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1 **Background mortality drivers of European tree species: climate change matters**

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10 **Increases of tree mortality rates have been highlighted in different biomes over the**
11 **past decades. However, disentangling the effects of climate change on the temporal**
12 **increase of tree mortality from those of management and forest dynamics remains a**
13 **challenge. Using a modeling approach taking tree and stand characteristics into**
14 **account, we sought to evaluate the impact of climate change on background mortality**
15 **for the most common European tree species. We focused on background mortality,**
16 **which is the mortality observed in a stand in the absence of abrupt disturbances, to**
17 **avoid confusion with mortality events unrelated with long-term changes in**
18 **temperature and rainfall. We studied 372,974 trees including 7,312 dead trees from**
19 **forest inventory data surveyed across France between 2009 and 2015. Factors related**
20 **with competition, stand characteristics, management intensity, and site conditions**
21 **were the expected preponderant drivers of mortality. Taking these main drivers into**
22 **account, we detected a climate change signal on 45% of the 43 studied species,**
23 **explaining an average 6% of the total modeled mortality. For 18 out of the 19 species**
24 **sensitive to climate change, we evidenced greater mortality with increasing**
25 **temperature or decreasing rainfall. By quantifying the mortality excess linked to the**
26 **current climate change for European temperate forest tree species, we provide new**
27 **insights into forest vulnerability that will prove useful for adapting forest management**
28 **to future conditions.**

29 Forests are among the most important terrestrial providers of ecosystem services. Therefore,
30 understanding how climate change could affect their functioning is an urgent challenge. Climate
31 change can influence tree mortality through extreme events such as storms, forest fires,
32 flooding, avalanches or pest outbreaks, that can locally lead to important forest dieback (1). At
33 the opposite end of catastrophe-related mortality, the mortality rates observed in stands in the
34 absence of severe disturbances are called background mortality. While the link between
35 extreme climatic events and tree mortality has been extensively studied (2, 3), the extent to
36 which background mortality increases are related to climate change remains unclear.

37 The link between current climatic conditions and background tree mortality was
38 established in the field through spatial approaches aimed at correlating the spatial variations of
39 observed mortality with those of average climatic conditions over a given period. These studies
40 lead to contrasting results. Tree mortality was found to be positively correlated with water stress
41 in forests of North America (4), positively correlated with warm summers in Europe (5), while
42 significant but highly heterogeneous and species-dependent responses to climate conditions
43 were evidenced in forests of the eastern United States (6, 7) and Spain (8). At the stand scale,
44 aerial observations of dieback patterns were found positively correlated with the intensity of
45 climatic water deficit in temperate (9) and boreal forests (10). Although these studies
46 highlighted average climate effects on background tree mortality, they did not take the evolution
47 of climatic conditions over time into account.

48 Other approaches characterized the evolution of background tree mortality based on the
49 analysis of longitudinal data, i.e. the monitoring of the tree or stand health status over long time
50 periods, with repeated aerial or ground surveys. Several such studies showed significant
51 background tree mortality increases over the last decades for all tree sizes and at different
52 altitudinal and latitudinal ranges in forests of the western and central United States (11) and in

53 boreal forests of Canada (12). In Central Europe, the analysis of Landsat data covering the years
54 1984 to 2016 showed that canopy mortality rates doubled over that period (13).

55 It is quite hard to disentangle the different drivers of background tree mortality over
56 long time periods in such temporal studies in a context of forest transition (14, 15). In North
57 America, because the stand development dynamics of old-growth forests have been assumed to
58 be at equilibrium, temporal increases of tree mortality in these stands were mainly attributed to
59 increasing temperature and decreasing water availability (11, 16). However, other temporal
60 studies in boreal and subalpine Canadian forests found that mortality increases were not related
61 to temperature increases, but only to increases in basal area and stand density (17), even in
62 mature stands (18). Additional studies in the same areas highlighted a predominant effect of
63 increased competition on increased tree mortality, with changes in climate conditions playing
64 a secondary role (12, 19). Furthermore, many additional factors such as species composition,
65 spatial structure, species interactions (20), or silvicultural practices and management intensity
66 (21) impact tree mortality and have evolved over the past decades, preventing temporal studies
67 from fully disentangling the drivers of mortality. Despite the stakes, the extent to which recent
68 climate change has already affected background tree mortality in temperate forests remains
69 questionable.

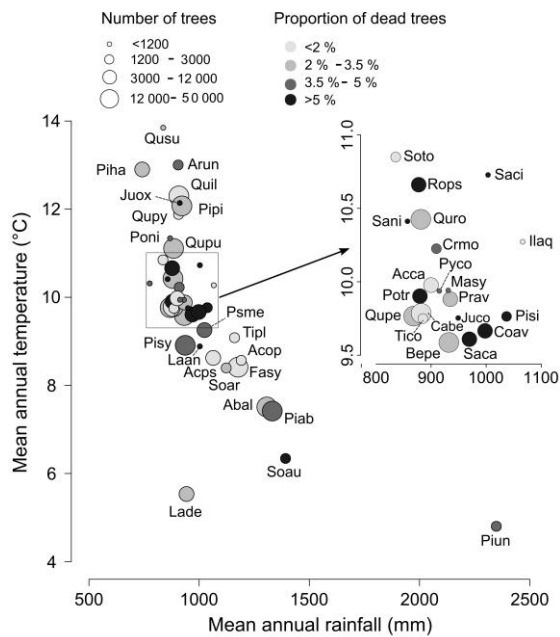
70 Previous studies based on spatial approaches did not consider the effects of climate
71 change intensity, while temporal studies could not reliably attribute mortality increases to
72 changes in the temperature and rainfall regimes owing to the difficulties in disentangling the
73 different drivers over long time periods. So far, no study combining both an accurate description
74 of tree and stand characteristics and climate change data has been performed on temperate
75 forests. We examined the relationships between the spatial patterns of climate change since the
76 1960s and the current distribution of dead trees using ground survey data from the French
77 national forest inventory program (NFI). This dataset provides an accurate description of tree

78 and stand characteristics, including previously unexplored potential mortality factors like
79 logging intensity, stand structure, and species composition for a large number of plots. We used
80 a modeling approach for a large number of species representative of the European temperate
81 forests to disentangle site, tree and stand characteristics effects from climate change effects on
82 mortality. European forests represent 26% of the world forests in terms of growing stock (15),
83 while a majority of European tree species are threatened by future global warming on a large
84 part of their distribution range (22).

85 **Materials and Methods**

86 **Study sites and species**

87 We used information from 41,692 forest plots with 554,133 trees, including 37,767 dead trees
88 inventoried in the national forest inventory program (NFI) over the 2009-2015 period in France.
89 Because our study focused on the effects of temperature and rainfall on background tree
90 mortality, we removed plots affected by storms, fires, avalanches, floods, and broken or felled
91 dead trees, to focus on standing dead trees (Electronic Supplementary Material, Panel 1a).
92 Salvage-logged trees were not taken into account because no information about the tree status
93 (living or dead) before harvesting was available. We studied a broad range of species
94 representative of contrasting ecological contexts (dry or wet and siliceous or calcareous)
95 representative of different biomes (lowland / mountain / Mediterranean forests). Among the
96 most common species present in the NFI database, we removed 5 species affected by severe
97 health issues (Electronic Supplementary Material, Panel 1b) to study 43 species (**Figure 1**) that
98 compose around 80% of the total forest cover of Europe (23). We finally considered 372,974
99 trees with diameter >7.5 cm including 7,312 dead trees located in 34,097 plots scattered across
100 the afforested territory of France.



Code	Species	Code	Species
Abal	<i>Abies alba</i>	Poni	<i>Populus nigra</i>
Acca	<i>Acer campestre</i>	Potr	<i>Populus tremula</i>
Acop	<i>Acer opalus</i>	Prav	<i>Prunus avium</i>
Acps	<i>Acer pseudoplatanus</i>	Psme	<i>Pseudotsuga menziesii</i>
Arun	<i>Arbutus unedo</i>	Pyco	<i>Pyrus communis</i>
Bepe	<i>Betula pendula</i>	Quil	<i>Quercus ilex</i>
Cabe	<i>Carpinus betulus</i>	Qupe	<i>Quercus petraea</i>
Coav	<i>Corylus avellana</i>	Qupu	<i>Quercus pubescens</i>
Crmo	<i>Crataegus monogyna</i>	Qupy	<i>Quercus pyrenaica</i>
Fasy	<i>Fagus sylvatica</i>	Quro	<i>Quercus robur</i>
Ilaq	<i>Ilex aquifolium</i>	Qusu	<i>Quercus suber</i>
Juco	<i>Juniperus communis</i>	Rops	<i>Robinia pseudoacacia</i>
Juox	<i>Juniperus oxycedrus</i>	Saal	<i>Salix alba</i>
Laan	<i>Laburnum anagyroides</i>	Saca	<i>Salix caprea</i>
Lade	<i>Larix decidua</i>	Saci	<i>Salix cinerea</i>
Masy	<i>Malus sylvestris</i>	Sani	<i>Sambucus nigra</i>
Piab	<i>Picea abies</i>	Soar	<i>Sorbus aria</i>
Pisi	<i>Picea sitchensis</i>	Soau	<i>Sorbus aucuparia</i>
Piha	<i>Pinus halepensis</i>	Soto	<i>Sorbus torminalis</i>
Pipi	<i>Pinus pinaster</i>	Tico	<i>Tilia cordata</i>
Pisy	<i>Pinus sylvestris</i>	Tipl	<i>Tilia platyphyllos</i>
Piun	<i>Pinus uncinata</i>		

101

102 **Figure 1. Number of trees and proportion of dead individuals *per* species along mean annual**
 103 **temperature and rainfall gradients over the 1961-1987 period.** The circle size corresponds to the
 104 total number of trees *per* species (alive or dead) in the sample surveyed between the years 2009 and
 105 2015. The circle color corresponds to the proportion of dead trees *per* species. Species are located at
 106 their mean temperature and rainfall over the 1961-1987 period. Correspondence is provided between
 107 the species names and the abbreviations used in this figure, in figure 5, in electronic supplementary
 108 material, table S2 and figure S2

109 The plot altitudes ranged from 1 m to 2,533 m (mean = 432 m), longitude from 5°W to 10°E,
 110 and latitude from 41°N to 51°N. The proportion of dead trees over the 2009-2015 period varied
 111 from 0.6% to 18% (**Figure 1**) of the total number of surveyed trees depending on the species
 112 (mean \pm s.d = 4.1% \pm 3.0%) and was not related to average 1961-1987 temperature ($R^2=0.06$,
 113 $P=0.62$), rainfall ($R^2=0.02$, $P=0.88$) or to the frequency of species ($R^2=0.09$, $P=0.08$; **Figure 1**).

114 Variables considered

115 Mortality models were built using 36 variables covering the main drivers of tree mortality
 116 identified at the tree and stand scales in various studies [**Table 1**, (24, 25)]. To assess the effects
 117 of competitive interactions at the tree level, we used the circumference at 1.3 m height (*Circ*,

118 cm) and calculated the relative circumference (*RelCirc*, %), which is the ratio of the
 119 circumference of each tree over the average circumference of the other trees in the plot. To
 120 assess the effects of stand structure and composition, we computed seven indices from the field-
 121 measured variables (*Circ* and tree canopy cover). The total basal area of all the trees within
 122 each plot was calculated from the tree circumference and summed to give the plot basal area
 123 (*BA*, m²/ha). The number of trees per hectare (*NB*, Nb/ha) was calculated from the sum of
 124 inventoried trees on the plot. The plot canopy cover (*CC*, %) is the proportion of the plot
 125 covered by the vertical projection of all measured tree crowns. We computed the total number
 126 of tree species (*Nb_sp*) and the proportion of basal area occupied by each species within each
 127 plot (*PropBA*, %) as indicators of forest composition. To evaluate stand structure heterogeneity,
 128 we calculated the Gini index of inequality of tree circumferences on the plot (26) (*Gini*) that
 129 ranges between 0 and 1, with increasing diameter unevenness.

$$130 \quad Gini = \frac{1}{\sum_{i=1}^n Ci (n-1)} \sum_{i=1}^n (2i - n - 1) Ci$$

131 *Ci* = Circumference of tree *i* in the plot

132 *n* = total number of trees in the plot

133 We assessed the effects of site environmental conditions with bio-indicated estimates of
 134 the soil pH, the carbon-to-nitrogen ratio, permanent and temporary waterlogging indices and 6
 135 climate variables describing average seasonal temperatures (*Tm_{winter}Ref*, *Tm_{spring}Ref*, *Tm_{summer}Ref*,
 136 *Tm_{autumn}Ref*) and spring and summer rainfall (*RF_{spring}Ref*, *RF_{summer}Ref*) over the 1961-1987 period
 137 (Electronic Supplementary Material, Panel 1c for additional details about the calculation of
 138 environmental condition variables).

139 Finally, we assessed the effects of climate change intensity by calculating the evolution
 140 of the same 6 climate variables between the 1961-1987 historic period and contemporary
 141 periods at each plot location using historic homogenized climate series spanning the 1961-2015
 142 period (27). Because delayed mortality can occur several years after a climatic disturbance (28),

143 and because the forest inventory program records trees that are supposed to have died in the
144 five years preceding their survey, we considered the fifteen years preceding each plot survey as
145 contemporary periods (e.g. the 1994-2009 period for a survey carried out in 2009). We obtained
146 6 variables describing the evolution of temperature and rainfall *per* season, calibrated on the
147 fifteen years preceding the date of the survey ($Tm_{win}Evo$, $Tm_{spr}Evo$, $Tm_{sum}Evo$, $Tm_{aut}Evo$,
148 $RF_{spr}Evo$ and $RF_{sum}Evo$, **Table 1**, and see Electronic Supplementary material, Panel 1d for
149 details about the calculation of climate change intensity variables).

150 We hypothesized that for a given temperature increase or rainfall decrease, impacts on
151 trees were greater in areas with a high temperature or low rainfall over the reference period. To
152 assess the potential influence of initial climate conditions on the effects of climate change on
153 tree mortality, we considered the product between $TmRef$ and $TmEvo$ and the $RfEvo$ -over- $RfRef$
154 ratio as additional candidate variables (**Table 1**).

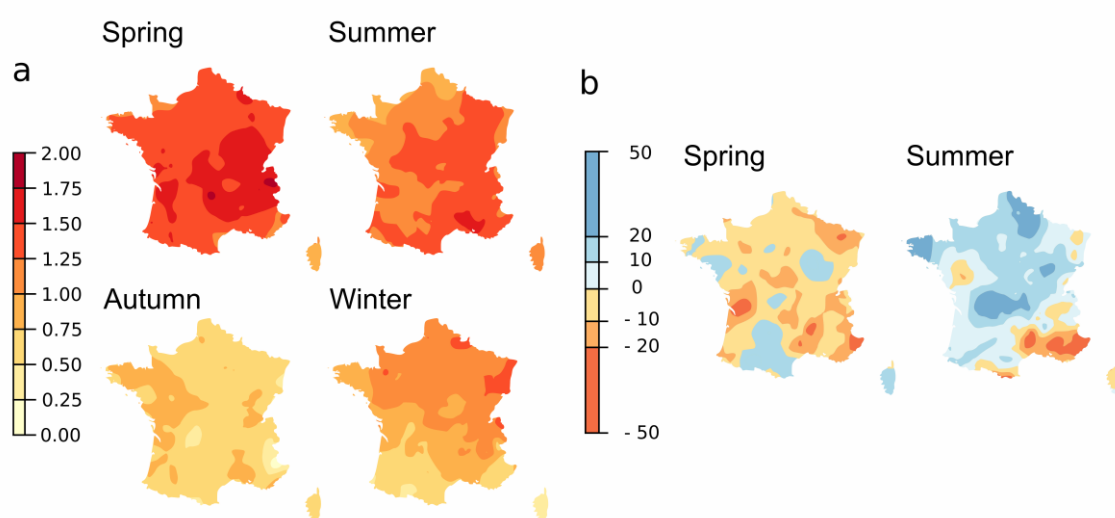
Variable name	Code	Description	Units	Source
Tree status				
Circumference	Circ	Circumference of the tree measured at 1.30m height.	cm	Field
Relative circumference	RelCirc	Ratio of the tree circumference over the mean circumference of all the trees in the plot.	/	Calc.
Stand characteristics and structure				
Plot basal area	BA	Sum of the tree basal areas in the plot.	m ²	Calc.
Number of trees <i>per</i> hectare	NB	Number of trees, all species considered, with a diameter ≥ 7.5 cm measured in the plot and related to a value <i>per</i> hectare.	nb.ha ⁻¹	Calc.
Canopy Cover	CC	Proportion of the forest floor covered by the vertical projection of the tree crowns.	%	Calc.
Quadratic mean diameter	QMD	Quadratic mean diameter of the trees on the plot.	cm	Calc.
Gini coefficient	Gini	Gini coefficient of the tree circumferences in each plot.	/	Calc.
Proportion of BA occupied by the species growing in the plot	PropBA	Percent of basal area occupied by the species in each plot.	%	Calc.
Number of tree species	Nb_sp	Total number of tree species in each plot.	/	Calc.
Stand management intensity				
Skidding distance	Dist	Indicator of the distance from the center of the plot to the nearest existing skid trail.	/	Field
Skid trails	Trails	Indicator of the presence of already existing skid trails and of the possibility to create new ones.	/	Field
Recent cut	Cut	Type and intensity of a recent cut in the plot (less than 5 years).	/	Field
Soil properties				
Available Water Content	AWC	Maximum volume of water that can be stored in the soil calculated from the Al-Majjou pedotransfer functions.	mm	Mod.
Permanent waterlogging	PW	pH, C/N, Permanent and temporary waterlogging index: bio-indicator values calculated from the floristic survey of each plot.	/	Mod.
Temporary waterlogging	TW		/	Mod.
pH	pH		/	Mod.
carbon-to-nitrogen ratio	CN		/	Mod.
Surface runoff	Topo	Surface runoff estimated from the site topography		Field
Climate conditions				
Winter mean T° 1961-1987	Tm _{win} Ref	Mean seasonal temperatures in winter, spring, summer, and autumn, and mean total seasonal rainfall in spring and summer calculated over the 1961-1987 reference period.	°C	Mod
Spring mean T° 1961-1987	Tm _{spr} Ref		°C	Mod.
Summer mean T° 1961-1987	Tm _{sum} Ref		°C	Mod.
Autumn mean T° 1961-1987	Tm _{aut} Ref		°C	Mod.
Spring rainfall 1961-1987	RF _{spr} Ref		mm	Mod.
Summer rainfall 1961-1987	RF _{sum} Ref		mm	Mod.
Intensity of climate change				
Winter mean T° evolution	Tm _{win} Evo	Climate change anomalies between the 1961-1987 reference period and shifting fifteen-year sub-periods based on the date of the survey of each plot for the same variables and seasons as for the reference period.	°C	Mod.
Spring mean T° evolution	Tm _{spr} Evo		°C	Mod.
Summer mean T° evolution	Tm _{sum} Evo		°C	Mod.
Autumn mean T° evolution	Tm _{aut} Evo		°C	Mod.
Spring Rainfall evolution	RF _{spr} Evo		mm	Mod.
Summer Rainfall evolution	RF _{sum} Evo		mm	Mod.
Interaction between temperature and its evolution	Tm _{win} Ref * Tm _{win} evo Tm _{spr} Ref * Tm _{spr} evo Tm _{sum} Ref * Tm _{sum} evo Tm _{aut} Ref * Tm _{aut} evo	Interaction between temperature evolution and the reference period temperature calculated as a product of these two values for each season. Relative rainfall evolution calculated as the ratio of rainfall evolution over the reference-period rainfall, for spring and summer.	°C ²	Mod.
Relative rainfall evolution	RF _{spr} evo / RF _{spr} Ref RF _{sum} evo / RF _{sum} Ref		%	Mod.

155

156 **Table 1. Description of the 36 explanatory variables used in the models.** *Code* =
157 abbreviation. The *Source* column indicates the origin of the data: collected on field (*Field*),
158 calculated using field data (*Calc*), or extracted from models available from Geographic
159 Information Systems (*Mod.*)

160 **Observed climate change patterns**

161 In our study area, mean annual temperature significantly increased by 1.1°C between 1961-
162 1987 and 1988-2015, (t-test: $P < 0.0001$), from 9.9°C ($\pm 0.4^\circ\text{C}$) to 11.0°C ($\pm 0.5^\circ\text{C}$; Electronic
163 Supplementary Material Figure 1a), while mean annual rainfall did not change significantly (t-
164 test: $P = 0.53$), from 974 mm (± 110 mm) to 990 mm (± 115 mm; Electronic Supplementary
165 Material Figure 1c). Important seasonal and spatial variations exist, and climate change
166 intensity was not uniform across the distribution of the plots (Electronic Supplementary
167 Material Figure 1b and 1d). The mapping of seasonal climate change variables between 1961-
168 1987 and 1988-2015 revealed that average temperature increases were more intense in spring
169 and summer, (between $+0.75^\circ\text{C}$ and $+2^\circ\text{C}$) than in autumn and winter (between $+0.25$ and
170 $+1^\circ\text{C}$; **Figure 2a**), with important spatial variations. Concerning changes in rainfall regimes
171 over this period, average spring rainfall decreased over most of the study area (**Figure 2b**),
172 while summer rainfall sharply decreased only in parts of south-eastern France, with sharp
173 increases observed elsewhere.



174
175 **Figure 2. Climate change between the 1961-1987 reference period and the 1988-2015 period per**
176 **season 1-A: for temperature (°C) 1-B: for rainfall (mm).**

177 **Statistical model**

178 We modeled the status of each tree (0: alive, 1: dead) for each of the 43 species with logistic
179 regression models. Logistic regression was used to model binary dependent variables (29) and
180 has been widely used in previous mortality models at the tree scale (30, 31). The output of each
181 logistic regression model is a probability of mortality ranging between 0 and 1. The most
182 common way to assess the goodness of fit of a logistic regression model is to use the Area
183 Under the Curve (AUC) (32). The AUC value varies between 0.5, indicating a prediction
184 equivalent to a random classification model, and 1, indicating that the model perfectly
185 differentiates between live and dead trees. As the AUC value is dependent on the geographical
186 extent and the number of predictors (33), we additionally provided the True Skill Statistics
187 (TSS), which is a goodness-of-fit indicator independent of the prevalence level (34). Its value
188 varies between -1, indicating that the model does not perform better than random, and 1,
189 indicating perfect agreement.

190 Variable selection for each species was made with a forward procedure (35) based on
191 residual deviance decrease using a set of 36 potential predictors (**Table 1**). At each step, we
192 selected the variable that induced the highest significant decrease in residual deviance
193 (Likelihood Ratio Test [LRT], $p < 0.01$). We only kept variables with correlation coefficients
194 (R^2) with variables previously selected in the model lower than 0.75. We continued the variable
195 selection process until no variable added a significant deviance reduction. We calibrated the
196 models on 298,379 trees. We then validated them on 74,595 independent trees randomly
197 selected from the full sampling. The trees used for validation were not used for calibration. To
198 evaluate the relative importance (RI) of the predictors, we calculated the drop contribution of
199 each variable used in the models (Electronic Supplementary Material, Panel 1e). To fully
200 characterize commonly observed U-shaped or bell-shaped responses of tree mortality to tree

201 size, competition intensity (36) and soil chemical and physical properties (37), we tested
202 quadratic forms for variables describing tree status, stand structure and soil properties (38).

203 We modeled tree mortality for each of the 43 species with logistic regression and
204 assessed the goodness of fit of the models with both AUC and TSS. First, we compared the
205 average values of these indicators between the calibration and the validation datasets. Second,
206 we presented which categories of variables were the most preponderant determinants of
207 background tree mortality. Finally, we detailed how climate change influenced background tree
208 mortality in terms of the amount of species affected, of the relative importance of the variables
209 in the models, and of the climate-change-related excess probability of induced mortality.

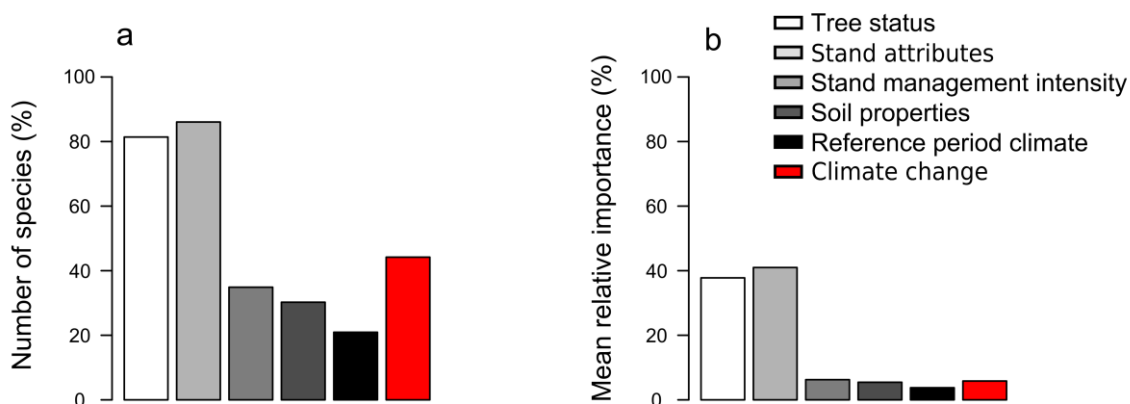
210 **Results**

211 For a vast majority of species, background tree mortality was highly predictable, with
212 high values of both AUC and TSS. We were able to quantify the relative importance of each
213 category of mortality drivers. As expected, factors related with the tree status and the stand
214 characteristics were the main drivers of mortality. Taking these factors into account, we also
215 detected a significant climate change effect on 45% of the species, leading for some species to
216 important excess probabilities of mortality as compared to a climate-change-free context.

217 The AUC for the 43 mortality models varied from 0.65 to 0.90 (mean \pm s.d of $0.81 \pm$
218 0.06) and the TSS from 0.21 to 0.69 (0.51 ± 0.11) in the calibration dataset and from 0.64 to
219 0.91 (0.78 ± 0.06) and the TSS from 0.16 to 0.49 (0.56 ± 0.12 ; Electronic Supplementary
220 Material, Table 1) in the validation dataset. AUC and TSS values did not significantly differed
221 between calibration and validation datasets (t-test, $P=0.11$ and $P=0.10$, respectively).

222 Tree status and stand attributes variables were the most frequently selected during model
223 building (LRT, $p < 0.01$), with 81% (for tree status) and 86% (for stand attributes) of the species
224 with one or more variables from these categories (**Figure 3a**), and 98% of the species with at

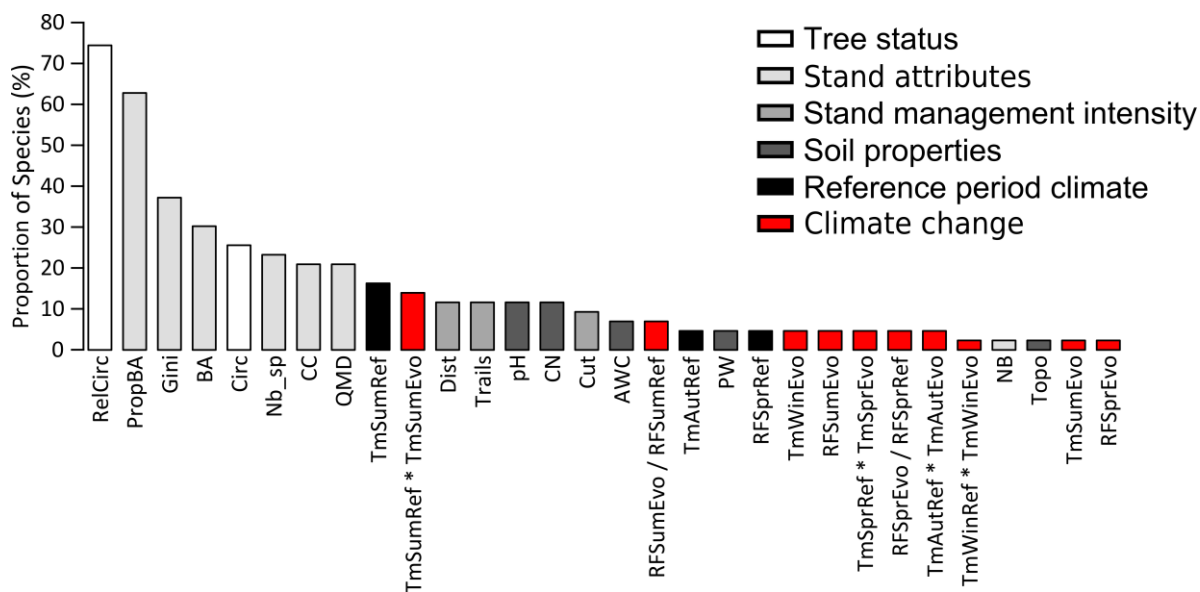
225 least one variable from both categories. All species considered, these variables had a relative
 226 importance of 79% in the mortality models (**Figure 3b**).



227
 228 **Figure 3: Frequency and importance of the different categories of factors explaining tree mortality**
 229 **in the models for the 43 tree species. (a)** Proportion of species with one or more significant variables
 230 *per* category, and **(b)** mean importance of the variables *per* category for all tree species.

231 *RelCirc* was the most frequently selected variable, with 74% of the species affected
 232 (**Figure 4**, and detailed model coefficients available in **Electronic Supplementary Material,**
 233 **Table 2**). All these species displayed decreasing mortality with increasing relative tree
 234 circumference, with a slight mortality increase at the highest values for 47% of the species.
 235 Stand density and spatial structure influenced tree mortality to a lesser extent, with important
 236 effects of tree species composition (*PropBA*, 63% of the species and *Nb_sp*, 23%), size
 237 heterogeneity (*Gini*, 37%), total basal area (*BA*, 30%), and canopy cover (*CC*, 21%). Stand
 238 management intensity variables (*Dist*, *Trails*, and *Cut*) were significant for 33% of the species,
 239 with observed mortality consistently decreasing with increasing management intensity. Effects
 240 of soil characteristics on tree mortality were rare, with responses to *pH* and *CN* for 12% of the
 241 species each. Reference period climate effects affected 23% of the species and had a low
 242 relative importance (**Figure 3b**). Among these effects, those of mean temperature were the most

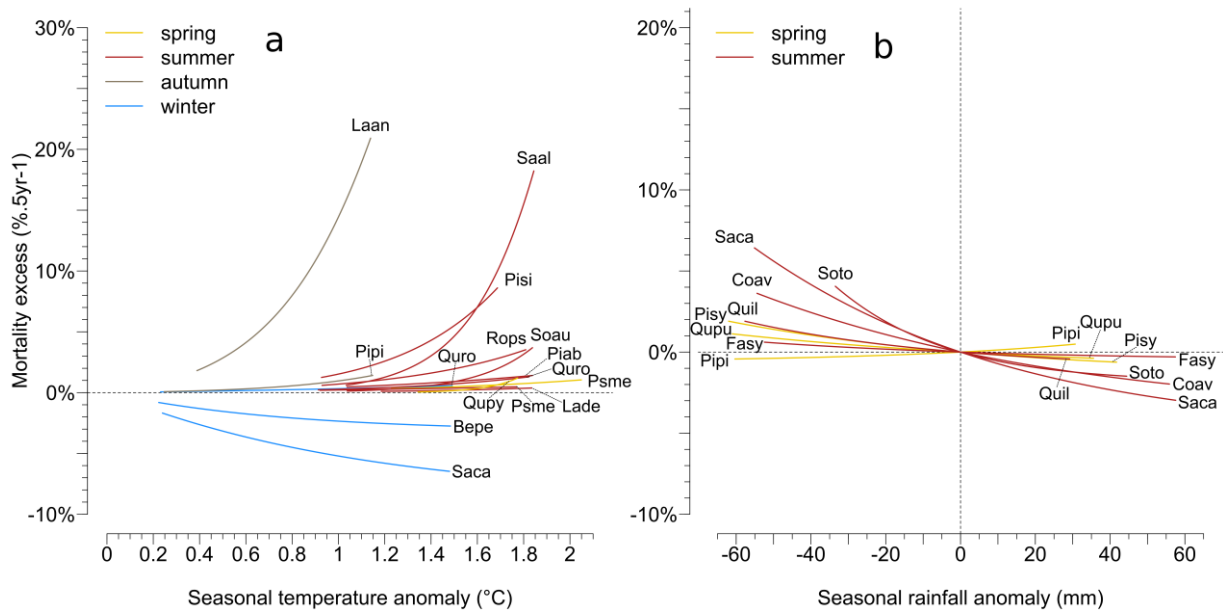
243 frequent ones (**Figure 4**), with 21% (n=9) of the species affected and mainly a mortality
 244 increase at the highest mean summer temperatures for 14% (n=6) of the species.



245
 246 **Figure 4. Frequency of the different variables explaining tree mortality and selected in the**
 247 **mortality models for the 43 species.** The colors represent the different categories of variables.

248 Climate-change-related effects were frequent and highly species-dependent, with 45%
 249 (n=19) of the species with one or several significant climate change variables selected (LRT, p
 250 < 0.01). The mean relative importance of climate change variables reached 6% (**Figures 3a** and
 251 **3b**) and was lower than that of the tree or stand characteristics (Electronic Supplementary
 252 Material, Figure 2). With 30% (n=13) of the species affected, the effects of temperature change
 253 were more frequent than those of rainfall change that concerned 19% (n=8) of the species.
 254 Among temperature effects, increasing mortality with increasing temperature was the most
 255 frequent one, with 26% (n=11) of the species affected (**Figure 5a**, see Electronic
 256 Supplementary Material, Figure 3a for the excess probability of mortality curves with 95%
 257 confidence intervals) and average excess probability of mortality ranging from +0.7% to
 258 +15.1% (mean = 3.9%) depending on the species as compared to a climate-change-free context
 259 (see Electronic Supplementary Material, Panel 2 for the calculation of average excess
 260 probability of mortality). Mean summer temperature was the most often selected effect, with

261 19% (n=8) of the species concerned. Decreasing mortality with increasing winter temperature
 262 affected 5% (n=2) of the species, leading to an average decrease of probability of mortality
 263 ranging from -21.9% to -6.5% (mean = -14.2%). Rainfall effects were less frequent than
 264 temperature effects and affected 19% (n=8) of the species (**Figure 5b** and Electronic
 265 Supplementary Material, Figure 3b); the main one was increasing mortality with decreasing
 266 rainfall, mainly in summer. Rainfall increase led to average changes in probability of mortality
 267 ranging from -1.1% to +0.3% (mean = -0.4%), while rainfall decrease led to changes in
 268 probability of mortality ranging from -0.3% to +1% (mean = +0.5%).



269
 270 **Figure 5. Excess probability of mortality along temperature (a, n=13 species) and rainfall (b, n=8**
 271 **species) anomaly gradients for the species with significant climate change effects.** For each species
 272 sensitive to climate change, we calculated the response curve corresponding to the climate change
 273 variable involved. To estimate the excess probability of mortality along each significant gradient of
 274 climate change variable, we calculated the difference between the response curve and the value
 275 corresponding to the mean predicted probability of mortality, with the target climate change effect fixed
 276 to 0. For species with several selected climate change variables, one curve *per* variable was plotted. We
 277 represented the four seasons in four different colors. For the correspondence table between the species
 278 names and the abbreviations, see **Figure 1**.

279 To ensure that our results were not biased by differences in management intensity or
280 only affected species with high base-mortality rates, we compared the relative importance of
281 climate change effects in our models among species with low and high base mortality rates
282 (Electronic Supplementary Material, Figure 4a) and among species with low and high harvest
283 intensities (Electronic Supplementary Material, Figure 4b). In neither case were the differences
284 significant (t-test: $P=0.699$ and $P=0.133$, respectively).

285 **Discussion**

286 By combining detailed information about tree competition, stand characteristics, management
287 intensity, and environmental conditions, we quantified for the first time the relative importance
288 of climate change effects on background tree mortality on a set of species representative of the
289 European forest. The climate change effects we highlighted were ecophysiologicaly consistent,
290 with a deleterious effect of both increasing temperature and decreasing rainfall on tree
291 mortality.

292 We found that the relative importance of factors related to the tree status and the stand
293 characteristics was on average more than 10 times higher than that of climate change variables.
294 The tree population on which we calibrated our models was composed of trees of all sizes and
295 ages. According to the self-thinning rule (39), the smallest trees are expected to die as a result
296 of competition and selection with stand ageing. For example, in pure and even-aged stands,
297 self-thinning relationships among 11 temperate forest species showed that up to 90% of small
298 trees naturally died with stand ageing (40). Therefore, the high importance of tree and stand
299 characteristic variables highlighted in our models was expected. Contrary to previous studies
300 attributing tree mortality solely to climate variability (5), recent climate change (11, 16), or
301 competition intensity (17), we emphasize that all these explanatory factors are potential
302 confounding factors that have to be studied jointly to properly predict tree mortality. Without
303 using temporal correlations that can be biased by changes in stand structure and composition

304 (12, 17), we found that when other causes of mortality are taken into account, a climate change
305 effect remains visible on 45% of the studied species. By removing the trees and plots affected
306 by forest fires, storms, avalanches, floods, wind events, and the species affected by the most
307 important health issues from our analysis, we removed major sources of catastrophe-related
308 mortality and ensured that the effects we highlighted could be confidently attributed to long-
309 term trends of climate change on background tree mortality.

310 From a physiological viewpoint, hydraulic failure has been identified as the main
311 process responsible for drought-related mortality, highly connected with trees' carbon balances
312 (41). This phenomenon results from xylem dysfunctioning due to cavitation, when water loss
313 from transpiration is higher than water uptake by roots (42). Embolism thresholds leading to
314 hydraulic failure were measured experimentally on a variety of tree species and turned out to
315 be highly species-dependent (43, 44). We found that the effects of increased temperature on
316 mortality were twice as frequent as those of rainfall decrease. Heat stress alone can diminish
317 photosynthetic activity and damage tree leaves, but only at extremely high temperatures
318 uncommon in temperate forests, and is unlikely to lead to tree death when not associated with
319 water shortage (45). However, when high temperatures are combined with low soil water
320 availability, the effects of drought can be exacerbated because of increased evapotranspiration,
321 and rapid tree death can occur (46). Additionally, as the soil water-holding capacity greatly
322 varied across the study area, rainfall intensity could be only weakly correlated to the actual soil
323 water content (47). Therefore, the effects of temperature increase on mortality could be direct
324 effects on the physiological functioning of trees, but they could also be proxies for water stress
325 effects. Thus, we suggest that future research further investigate the links between mortality
326 and the evolution of the soil water balance. Finally, the higher importance of temperature effects
327 over rainfall effects could also result from important differences in spatial patterns of climate
328 change across the French territory. While temperatures significantly and differently increased

329 across the whole study area, changes in rainfall regimes were more heterogeneous, with
330 decreases of summer rainfall only in a limited part of the study area. Therefore, our models
331 could have been more efficient at detecting widespread temperature increase effects rather than
332 rarer rainfall decrease effects. The detection of the sole effects of rainfall decrease can be
333 improved in future studies by studying broader geographical ranges, for example by combining
334 forest inventories from several European countries (48), provided that the levels of accuracy,
335 the survey protocols of the stand characteristics, and environmental conditions are similar.

336 Extreme events such as abnormal droughts or heat waves are important drivers of tree
337 mortality (49), and they are expected to increase in frequency and intensity with climate change
338 (1). The extent to which they affect tree functioning depends on their intensity, duration,
339 frequency, and timing. For example, the adverse effects of the 2003 drought on *Pinus sylvestris*
340 in Europe were amplified by repeated droughts in the following years (50). Under the same heat
341 sum, *Quercus rubra* seedlings were more vulnerable under short and intense stress than under
342 longer and lower intensity stress (51). We studied trees that died in the 5 years preceding their
343 survey, limiting the study of the relationships between the timing of extreme events and tree
344 death. Intense droughts and heat waves were indirectly taken into account as averaged values
345 over fifteen-year periods characterizing contemporary climate. Further studies using specific
346 methods to disentangle the effects of long term changes from extreme events, including drought
347 frequencies and intensities, coupled with the use of data from annually surveyed permanent
348 plots would allow better understanding the respective effects of extreme events and long term
349 tendencies on tree mortality.

350 Our study probably under-evaluated the effects of climate change on tree mortality.
351 Management effects were accounted for in our models but probably poorly evaluated, because
352 many dying or dead trees were preferentially cut during salvage loggings, clear or selective
353 cuts, and were not recorded in the forest inventory database. To avoid confusion with mortality

354 events unrelated with long-term changes in temperature and rainfall, we calibrated our models
355 on a tree population cleaned from trees that died from abrupt disturbances and from species
356 with the most important health issues. However, as climate change also likely increases fire and
357 windstorm frequency as well as outbreaks of insect or pathogenic disturbances (52), the death
358 of many trees removed from our analysis due to disturbances could be linked to climate change.
359 Therefore, our models of background tree mortality tended to underestimate rather than
360 overestimate the total effects of climate change on tree mortality.

361 Biotic factors interact with other causes of mortality to shape mortality patterns. Pests
362 and pathogens can trigger tree decline or only hit weakened trees that would have died even in
363 their absence. Due to these interactions between biotic and abiotic factors, we were not able to
364 explicitly take into account the probability that a tree died as a result of biotic factors alone.
365 Accurate modelling of the spatial distribution of pests and pathogens and of its evolution over
366 time appears critical to better disentangle biotic from abiotic causes of tree mortality.

367 **Conclusion**

368 A better understanding of forest vulnerability to climate change is critical to maintain the
369 ecosystem services they provide, including timber and non-timber products, erosion control, air
370 and water quality, carbon sequestration, or cultural services. With projections of increasing
371 temperatures up to +4.8°C by 2100 under the RCP8.5 scenario (53) and of increasing drought
372 frequencies and intensities (1), our results suggest that mortality rates will keep on increasing,
373 while species that have not responded to climate change yet could respond in the future,
374 suggesting important changes in future tree species composition. However, as tree and stand
375 characteristics remain the main drivers of tree mortality, changes in silvicultural practices must
376 be further explored to adapt forests to future climatic conditions.

377 **Data accessibility**

378 The dataset from the national forest inventory program including mortality data, tree status, and
379 stand attribute data are available at <https://inventaire-forestier.ign.fr/spip.php?rubrique153>. The
380 climatic and bio-indicator data used for modelling are available at
381 <https://silvae.agroparistech.fr/>.

382 **Competing interests**

383 We declare we have no competing interests.

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