated from  
280the SPAMM objects using a personal script adapted from the piecewise Package (Lefcheck, 2016)  
281according to Nakagawa methodology (Nakagawa & Schielzeth, 2013, Nakagawa, Johnson &  
282Schielzeth, 2017).

283

#### 284**2.4.7 Comparison of spatial predictions and climatic marginality**

285We used the selected models to predict mortality occurrence and intensity across the range of NFI  
286plots. To visually inspect the differences in the climatically marginal populations, we split the  
287predicted values into three groups based on the quartiles, to indicate high, medium and low levels of  
288mortality (Figure 3 and Supporting Information Tables S9, S10).

289To statistically test for heterogeneity in the distribution of the predicted probability among the three  
290areas (core, leading edge and trailing edge), we compared the predicted distribution (Figure 3) against

291the expected distribution under the assumption of no spatial structure in mortality occurrence (null  
292hypothesis) with a  $\chi$ -square test. Under the null hypothesis, we expected the distribution to be  
293uniformly distributed within the three areas (25% of the values in each quartile) (Supporting  
294Information Figure S4a). P-values  $< 0.05$  indicate that predicted mortality was different than expected  
295under the null hypothesis. The same approach was used to test for patterns across the three areas in  
296predicted mortality intensity (Supporting Information Figure S4b).

297

## 2983 RESULTS

### 2993.1 Climatic marginality across species ranges

300The variables that contributed the most in defining the core, trailing and leading areas were the annual  
301evapotranspiration for 10 out of the 20 species, the maximum temperature of the warmest month for  
302four species and annual precipitation for four species (Table S5). Marginal areas (leading and trailing  
303edges) were therefore areas exhibiting the highest or the lowest values for these climatic variables.

304We observed that our climatic marginality did not systematically match with the commonly used  
305geographic marginality (northern part of species distribution corresponding to the geographical  
306leading edge, and southern part to the geographical trailing edge), particularly in the mountainous  
307areas which were included in the climatic leading edge for most species although they were mostly  
308located in the central part of the range (geographical core) (Figure S2).

309

310

### 3113.2 Underlying drivers of occurrence and intensity of tree mortality

312Overall, the occurrence of mortality was mostly located at the trailing edge and related to drought  
313whereas the intensity of mortality was related to multiple drivers at the trailing edge and to the  
314warmest temperature at the leading edge. Bigger trees (likely to be older trees) showed higher  
315occurrence of mortality than smaller ones whereas intensity of mortality was similar across sizes (and  
316therefore ages).

317

318The variance explained by BIN models ranged from 6% for *Acer pseudoacacia* to 46% for *Pinus*  
319*pinaster* and the AUC ranged from 0.769 for *Quercus ilex* to 0.850 for *Acer pseudoplatanus* (Table  
3201). The variance explained by NB models ranged from 13% for *Castanea sativa* to 48% for *Fraxinus*  
321*excelsior* and the cross-validation scores ranged from 0.256 for *Quercus pyrenaica* to 0.735 for  
322*Betula pendula*. Accounting for spatial autocorrelation (SAC) in the models improved the capacity of  
323generalization of the three models (i.e. from 25.61% to 57.54% for *Quercus pyrenaica*, Table 1).

324

325Competition-related variables (stand basal area of the species and stand basal areas of the other  
326species at the plot) were the most frequently significant variables in BIN and NB models (significant  
327in 13 out of 20 species for interspecific competition and 10 species for intraspecific competition, see  
328estimated coefficients and their standard error in Supporting Information Table S11a,b and frequency  
329in Table S12a,b). Precipitation, temperature and SPEI variables were retained in BIN models for 16,  
33011 and 12 species respectively and in NB models for 11, 8 and 9 species (estimated coefficients and  
331their standard error of the associated coefficient in Table S11a,b and frequency in Table S12a,b).

332

333Climatic marginality was significant in the BIN model in 5 species in the trailing edge and in 7  
334species in the leading edge; and it was also significant in NB models in 3 species in the trailing edge  
335and in 7 species in the leading edge (magnitude and standard error of the associated coefficient are  
336shown in Table S11a,b and frequency in Table S12a,b).

337

338The average age of the plot (meanDBH) was significant in explaining both occurrence and intensity  
339of mortality (positive association in 14 species and 11 species respectively) meaning that larger (and  
340therefore older) trees were more affected by mortality. Average growth rate of the species of the plot  
341(meanBAI<sub>j</sub>) was also significant in both models (negative associations in 18 species for BIN models  
342and 7 in NB models) meaning that older plots (with the lowest average growth) are more likely to

343experience mortality. Tree density (treenumber) was positively associated in both models (14 and 12  
344species respectively for BIN and NB models). The number of years between surveys  
345(yearsbetweensurvey) was also significant in explaining both the mortality occurrence probability  
346between two census (6 species, BIN model) and the intensity of mortality (15 species, NB model)  
347(Magnitude and standard error of the associated coefficient in Table S11a,b and frequency in Table  
348S12a,b)

349  
350Interactions between marginality and SPEI variables were the most frequent in BIN models (17  
351significant interactions, 9 at the trailing edge and 7 at the leading edge) whereas the interaction  
352between climatic marginality and temperature-related variables was the most frequent in NB models  
353(12 significant interactions, 3 at the trailing edge and 9 at the leading edge) (Supporting Information  
354Table S11c,d). When drought conditions in the studied period were higher than in the reference  
355period (lower values of mean SPEI), predicted tree mortality occurrence probability (BIN models)  
356was higher in marginal than core areas, particularly at the trailing edge (for both temperate and  
357Mediterranean species *Abies alba*, *Picea abies*, *Pinus sylvestris*, *Castanea sativa* *Pinus pinea* and  
358*Pinus nigra*, Figure 1a-f). Under drier conditions than those experienced in the reference period (i.e.  
359negative SPEI values), the highest probability of mortality was found in the core area for some  
360temperate (*Populus tremula*, *Quercus robur*, *Betula pendula* (Supporting Information Figure S5a-c)  
361and Mediterranean species (*Pinus halepensis* and *Quercus pyrenaica* (Supporting Information Figure  
362S5d and Table S12c).

363  
364In addition to drought, a few species also showed the highest tree mortality probability during the  
365time between surveys at the climatic margins when precipitation were low or when temperatures were  
366high. This was the case for the temperate species *Fagus sylvatica* and *Fraxinus excelsior* (Supporting  
367Information Figure S6a and Table S12c) and the Mediterranean species *Pinus pinaster* and *Quercus*  
368*suber* (Supporting Information Figure S6b-c).

369

370The intensity of mortality (NB models) for the temperate species *A.alba*, *B.pendula*, *F.sylvatica* and  
371*P.abies* was generally higher in the trailing edge than in the core but not always associated with low  
372SPEI. It was associated with various variables as competition, lower SPEI, warmer temperatures or  
373lower precipitation than in the core, depending on the species (Figure 2a-c and Supporting  
374Information Figure S7a). In addition, a strong effect of high temperatures was observed in leading  
375edge areas. Under high temperatures, both temperate (*F.excelisior*, *Quercus petraea* and *Q.robur*,  
376Figure 2d-f) and Mediterranean species (*Quercus ilex*, *P.halepensis*, *P.nigra* and *P.pinea*; Supporting  
377Information Figure S7b-c and Table S12d) showed more intense predicted mortality at the leading  
378edge than in the core areas. Also, *P.tremula* populations are more likely to show high intensity of  
379mortality at the core of its distribution when drought in the studied period was higher than in the  
380reference period (lower values of mean SPEI) (Table S12d).

381

### 3823.3 Spatial patterns of occurrence and intensity of mortality across tree species ranges

383The predicted probability of mortality occurrence (BIN models) was the highest in the trailing edge  
384part of the range for eight temperate (*Alnus glutinosa*, *Betula pendula*, *Picea abies*, *Pinus .sylvestris*,  
385*Populus tremula*, *Fagus sylvatica*, *Quercus robur*, *Q. petraea*) and three Mediterranean species  
386(*Quercus ilex*, *Q.pyrenaica*, *Castanea sativa*) (Figure 3 and S4a). None of the species had a  
387significantly higher probability of mortality occurrence in the core than in the margins, while two  
388temperate species (*P.abies* and *P.sylvestris*) had lower probability of occurrence of mortality in the  
389core than expected under the assumption of uniformity across the species range (Figure 3 and S4a).  
390Four temperate species (*Alnus glutinosa*, *Pinus sylvetris*, *Populus nigra*, *Quercus robur*) and four  
391Mediterranean species (*Castanea sativa*, *Pinus nigra*, *P. pinea* and *Quercus ilex*) had a lower  
392probability of occurrence of mortality in the leading edge part of their range than the core (Figure 3  
393and S4a). We did not find any spatial patterns in the intensity of mortality (NB models) in temperate  
394species. However, the highest predicted intensity of mortality was at the leading edge part of the



395species range for 6 Mediterranean species (*P.halepensis*, *P.nigra*, *P.pinaster*, *P.pinea*, *Q.pyreneica*,  
396*Q.suber*) (Figure 3 and S4b)

397

398Only six species showed similarities between the occurrence and intensity of predicted mortality  
399(Figure 3): *Castanea sativa*, *Quercus robur* and *Quercus ilex* showed the lowest values of both types  
400of predicted mortality at their leading edge whereas *Acer pseudoplatanus* displayed the lowest values  
401at the trailing edge; the predicted intensity and occurrence of mortality predictions for *Quercus ilex*  
402showed the highest values at the trailing edge. *Picea abies* showed the lowest predictions of  
403occurrence and intensity of mortality in the core of the distribution and *Pinus pinaster* predicted  
404mortality of both types was highest at the leading edge.

405

406

407

#### 4084 DISCUSSION

##### 4094.1 Drivers of occurrence and intensity of tree mortality across European tree ranges

410

411Our results are in agreement with previous studies showing that the combination of drought and  
412competition exacerbate the probability of mortality occurrence (Ruiz-Benito et al. 2013, Young,  
4132017) (Tables S11a, S12a), while intense events are driven by multiple factors (including drought and  
414competition) (Anderegg et al., 2015; Jump et al. 2017; Seidl et al., 2017; Wood, Knapp, Muzika,  
415Stambaugh, & Gu, 2018). As expected, the most intense mortality events were associated with low  
416precipitation and high temperatures, the latter only for half of the species (Tables S11b, S12b). This  
417may be explained by the synergic effects of low precipitation and warm temperatures with insect  
418outbreaks (not included in our models) that may end into die-off events (Anderegg et al., 2015; Kurz  
419et al., 2008; McDowell et al., 2011; Wood et al., 2018).

420

421The importance of drought for the occurrence of mortality was higher in marginal populations that  
422experienced drier than average conditions during the study period, suggesting that these populations  
423are the most vulnerable to climate warming (Figure 1a-f and S6a-c). Although in exceptional cases,  
424the highest level of relative drought was more detrimental for core than marginal populations (Figure  
425S5a-d). Interestingly, high temperatures at the leading edge were correlated with the most intense  
426events of mortality for many species, whereas the combination of drought and climatic marginality  
427was less important in mortality intensity than occurrence (Figure 2d-f and S7b-c). Other studies have  
428already observed an increase in background mortality in mild climates and at the northern margin of  
429species ranges associated with warm temperature (Ruiz Benito et al. 2013; Neuman et al. 2017). The  
430less important role of drought in explaining intensity of mortality could be explained by the time lag  
431between stressful conditions and mortality responses, making it complicated to detect such small-time  
432scale effects (Jump et al., 2017). We found a larger effect of competition on intensity of mortality at  
433the trailing edge than at the core in temperate species (Figure 2a-c and S7a), which could be  
434explained by the presence of more competitive and less prone to hydraulic risk Mediterranean species  
435reaching their leading edge (Benito Garzón 2013, 2018).

436

#### 437**4.2 Placing tree mortality at large geographical gradients**

438Mortality is an important component of demography and as such, its geographical patterns can be  
439used to describe demographic and ecological differences of the core versus the peripheral populations  
440(Purves, 2009; Pironon et al., 2017). We showed that the occurrence of mortality is greater in  
441climatically marginal regions than at the climatic core of the species ranges. Furthermore, plots  
442containing largest trees (higher DBH classes) and trees with the lowest growth rate (lower meanBAI<sub>j</sub>)  
443were often associated with high mortality occurrence probability, suggesting that oldest trees are  
444more likely to die (Vanoni et al., 2019; Hülsmann et al., 2017; Cailleret et al., 2017) (Table S11a).

445The predicted probability of mortality occurrence was the highest in the trailing edge for most  
446temperate species and the lowest in the leading edge for half of the Mediterranean species (Figure 3

447and S4a). This suggest that the Mediterranean-temperate ecotone is a hotspot of forest composition  
448changes, as previously suggested on the European gradients of water availability (Ruiz-Benito et al.  
4492017). Furthermore, in Mediterranean species, mortality occurrence was more likely to be higher in  
450the trailing edge than in the core under intense drought (Figure 1d-f), suggesting that the southern part  
451of the species ranges can be delimited by drought-induced mortality (Benito-Garzón et al., 2013;  
452Benito Garzón et al., 2018; Gárate-Escamilla, Hampe, Vizcaíno-Palomar, Robson, & Benito Garzón,  
4532019; Kunstler et al., 2016). This result also highlights that drought increases in southern Europe are  
454boosting background mortality in the last years (Benito Garzón et al., 2018; Carnicer et al., 2011;  
455Druckenbrod et al., 2019; Neumann et al., 2017; Ruiz-Benito et al., 2013).

456

457Conversely, the most intense events of mortality are evenly distributed in the European extent studied  
458(Allen et al., 2015; Allen et al., 2010; Jump et al., 2009; Jump et al., 2017) and they are not related  
459with old trees (DBH classes) or slow growth (meanBAIj) (Table S11b), suggesting they can affect all  
460class of trees age and size as expected for die-off events. As such, die-off mortality can be affected by  
461other important factors such as large competition (Young et al. 2017), pest emergence, fires etc. and  
462result in unexpected demographic patterns. (Jump et al., 2017).

463

### 464**4.3 Limitations and perspectives**

465Although recently managed forests have been removed from our analysis according to management  
466information in forest inventories (Ruiz-Benito et al. 2020), further legacy effects for which no  
467information is available could affect mortality (Clark, Bell, Hersh, & Nichols, 2011; Csilléry et al.,  
4682013, Young 2017). In addition, disturbance magnitude and duration could have contrasting lag  
469effects and the differences in the time lag between surveys in our data can result in large uncertainties  
470(Druckenbrod et al., 2019).

471

472Our findings provide a new perspective to study tree mortality in forests from NFI data as both  
473demographic and stochastic processes are exacerbated to some extent by drought stress but also by an  
474interaction of climatic drivers that change across species ranges.

475

#### 476**Acknowledgements**

477This study was funded by the “Investments for the Future” program IdEx Bordeaux (ANR-10-IDEX-  
47803-02) and the ATHENEE project (Nouvelle-Aquitaine Région). We thank the FunDivEUROPE  
479project (European Union Seventh Framework Programme ([FP7/2007-2013](#)) under grant agreement no  
480265171) for the previous harmonization of the National Forest Inventory data used in this study.  
481MAZ and PRB were supported by grant DARE; RTI2018-096884-B-C32 (MICINN, Spain).

482

#### 483**REFERENCES**

484

- 485Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global  
486 vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene.  
487 *Ecosphere*, 6(8), 1–55. <https://doi.org/10.1890/ES15-00203.1>
- 488Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., ... Cobb,  
489 N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging  
490 climate change risks for forests. *Forest Ecology and Management*, 259(4), 660–684.  
491 <https://doi.org/10.1016/j.foreco.2009.09.001>
- 492Anderegg, W. R., Hicke, J. A., Fisher, R. A., Allen, C. D., Aukema, J., Bentz, B., ... & Pan, Y.  
493 (2015). Tree mortality from drought, insects, and their interactions in a changing climate. *New*  
494 *Phytologist*, 208(3), 674-683. <https://doi.org/10.1111/nph.13477>
- 495Archambeau, J., Ruiz-Benito, P., Ratcliffe, S., Fréjaville, T., Changenet, A., Castañeda, J. M. M., ...  
496 & Garzón, M. B. (2020). Similar patterns of background mortality across Europe are mostly  
497 driven by drought in European beech and a combination of drought and competition in Scots  
498 pine. *Agricultural and Forest Meteorology*, 280, 107772.  
499 <https://doi.org/10.1016/j.agrformet.2019.107772>
- 500Baeten, L., Verheyen, K., Wirth, C., Bruelheide, H., Bussotti, F., Finér, L., ... & Ampoorter, E.  
501 (2013). A novel comparative research platform designed to determine the functional significance  
502 of tree species diversity in European forests. *Perspectives in Plant Ecology, Evolution and*  
503 *Systematics*, 15(5), 281-291. <https://doi.org/10.1016/j.ppees.2013.07.002>
- 504Benito-Garzón, M., Ruiz-Benito, P., & Zavala, M. A. (2013). Interspecific differences in tree growth  
505 and mortality responses to environmental drivers determine potential species distributional limits

506 in Iberian forests. *Global Ecology and Biogeography*, 22(10), 1141–1151.  
507 <https://doi.org/10.1111/geb.12075>

508 Benito-Garzón, M., Leadley, P. W., & Fernández-Manjarrés, J. F. (2014). Assessing global biome  
509 exposure to climate change through the Holocene–Anthropocene transition. *Global Ecology  
510 and Biogeography*, 23(2), 235–244. <https://doi.org/10.1111/geb.12097>

511 Benito Garzón, M., González Muñoz, N., Wigneron, J. P., Moisy, C., Fernández–Manjarrés, J., &  
512 Delzon, S. (2018). The legacy of water deficit on populations having experienced negative  
513 hydraulic safety margin. *Global Ecology and Biogeography*, 27(3), 346–356.  
514 <https://doi.org/10.1111/geb.12701>

515 Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., ... Meyer, C. W.  
516 (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of  
517 the National Academy of Sciences*, 102(42), 15144–15148.  
518 <https://doi.org/10.1073/pnas.0505734102>

519 Bugmann, H., Seidl, R., Hartig, F., Bohn, F., Brůna, J., Cailleret, M., ... Reyer, C. P. O. (2019). Tree  
520 mortality submodels drive simulated long-term forest dynamics: assessing 15 models from the  
521 stand to global scale. *Ecosphere*, 10(2). <https://doi.org/10.1002/ecs2.2616>

522 Cailleret, M., Jansen, S., Robert, E. M. R., Desoto, L., Aakala, T., Antos, J. A., ... Martínez-Vilalta, J.  
523 (2017). A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology*,  
524 23(4), 1675–1690. <https://doi.org/10.1111/gcb.13535>

525 Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sanchez, G., & Penuelas, J. (2011). Widespread  
526 crown condition decline, food web disruption, and amplified tree mortality with increased  
527 climate change-type drought. *Proceedings of the National Academy of Sciences*, 108(4), 1474–  
528 1478. <https://doi.org/10.1073/pnas.1010070108>

529 Caudullo, G., Welk, E., & San-Miguel-Ayanz, J. (2017). Chorological maps for the main European  
530 woody species. *Data in brief*, 12, 662–666. <https://doi.org/10.1016/j.dib.2017.05.007>

531 Clark, J. S., Bell, D. M., Hersh, M. H., & Nichols, L. (2011). Climate change vulnerability of forest  
532 biodiversity: Climate and competition tracking of demographic rates. *Global Change Biology*,  
533 17(5), 1834–1849. <https://doi.org/10.1111/j.1365-2486.2010.02380.x>

534 Csilléry, K., Seignobosc, M., Lafond, V., Kunstler, G., & Courbaud, B. (2013). Estimating long-term  
535 tree mortality rate time series by combining data from periodic inventories and harvest reports in  
536 a Bayesian state-space model. *Forest Ecology and Management*, 292, 64–74.  
537 <https://doi.org/10.1016/j.foreco.2012.12.022>

538 Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... & Münkemüller, T.  
539 (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their  
540 performance. *Ecography*, 36(1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>

541 Druckenbrod, D. L., Martin–Benito, D., Orwig, D. A., Pederson, N., Poulter, B., Renwick, K. M., &  
542 Shugart, H. H. (2019). Redefining temperate forest responses to climate and disturbance in the  
543 eastern United States: New insights at the mesoscale. *Global Ecology and Biogeography*, 28(5),  
544 557–575. <https://doi.org/10.1111/geb.12876>

- 545 Franklin, J. F., Shugart, H. H., & Harmon, M. E. (1987). Tree Death as an Ecological Process.  
546 *BioScience*, 37(8), 550–556. <https://doi.org/10.2307/1310665>
- 547 Fréjaville, T., & Benito Garzón, M. (2018). The EuMedClim database: Yearly climate data (1901–  
548 2014) of 1 km resolution grids for Europe and the Mediterranean basin. *Frontiers in Ecology and*  
549 *Evolution*, 6, 31. <https://doi.org/10.3389/fevo.2018.00031>
- 550 Gárate-Escamilla, H., Hampe, A., Vizcaíno-Palomar, N., Robson, T. M., & Benito Garzón, M.  
551 (2019). Range-wide variation in local adaptation and phenotypic plasticity of fitness-related  
552 traits in *Fagus sylvatica* and their implications under climate change. *Global Ecology and*  
553 *Biogeography*, (April), 1336–1350. <https://doi.org/10.1111/geb.12936>
- 554 Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C. D., ... &  
555 Kraft, N. J. (2017). Tree mortality across biomes is promoted by drought intensity, lower wood  
556 density and higher specific leaf area. *Ecology Letters*, 20(4), 539-553.  
557 <https://doi.org/10.1111/ele.12748>
- 558 Hartmann, H., Schuldt, B., Sanders, T. G. M., Macinnis-Ng, C., Boehmer, H. J., Allen, C. D., ...  
559 Anderegg, W. R. L. (2018). Monitoring global tree mortality patterns and trends. Report from  
560 the VW symposium ‘Crossing scales and disciplines to identify global trends of tree mortality as  
561 indicators of forest health.’ *New Phytologist*, 217(3), 984–987.  
562 <https://doi.org/10.1111/nph.14988>
- 563 Hülsmann, L., Bugmann, H., & Brang, P. (2017). How to predict tree death from inventory data—  
564 lessons from a systematic assessment of European tree mortality models. *Canadian Journal of*  
565 *Forest Research*, 47(7), 890-900. <https://doi.org/10.1139/cjfr-2016-0224>
- 566 Hurst, J. M., Allen, R. B., Coomes, D. A., & Duncan, R. P. (2011). Size-specific tree mortality varies  
567 with neighbourhood crowding and disturbance in a montane *Nothofagus* forest. *PloS one*, 6(10).  
568 <https://doi.org/10.1371/journal.pone.0026670>
- 569 IPCC. (2014). Climate change 2014. Synthesis report. Versión inglés. Climate Change 2014:  
570 Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report  
571 of the Intergovernmental Panel on Climate Change. <https://doi.org/10.1017/CBO9781107415324>
- 572 Jombart, T. (2008). adegenet: a R package for the multivariate analysis of genetic  
573 markers. *Bioinformatics*, 24(11), 1403-1405. <https://doi.org/10.1093/bioinformatics/btn129>
- 574 Jump, A. S., Mátyás, C., & Peñuelas, J. (2009). The altitude-for-latitude disparity in the range  
575 retractions of woody species. *Trends in ecology & evolution*, 24(12), 694-701.  
576 <https://doi.org/10.1016/j.tree.2009.06.007>
- 577 Jump, A. S., Ruiz-Benito, P., Greenwood, S., Allen, C. D., Kitzberger, T., Fensham, R., ... Lloret, F.  
578 (2017). Structural overshoot of tree growth with climate variability and the global spectrum of  
579 drought-induced forest dieback. *Global Change Biology*, 23(9), 3742–3757.  
580 <https://doi.org/10.1111/gcb.13636>
- 581 Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., ... Westoby, M.  
582 (2016). Plant functional traits have globally consistent effects on competition. *Nature*,  
583 529(7585), 204–207. <https://doi.org/10.1038/nature16476>

- 584Kurz, W. A., Dymond, C. C., Stinson, G., Rampley, G. J., Neilson, E. T., Carroll, A. L., ... Safranyik,  
585 L. (2008). Mountain pine beetle and forest carbon feedback to climate change. *Nature*,  
586 452(7190), 987–990. <https://doi.org/10.1038/nature06777>
- 587Lee, Y., Nelder, J. A., & Pawitan, Y. (2018). Generalized linear models with random effects: unified  
588 analysis via H-likelihood. Chapman and Hall/CRC.
- 589Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology,  
590 evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573-579.  
591 <https://doi.org/10.1111/2041-210X.12512>
- 592McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., ... & Yezzer, E.  
593 A. (2008). Mechanisms of plant survival and mortality during drought: why do some plants  
594 survive while others succumb to drought?. *New phytologist*, 178(4), 719-739.  
595 <https://doi.org/10.1016/j.biocon.2016.01.028>
- 596McDowell, N., Allen, C. D., Anderson-Teixeira, K., Brando, P., Brienen, R., Chambers, J., ... &  
597 Espirito-Santo, F. (2018). Drivers and mechanisms of tree mortality in moist tropical  
598 forests. *New Phytologist*, 219(3), 851-869. <https://doi.org/10.1111/nph.15027>
- 599McDowell, N. G., Beerling, D. J., Breshears, D. D., Fisher, R. A., Raffa, K. F., & Stitt, M. (2011).  
600 The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in*  
601 *Ecology and Evolution*, 26(10), 523–532. <https://doi.org/10.1016/j.tree.2011.06.003>
- 602Mueller-Dombois, D. (1987). Natural dieback in forests. *BioScience*, 37(8), 575-583.  
603 <https://doi.org/10.2307/1310668>
- 604Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R<sup>2</sup> from  
605 generalized linear mixed-effects models. *Methods in ecology and evolution*, 4(2), 133-142.  
606 <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- 607Nakagawa, S., Johnson, P. C., & Schielzeth, H. (2017). The coefficient of determination R<sup>2</sup> and  
608 intra-class correlation coefficient from generalized linear mixed-effects models revisited and  
609 expanded. *Journal of the Royal Society Interface*, 14(134), 20170213.  
610 <https://doi.org/10.1098/rsif.2017.0213>
- 611Neumann, M., Mues, V., Moreno, A., Hasenauer, H., & Seidl, R. (2017). Climate variability drives  
612 recent tree mortality in Europe. *Global Change Biology*, 23(11), 4788–4797.  
613 <https://doi.org/10.1111/gcb.13724>
- 614Pironon, S., Papuga, G., Vilellas, J., Angert, A. L., García, M. B., & Thompson, J. D. (2017).  
615 Geographic variation in genetic and demographic performance: new insights from an old  
616 biogeographical paradigm. *Biological Reviews*, 92(4), 1877–1909.  
617 <https://doi.org/10.1111/brv.12313>
- 618Purves, D. W. (2009). The demography of range boundaries versus range cores in eastern US tree  
619 species. *Proceedings of the Royal Society B: Biological Sciences*, 276(1661), 1477–1484.  
620 <https://doi.org/10.1098/rspb.2008.1241>
- 621Rousset, F., Ferdy, J. B., & Courtiol, A. (2016). spaMM: Mixed models, particularly spatial  
622 GLMMs. R package version, 1(2).

623 Ruiz-Benito, P., Lines, E. R., Gómez-Aparicio, L., Zavala, M. A., & Coomes, D. A. (2013). Patterns  
624 and Drivers of Tree Mortality in Iberian Forests: Climatic Effects Are Modified by Competition.  
625 PLoS ONE, 8(2). <https://doi.org/10.1371/journal.pone.0056843>

626 Ruiz-Benito, P., Ratcliffe, S., Jump, A. S., Gómez-Aparicio, L., Madrigal-Gonzalez, J., Wirth, C., ...  
627 Zavala, M. A. (2017). Functional diversity underlies demographic responses to environmental  
628 variation in European forests. *Global Ecology and Biogeography*, 26(2), 128–141.  
629 <https://doi.org/10.1111/geb.12515>

630 Ruiz-Benito, P., Vacchiano, G., Lines, E. R., Reyer, C. P., Ratcliffe, S., Morin, X., ... & Palacios-  
631 Orueta, A. (2020). Available and missing data to model impact of climate change on European  
632 forests. *Ecological Modelling*, 416, 108870. <https://doi.org/10.1016/j.ecolmodel.2019.108870>

633 Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., ... O Reyer, C. P.  
634 (2017). Forest disturbances under climate change Europe PMC Funders Group. *Nat Clim*  
635 *Change*, 7, 395–402. <https://doi.org/10.1038/nclimate3303>

636 Vanoni, M., Cailleret, M., Hülsmann, L., Bugmann, H., & Bigler, C. (2019). How do tree mortality  
637 models from combined tree-ring and inventory data affect projections of forest succession?  
638 *Forest Ecology and Management*, 433(November 2018), 606–617.  
639 <https://doi.org/10.1016/j.foreco.2018.11.042>

640 Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought index  
641 sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal of*  
642 *climate*, 23(7), 1696-1718. <https://doi.org/10.1175/2009JCLI2909.1>

643 Wood, J. D., Knapp, B. O., Muzika, R. M., Stambaugh, M. C., & Gu, L. (2018). The importance of  
644 drought–pathogen interactions in driving oak mortality events in the Ozark Border  
645 Region. *Environmental Research Letters*, 13(1), 015004.  
646 <https://doi.org/10.1088/1748-9326/aa94fa>

647 Young, D. J. N., Stevens, J. T., Earles, J. M., Moore, J., Ellis, A., Jirka, A. L., & Latimer, A. M.  
648 (2017). Long-term climate and competition explain forest mortality patterns under extreme  
649 drought. *Ecology Letters*, 20(1), 78–86. <https://doi.org/10.1111/ele.12711>

650



Figure 1: Effect of the interaction between drought (mean SPEI index) and marginality on predicted mortality occurrence per plot (expressed as a probability) across the core (black lines), trailing (red lines) and leading edge (blue lines) of three temperate species: a) *Abies alba*, b) *Picea abies*, c) *Pinus sylvestris*; and three Mediterranean – warm temperate species: d) *Castanea sativa*, e) *Pinus pinea*, f) *Pinus nigra*. Predictions within the ranges of the environmental gradients covered by the species are shown by solid colors and extrapolations outside the environmental gradients covered by the species are shown in transparent colors. For the case of *Castanea sativa* our data did not cover the leading edge of the species. T-values of the main effects interacting with marginality are reported.

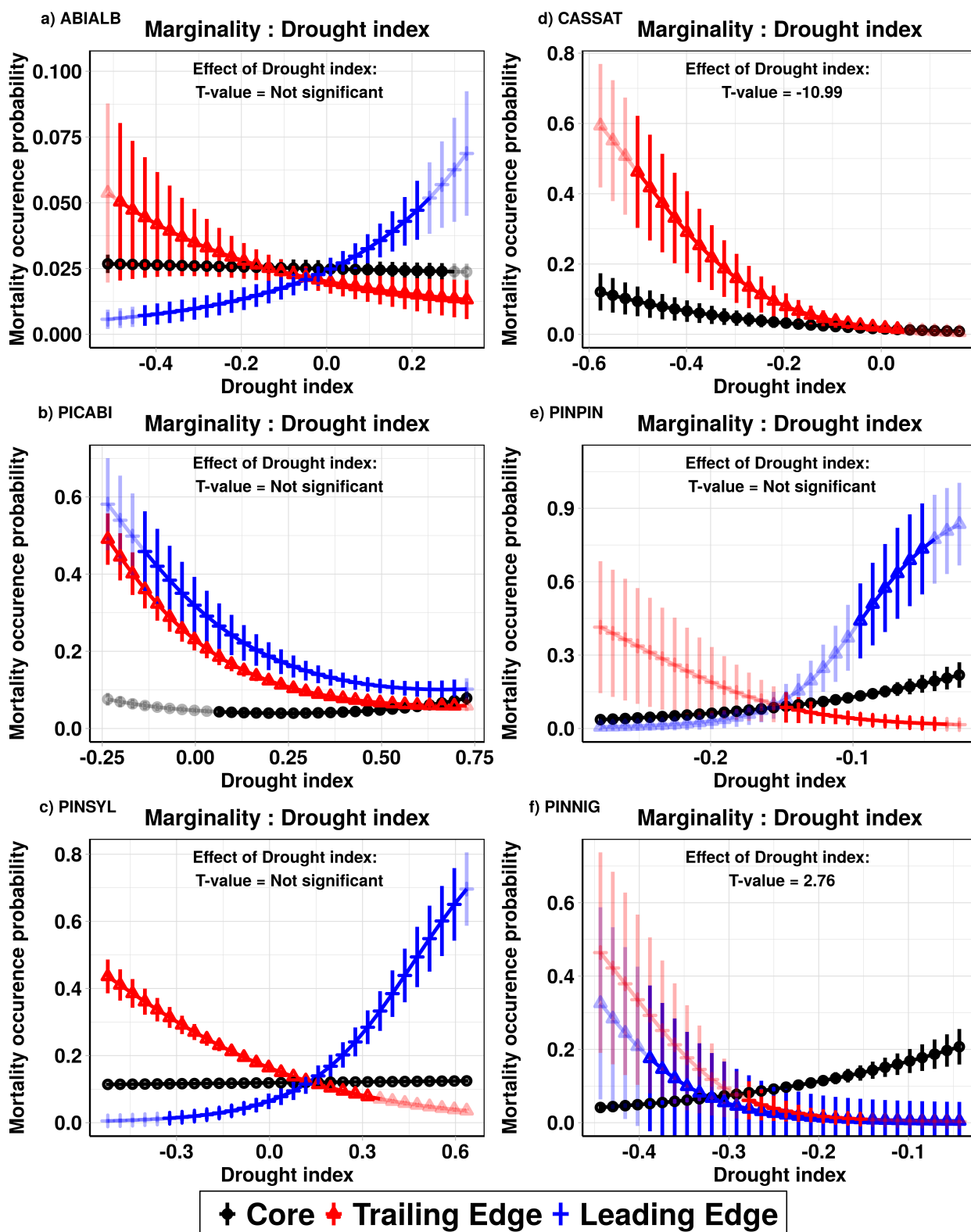


Figure 2: Effect of the interaction between climatic variables on the predicted intensity of mortality across the core (black lines), trailing (red lines) and leading edge (blue lines) of six temperate species: a) *Abies alba*, b) *Betula pendula*, c) *Fagus sylvatica*, d) *Fraxinus excelsior*, e) *Quercus petraea*, f) *Quercus robur*, expressed as the proportion (‰), by year and by plot. Predictions within the ranges of the environmental gradients covered by the species are shown by solid colors and extrapolations outside the environmental gradients covered by the species are shown in light colors. T-values of the main effects interacting with marginality are reported.

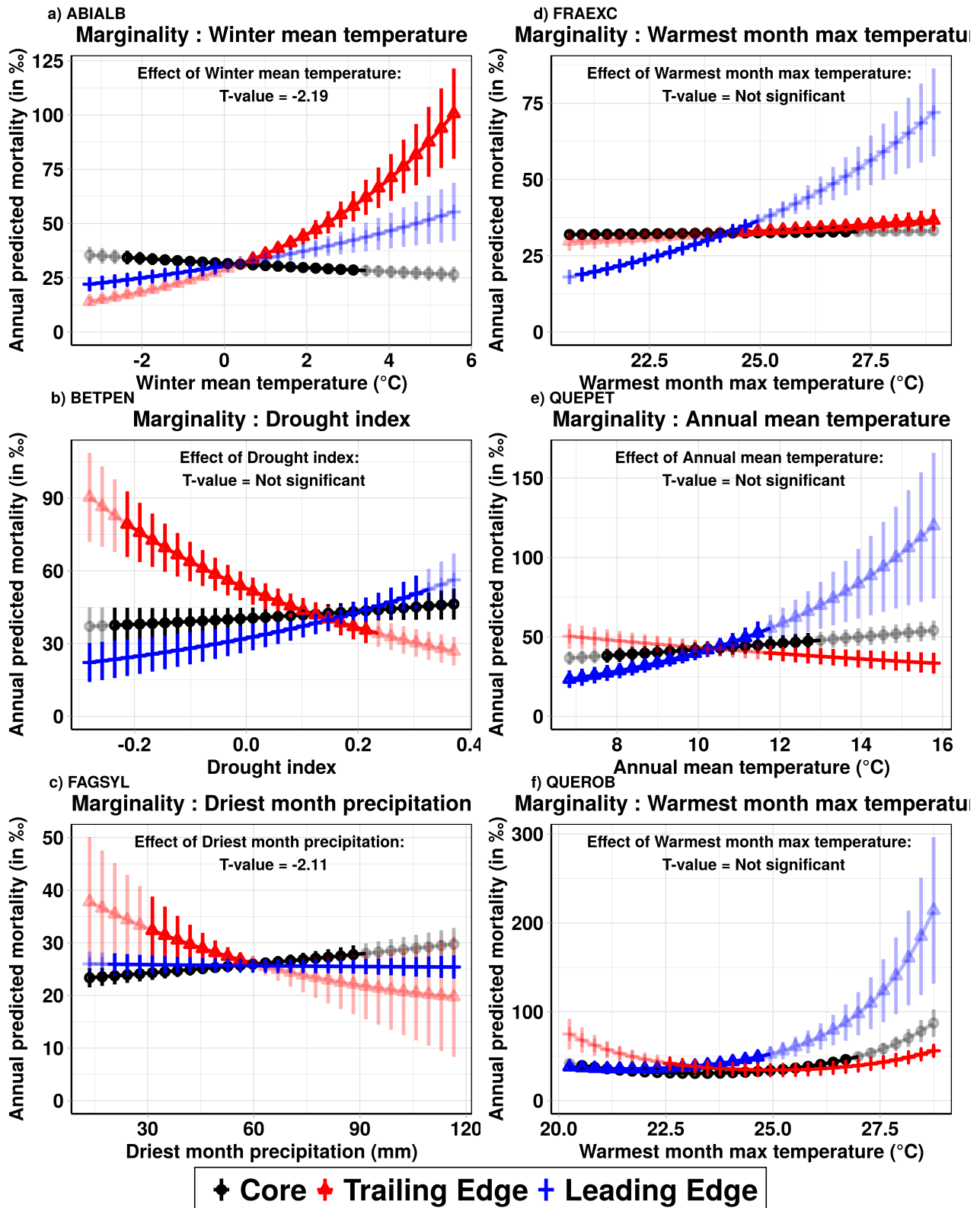


Table 1: Statistical evaluation of occurrence and intensity of mortality models, by species. Species: Name of the species. Code: Code used for each species Model: model type: Occurrence, intensity or intensity of mortality model including spatial autocorrelation (intensity + SAC - Spatial Autocorrelation -). R2M: Marginal r-squared. R2C: conditional r-squared. PCVObs: proportion change in variance between null model and fixed effect model (in %). COG: capacity of generalization. AUC (Area Under the Curve) for mortality occurrence models and CV (Cross Validation score) for intensity of mortality models.

Species	Code	Model	R2M	R2C	PCVObs	COG (AUC/CV)
<i>Abies alba</i> Mill.	ABIALB	Occurrence	0.13	0.42	-1.98	0.82
<i>Acer pseudoplatanus</i> L.	ACEPSE	Occurrence	0.06	0.2	-9.25	0.85
<i>Alnus glutinosa</i> (L.) Gaertn.	ALNGLU	Occurrence	0.2	0.26	-1.45	0.81
<i>Betula pendula</i> Roth.	BETPEN	Occurrence	0.09	0.34	-5.55	0.83
<i>Castanea sativa</i> Mill.	CASSAT	Occurrence	0.21	0.56	-1.18	0.82
<i>Fagus sylvatica</i> L.	FAGSYL	Occurrence	0.11	0.12	-3.55	0.82
<i>Fraxinus excelsior</i> L.	FRAEXC	Occurrence	0.07	0.38	-5.59	0.84
<i>Picea abies</i> (L.) H.Karst.	PICABI	Occurrence	0.15	0.19	-1.68	0.78
<i>Pinus halepensis</i> Mill.	PINHAL	Occurrence	0.22	0.22	-1.46	0.80
<i>Pinus nigra</i> J.F.Arnold.	PINNIG	Occurrence	0.19	0.24	-1.74	0.81
<i>Pinus pinaster</i> Aiton.	PINPINA	Occurrence	0.46	0.46	-0.52	0.85
<i>Pinus pinea</i> L.	PINPIN	Occurrence	0.24	0.24	-1.2	0.81
<i>Pinus sylvestris</i> L.	PINSYL	Occurrence	0.22	0.26	-1.17	0.80
<i>Populus nigra</i> L.	POPNEG	Occurrence	0.19	0.46	-1.39	0.84
<i>Populus tremula</i> L.	POPTRE	Occurrence	0.12	0.24	-2.83	0.82
<i>Quercus ilex</i> L.	QUEILE	Occurrence	0.12	0.37	-2.98	0.77
<i>Quercus petraea</i> Liebl.	QUEPET	Occurrence	0.13	0.36	-2.63	0.83
<i>Quercus pyrenaica</i> Willd.	QUEPYR	Occurrence	0.17	0.17	-2.04	0.79
<i>Quercus robur</i> L.	QUEROB	Occurrence	0.28	0.52	-1.37	0.83
<i>Quercus suber</i> L.	QUESUB	Occurrence	0.15	0.15	-1.2	0.77
<i>Abies alba</i> Mill.	ABIALB	Intensity	0.2	0.5	0.31	0.58
<i>Acer pseudoplatanus</i> L.	ACEPSE	Intensity	0.21	0.92	0.7	0.51
<i>Alnus glutinosa</i> (L.) Gaertn.	ALNGLU	Intensity	0.39	0.44	0.4	0.53
<i>Betula pendula</i> Roth.	BETPEN	Intensity	0.42	0.66	0.53	0.73
<i>Betula pendula</i> Roth.	BETPEN	Intensity + SAC	0.42	0.71	0.6	NA
<i>Castanea sativa</i> Mill.	CASSAT	Intensity	0.13	0.78	0.38	0.57
<i>Fagus sylvatica</i> L.	FAGSYL	Intensity	0.23	0.46	0.25	0.37
<i>Fraxinus excelsior</i> L.	FRAEXC	Intensity	0.46	0.46	0.52	0.64
<i>Fraxinus excelsior</i> L.	FRAEXC	Intensity + SAC	0.48	0.52	0.51	NA
<i>Picea abies</i> (L.) H.Karst.	PICABI	Intensity	0.22	0.41	0.33	0.57

<i>Pinus halepensis</i> Mill.	PINHAL	Intensity	0.26	0.26	0.33	0.60
<i>Pinus nigra</i> J.F.Arnold.	PINNIG	Intensity	0.2	0.41	0.32	0.32
<i>Pinus pinaster</i> Aiton.	PINPINA	Intensity	0.29	0.29	0.38	0.62
<i>Pinus pinea</i> L.	PINPIN	Intensity	0.24	0.34	0.3	0.56
<i>Pinus sylvestris</i> L.	PINSYL	Intensity	0.27	0.51	0.35	0.57
<i>Populus tremula</i> L.	POPTRE	Intensity	0.29	0.29	0.34	0.59
<i>Quercus ilex</i> L.	QUEILE	Intensity	0.26	0.48	0.35	0.40
<i>Quercus petraea</i> Liebl.	QUEPET	Intensity	0.29	0.77	0.4	0.57
<i>Quercus pyrenaica</i> Willd.	QUEPYR	Intensity	0.26	0.26	0.32	0.26
<i>Quercus pyrenaica</i> Willd.	QUEPYR	Intensity + SAC	0.26	0.26	0.29	0.57
<i>Quercus robur</i> L.	QUEROB	Intensity	0.26	0.38	0.33	0.61
<i>Quercus suber</i> L.	QUESUB	Intensity	0.33	0.33	0.34	0.73

Figure 3: First and third columns show the predicted mortality occurrence (GLMM) and second and fourth columns are the predicted intensity of mortality (ZTNBGLMM) for the twenty species. Blues dots correspond to mortality predictions values lower than the first quartile (lowest values), green dots represent values ranging from the first to the third quartile (medium values) and red dots represent values higher than the third quartile (highest values) (Table S10). Light grey areas display species distribution ranges.

