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Adrien Taccoen, Christian C. Piedallu, Ingrid Seynave, Vincent V. Perez, Anne Gégout-Petit, et al.. Background mortality drivers of European tree species : climate change matters. Proceedings of the Royal Society B: Biological Sciences, 2019, 286 (1900), pp.20190386. 10.1098/rspb.2019.0386 . hal-02095574v2

HAL Id: hal-02095574

<https://hal.science/hal-02095574v2>

Submitted on 14 Dec 2020

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Cite this article: Taccoen A, Piedallu C, Seynave I, Perez V, Gégout-Petit A, Nageleisen L-M, Bontemps J-D, Gégout J-C. 2019 Background mortality drivers of European tree species: climate change matters. *Proc. R. Soc. B* **286**: 20190386.
<http://dx.doi.org/10.1098/rspb.2019.0386>

Received: 14 February 2019

Accepted: 13 March 2019

Subject Category:

Global change and conservation

Subject Areas:

ecology, environmental science, plant science

Keywords:

global change, mortality, temperate forest, tree species, climate change, forest inventory

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Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.4441907>.

Background mortality drivers of European tree species: climate change matters

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Increases in tree mortality rates have been highlighted in different biomes over the past decades. However, disentangling the effects of climate change on the temporal increase in tree mortality from those of management and forest dynamics remains a challenge. Using a modelling approach taking tree and stand characteristics into account, we sought to evaluate the impact of climate change on background mortality for the most common European tree species. We focused on background mortality, which is the mortality observed in a stand in the absence of abrupt disturbances, to avoid confusion with mortality events unrelated to long-term changes in temperature and rainfall. We studied 372 974 trees including 7312 dead trees from forest inventory data surveyed across France between 2009 and 2015. Factors related to competition, stand characteristics, management intensity, and site conditions were the expected preponderant drivers of mortality. Taking these main drivers into account, we detected a climate change signal on 45% of the 43 studied species, explaining an average 6% of the total modelled mortality. For 18 out of the 19 species sensitive to climate change, we evidenced greater mortality with increasing temperature or decreasing rainfall. By quantifying the mortality excess linked to the current climate change for European temperate forest tree species, we provide new insights into forest vulnerability that will prove useful for adapting forest management to future conditions.

1. Introduction

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

The link between current climatic conditions and background tree mortality was established in the field through spatial approaches aimed at correlating the spatial variations of observed mortality with those of average climatic conditions over a given period. These studies lead to contrasting results. Tree mortality was found to be positively correlated with water stress in forests of North America [4], positively correlated with warm summers in Europe [5], while significant but highly heterogeneous and species-dependent responses

to climate conditions were evidenced in forests of the eastern United States [6,7] and Spain [8]. At the stand scale, aerial observations of dieback patterns were found to be positively correlated with the intensity of climatic water deficit in temperate [9] and boreal forests [10]. Although these studies highlighted average climate effects on background tree mortality, they did not take the evolution of climatic conditions over time into account.

Other approaches characterized the evolution of background tree mortality based on the analysis of longitudinal data, i.e. the monitoring of the tree or stand health status over long time periods, with repeated aerial or ground surveys. Several such studies showed significant background tree mortality increases over the last decades for all tree sizes and at different altitudinal and latitudinal ranges in forests of the western and central United States [11] and in boreal forests of Canada [12]. In Central Europe, the analysis of Landsat data covering the years 1984 to 2016 showed that canopy mortality rates doubled over that period [13].

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

Previous studies based on spatial approaches did not consider the effects of climate change intensity, while temporal studies could not reliably attribute mortality increases to changes in the temperature and rainfall regimes owing to the difficulties in disentangling the different drivers over long time periods. So far, no study combining both an accurate description of tree and stand characteristics and climate change data has been performed on temperate forests. We examined the relationships between the spatial patterns of climate change since the 1960s and the current distribution of dead trees using ground survey data from the French national forest inventory programme (NFI). This dataset provides an accurate description of tree and stand characteristics, including previously unexplored potential mortality factors like logging intensity, stand structure, and species composition for a large number of plots. We used a modelling approach for a large number of species representative of the European temperate forests to disentangle site, tree, and stand characteristics effects from climate change effects on mortality. European forests represent 26% of the world forests in terms of growing stock [15], while a majority of European

tree species are threatened by future global warming on a large part of their distribution range [22].

2. Material and methods

(a) Study sites and species

We used information from 41 692 forest plots with 554 133 trees, including 37 767 dead trees inventoried in the NFI over the 2009–2015 period in France. Because our study focused on the effects of temperature and rainfall on background tree mortality, we removed plots affected by storms, fires, avalanches, floods, and broken or felled dead trees, to focus on standing dead trees (electronic supplementary material, panel S1a). Salvage-logged trees were not taken into account because no information about the tree status (living or dead) before harvesting was available. We studied a broad range of species representative of contrasting ecological contexts (dry or wet and siliceous or calcareous) representative of different biomes (lowland/mountain/Mediterranean forests). Among the most common species present in the NFI database, we removed five species affected by severe health issues (electronic supplementary material, panel S1b) to study 43 species (figure 1) that compose around 80% of the total forest cover of Europe [23]. We finally considered 372 974 trees with a diameter greater than 7.5 cm including 7312 dead trees located in 34 097 plots scattered across the afforested territory of France.

The plot altitudes ranged from 1 to 2533 m (mean = 432 m), longitude from 5°W to 10°E, and latitude from 41°N to 51°N. The proportion of dead trees over the 2009–2015 period varied from 0.6 to 18% (figure 1) of the total number of surveyed trees depending on the species (mean \pm s.d. = $4.1 \pm 3.0\%$) and was not related to average 1961–1987 temperature ($R^2 = 0.06$, $p = 0.62$), rainfall ($R^2 = 0.02$, $p = 0.88$), or to the frequency of species ($R^2 = 0.09$, $p = 0.08$; figure 1).

(b) Variables considered

Mortality models were built using 36 variables covering the main drivers of tree mortality identified at the tree and stand scales in various studies (table 1, [24,25]). To assess the effects of competitive interactions at the tree level, we used the circumference at 1.3 m height (*Circ*, cm) and calculated the relative circumference (*RelCirc*, %), which is the ratio of the circumference of each tree over the average circumference of the other trees in the plot. To assess the effects of stand structure and composition, we computed seven indices from the field-measured variables (*Circ* and tree canopy cover (CC)). The total BA of all the trees within each plot was calculated from the tree circumference and summed to give the plot BA ($\text{m}^2 \text{ha}^{-1}$). The number of trees per hectare (*NB*, Nb ha^{-1}) was calculated from the sum of inventoried trees on the plot. The plot CC (%) is the proportion of the plot covered by the vertical projection of all measured tree crowns. We computed the total number of tree species (*Nb_sp*) and the proportion of basal area occupied by each species within each plot (*PropBA*, %) as indicators of forest composition. To evaluate stand structure heterogeneity, we calculated the Gini index of inequality of tree circumferences on the plot [26] (*Gini*) that ranges between 0 and 1, with increasing diameter unevenness.

$$Gini = \frac{1}{\sum_{i=1}^n C_i(n-1)} \sum_{i=1}^n (2i - n - 1)C_i,$$

C_i = circumference of tree i in the plot; n = total number of trees in the plot.

We assessed the effects of site environmental conditions with bio-indicated estimates of the soil pH, the carbon-to-nitrogen

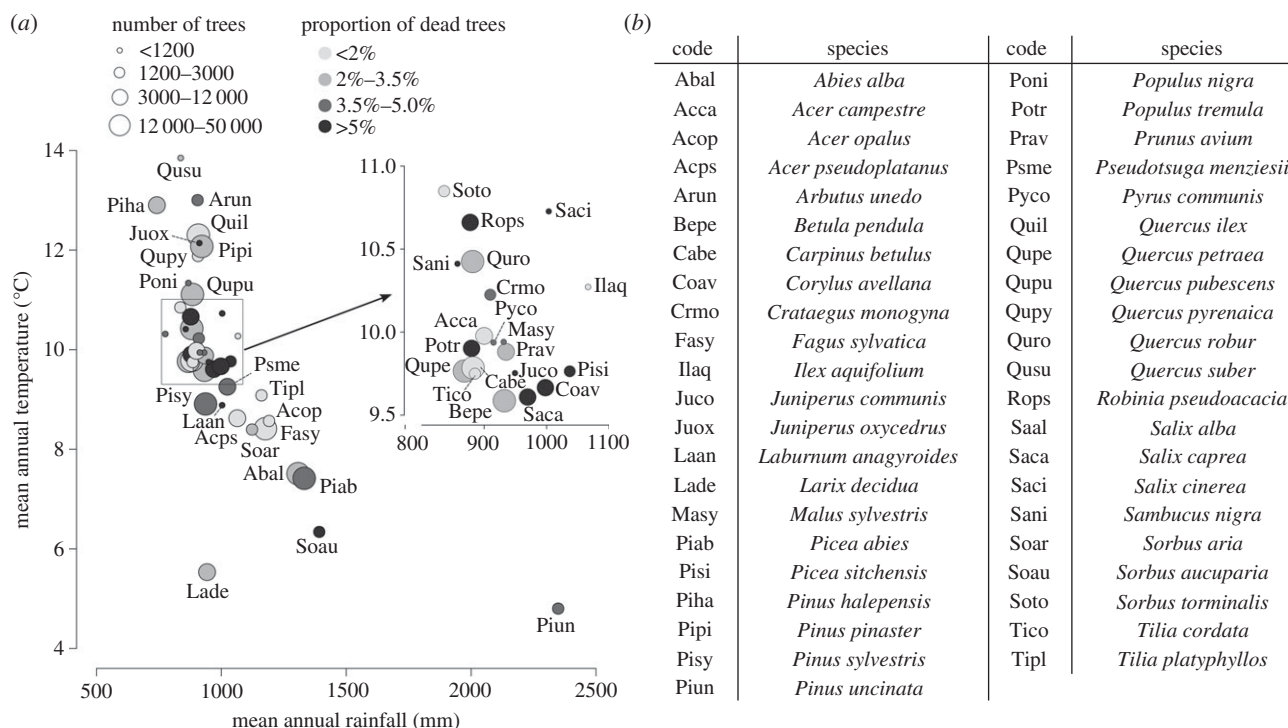


Figure 1. (a,b) Number of trees and proportion of dead individuals *per* species along mean annual temperature and rainfall gradients over the 1961–1987 period. The circle size corresponds to the total number of trees *per* species (alive or dead) in the sample surveyed between the years 2009 and 2015.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

ratio, permanent and temporary waterlogging indices, and six climate variables describing average seasonal temperatures ($T_{m_{win}Ref}$, $T_{m_{spr}Ref}$, $T_{m_{sum}Ref}$, $T_{m_{aut}Ref}$) and spring and summer rainfall ($RF_{spr}Ref$, $RF_{sum}Ref$) over the 1961–1987 period (electronic supplementary material, panel S1c for additional details about the calculation of environmental condition variables).

Finally, we assessed the effects of climate change intensity by calculating the evolution of the same six climate variables between the 1961–1987 historic period and contemporary periods at each plot location using historic homogenized climate series spanning the 1961–2015 period [27]. Because delayed mortality can occur several years after a climatic disturbance [28], and because the forest inventory programme records trees that are supposed to have died in the 5 years preceding their survey, we considered the 15 years preceding each plot survey as contemporary periods (e.g. the 1994–2009 period for a survey carried out in 2009). We obtained six variables describing the evolution of temperature and rainfall *per* season, calibrated on the 15 years preceding the date of the survey ($T_{m_{win}Evo}$, $T_{m_{spr}Evo}$, $T_{m_{sum}Evo}$, $T_{m_{aut}Evo}$, $RF_{spr}Evo$, and $RF_{sum}Evo$, table 1, and see electronic supplementary material, panel S1d for details about the calculation of climate change intensity variables).

We hypothesized that for a given temperature increase or rainfall decrease, impacts on trees were greater in areas with a high temperature or low rainfall over the reference period. To assess the potential influence of initial climate conditions on the effects of climate change on tree mortality, we considered the product between T_{mRef} and T_{mEvo} and the $RfEvo$ -over- $RfRef$ ratio as additional candidate variables (table 1).

(c) Observed climate change patterns

In our study area, the mean annual temperature significantly increased by 1.1°C between 1961–1987 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

supplementary material, figure S1a), while the mean annual rainfall did not change significantly (t -test: $p = 0.53$), from 974 mm (± 110 mm) to 990 mm (± 115 mm; electronic supplementary material, figure S1c). Important seasonal and spatial variations exist, and climate change intensity was not uniform across the distribution of the plots (electronic supplementary material, figure S1b,d). The mapping of seasonal climate change variables between 1961–1987 and 1988–2015 revealed that average temperature increases were more intense in spring and summer (between +0.75°C and +2°C) than in autumn and winter (between +0.25 and +1°C; figure 2a), with important spatial variations. Concerning changes in rainfall regimes over this period, average spring rainfall decreased over most of the study area (figure 2b), while summer rainfall sharply decreased only in parts of southeastern France, with sharp increases observed elsewhere.

(d) Statistical model

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

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

variable name	code	description	units	source
tree status				
circumference	<i>Circ</i>	circumference of the tree measured at 1.30 m height	cm	<i>Field</i>
relative circumference	<i>RelCirc</i>	ratio of the tree circumference over the mean circumference of all the trees in the plot	cm	<i>Calc.</i>
stand characteristics and structure				
plot basal area	<i>BA</i>	sum of the tree basal areas in the plot	m ²	<i>Calc.</i>
number of trees <i>per</i> hectare	<i>NB</i>	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	<i>Calc.</i>
canopy cover	<i>CC</i>	proportion of the forest floor covered by the vertical projection of the tree crowns	%	<i>Calc.</i>
quadratic mean diameter	<i>QMD</i>	quadratic mean diameter of the trees on the plot	cm	<i>Calc.</i>
Gini coefficient	<i>Gini</i>	Gini coefficient of the tree circumferences in each plot	/	<i>Calc.</i>
proportion of BA occupied by the species growing in the plot	<i>PropBA</i>	per cent of basal area occupied by the species in each plot	%	<i>Calc.</i>
number of tree species	<i>Nb_sp</i>	total number of tree species in each plot	/	<i>Calc.</i>
stand management intensity				
skidding distance	<i>Dist</i>	indicator of the distance from the centre of the plot to the nearest existing skid trail	/	<i>Field</i>
skid trails	<i>Trails</i>	indicator of the presence of already existing skid trails and of the possibility to create new ones	/	<i>Field</i>
recent cut	<i>Cut</i>	type and intensity of a recent cut in the plot (less than 5 years)	/	<i>Field</i>
soil properties				
available water content	<i>AWC</i>	maximum volume of water that can be stored in the soil calculated from the Al-Majou pedotransfer functions	mm	<i>Mod.</i>
permanent waterlogging	<i>PW</i>	pH, C/N, permanent and temporary waterlogging index: bio-indicator values calculated from the floristic survey	/	<i>Mod.</i>
temporary waterlogging	<i>TW</i>		/	<i>Mod.</i>
pH	<i>pH</i>	of each plot	/	<i>Mod.</i>
carbon-to-nitrogen ratio	<i>CN</i>		/	<i>Mod.</i>
surface runoff	<i>Topo</i>	surface run-off estimated from the site topography		<i>Field</i>
climate conditions				
winter mean T° 1961–1987	<i>Tm_{win}Ref</i>	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	<i>Mod.</i>
spring mean T° 1961–1987	<i>Tm_{spr}Ref</i>		°C	<i>Mod.</i>
summer mean T° 1961–1987	<i>Tm_{sum}Ref</i>		°C	<i>Mod.</i>
autumn mean T° 1961–1987	<i>Tm_{aut}Ref</i>		°C	<i>Mod.</i>
spring rainfall 1961–1987	<i>RF_{spr}Ref</i>		mm	<i>Mod.</i>
summer rainfall 1961–1987	<i>RF_{sum}Ref</i>		mm	<i>Mod.</i>

(Continued)

Table 1. (Continued)

variable name	code	description	units	source
intensity of climate change				
winter mean T° evolution	$Tm_{win}Evo$	climate change anomalies between the 1961–1987	°C	Mod.
spring mean T° evolution	$Tm_{spr}Evo$	reference period and shifting 15-year sub-periods based	°C	Mod.
summer mean T° evolution	$Tm_{sum}Evo$	on the date of the survey of each plot for the same variables and seasons as for the reference period	°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	$Tm_{win}Ref \times Tm_{win}evo$	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.
	$Tm_{spr}Ref \times Tm_{spr}evo$		°C ²	Mod.
	$Tm_{sum}Ref \times Tm_{sum}evo$		°C ²	Mod.
	$Tm_{aut}Ref \times Tm_{aut}evo$		°C ²	Mod.
relative rainfall evolution	$RF_{spr}evo/RF_{spr}Ref$		%	Mod.
	$RF_{sum}evo/RF_{sum}Ref$			

Variable selection for each species was made with a forward procedure [35] based on residual deviance decrease using a set of 36 potential predictors (table 1). At each step, we selected the variable that induced the highest significant decrease in residual deviance (Likelihood Ratio Test [LRT], $p < 0.01$). We only kept variables with correlation coefficients (R^2) with variables previously selected in the model lower than 0.75. We continued the variable selection process until no variable added a significant deviance reduction. We calibrated the models on 298 379 trees. We then validated them on 74 595 independent trees randomly selected from the full sampling. The trees used for validation were not used for calibration. To evaluate the relative importance (RI) of the predictors, we calculated the drop contribution of each variable used in the models (electronic supplementary material, panel S1e). To fully characterize commonly observed U-shaped or bell-shaped responses of tree mortality to tree size, competition intensity [36], and soil chemical and physical properties [37], we tested quadratic forms for variables describing tree status, stand structure, and soil properties [38].

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

3. Results

For a vast majority of species, background tree mortality was highly predictable, with high values of both AUC and TSS. We were able to quantify the RI of each category of mortality

drivers. As expected, factors related to the tree status and the stand characteristics were the main drivers of mortality. Taking these factors into account, we also detected a significant climate change effect on 45% of the species, leading for some species to important excess probabilities of mortality as compared to a climate change-free context.

The AUC for the 43 mortality models varied from 0.65 to 0.90 (mean \pm s.d. of 0.81 ± 0.06) and the TSS from 0.21 to 0.69 (0.51 ± 0.11) in the calibration dataset and from 0.64 to 0.91 (0.78 ± 0.06) and the TSS from 0.16 to 0.49 (0.56 ± 0.12 ; electronic supplementary material, table S1) in the validation dataset. AUC and TSS values did not significantly differ between calibration and validation datasets (t -test, $p = 0.11$ and $p = 0.10$, respectively).

Tree status and stand attributes variables were the most frequently selected during model building (LRT, $p < 0.01$), with 81% (for tree status) and 86% (for stand attributes) of the species with one or more variables from these categories (figure 3a), and 98% of the species with at least one variable from both categories. All species considered, these variables had an RI of 79% in the mortality models (figure 3b).

RelCirc was the most frequently selected variable, with 74% of the species affected (figure 4, and detailed model coefficients available in the electronic supplementary material, table S2). All these species displayed decreasing mortality with increasing relative tree circumference, with a slight mortality increase at the highest values for 47% of the species. Stand density and spatial structure influenced tree mortality to a lesser extent, with important effects of tree species composition (*PropBA*, 63% of the species and *Nb_sp*, 23%), size heterogeneity (*Gini*, 37%), total BA (30%), and CC (21%). Stand management intensity variables (*Dist*, *Trails*, and *Cut*) were significant for 33% of the species, with observed mortality consistently decreasing with increasing management intensity. Effects of soil characteristics on tree

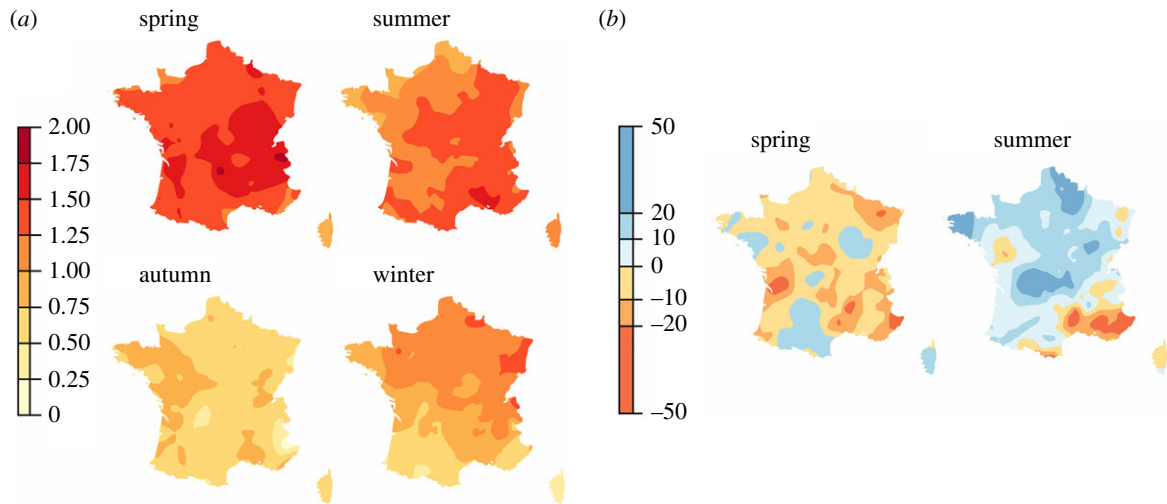


Figure 2. Climate change between the 1961–1987 reference period and the 1988–2015 period per season 1 (a): for temperature ($^{\circ}\text{C}$) and 1 (b): for rainfall (mm). (Online version in colour.)

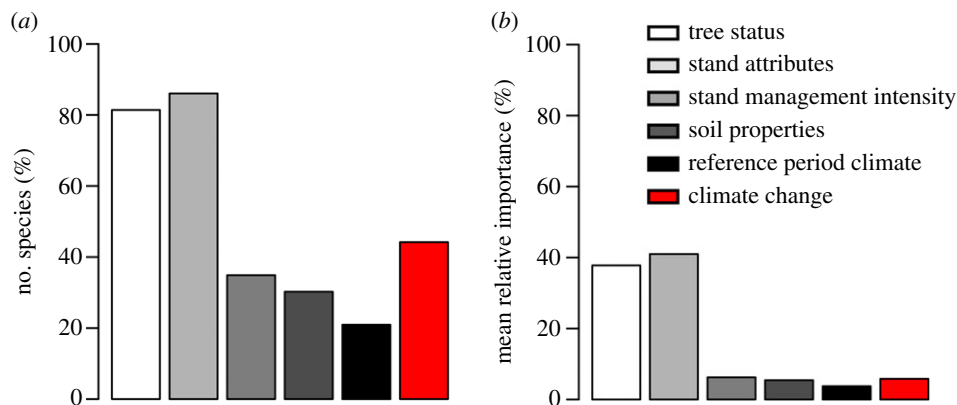


Figure 3. Frequency and importance of the different categories of factors explaining tree mortality in the models for the 43 tree species. (a) Proportion of species with one or more significant variables *per* category, and (b) mean importance of the variables *per* category for all tree species. (Online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

mortality were rare, with responses to *pH* and *CN* for 12% of the species each. Reference period climate effects affected 23% of the species and had a low RI (figure 3*b*). Among these effects, those of mean temperature were the most frequent ones (figure 4), with 21% ($n = 9$) of the species affected and mainly a mortality increase at the highest mean summer temperatures for 14% ($n = 6$) of the species.

Climate change-related effects were frequent and highly species dependent, with 45% ($n = 19$) of the species with one or several significant climate change variables selected (LRT, $p < 0.01$). The mean RI of climate change variables reached 6% (figures 3*a,b*) and was lower than that of the tree or stand characteristics (electronic supplementary material, figure S2). With 30% ($n = 13$) of the species affected, the effects of temperature change were more frequent than those of rainfall change that affected 19% ($n = 8$) of the species. Among temperature effects, increasing mortality with increasing temperature was the most frequent one, with 26% ($n = 11$) of the species affected (figure 5*a*, electronic supplementary material, figure S3*a* for the excess probability of mortality curves with 95% confidence intervals) and average excess probability of mortality ranging from +0.7% to +15.1% (mean = 3.9%) depending on the species as compared to a climate change-free context (see electronic supplementary

material, panel S2 for the calculation of average excess probability of mortality). Mean summer temperature was the most often selected effect, with 19% ($n = 8$) of the species affected. Decreasing mortality with increasing winter temperature affected 5% ($n = 2$) of the species, leading to an average decrease in the probability of mortality ranging from -21.9% to -6.5% (mean = -14.2%). Rainfall effects were less frequent than temperature effects and affected 19% ($n = 8$) of the species (figure 5*b*; electronic supplementary material, figure S3*b*); the main one was increasing mortality with decreasing rainfall, mainly in summer. Rainfall increase led to average changes in the probability of mortality ranging from -1.1% to $+0.3\%$ (mean = -0.4%), while rainfall decrease led to changes in the probability of mortality ranging from -0.3% to $+1\%$ (mean = $+0.5\%$).

To ensure that our results were not biased by differences in management intensity or only affected species with high base-mortality rates, we compared the RI of climate change effects in our models among species with low and high base-mortality rates (electronic supplementary material, figure S4*a*) and among species with low and high harvest intensities (electronic supplementary material, figure S4*b*). In neither case were the differences significant (t -test: $p = 0.699$ and $p = 0.133$, respectively).

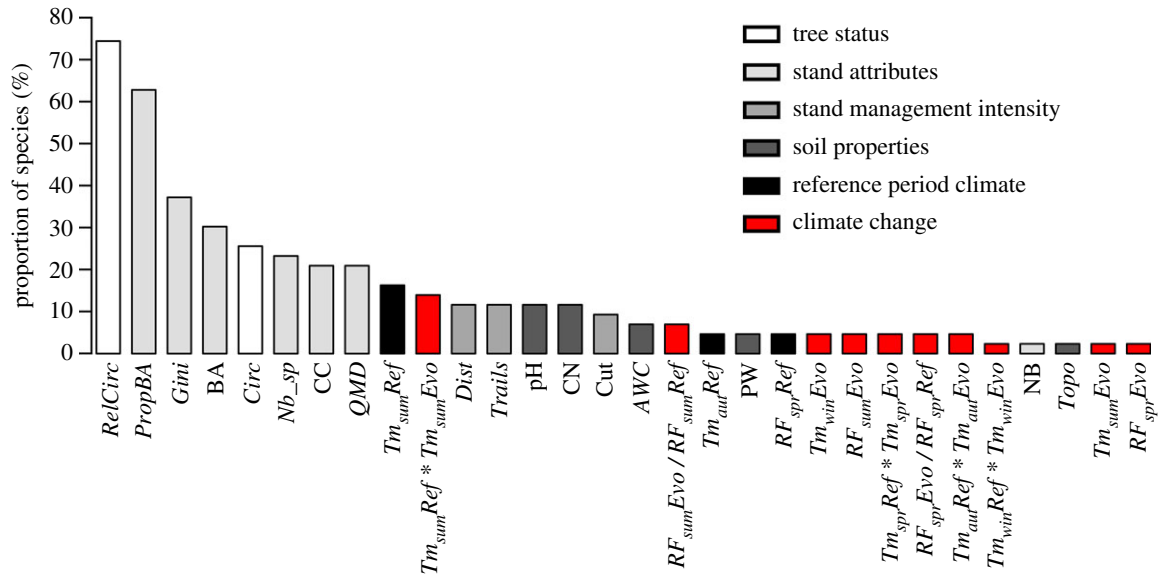


Figure 4. Frequency of the different variables explaining tree mortality and selected in the mortality models for the 43 species. The colours represent the different categories of variables. (Online version in colour.)

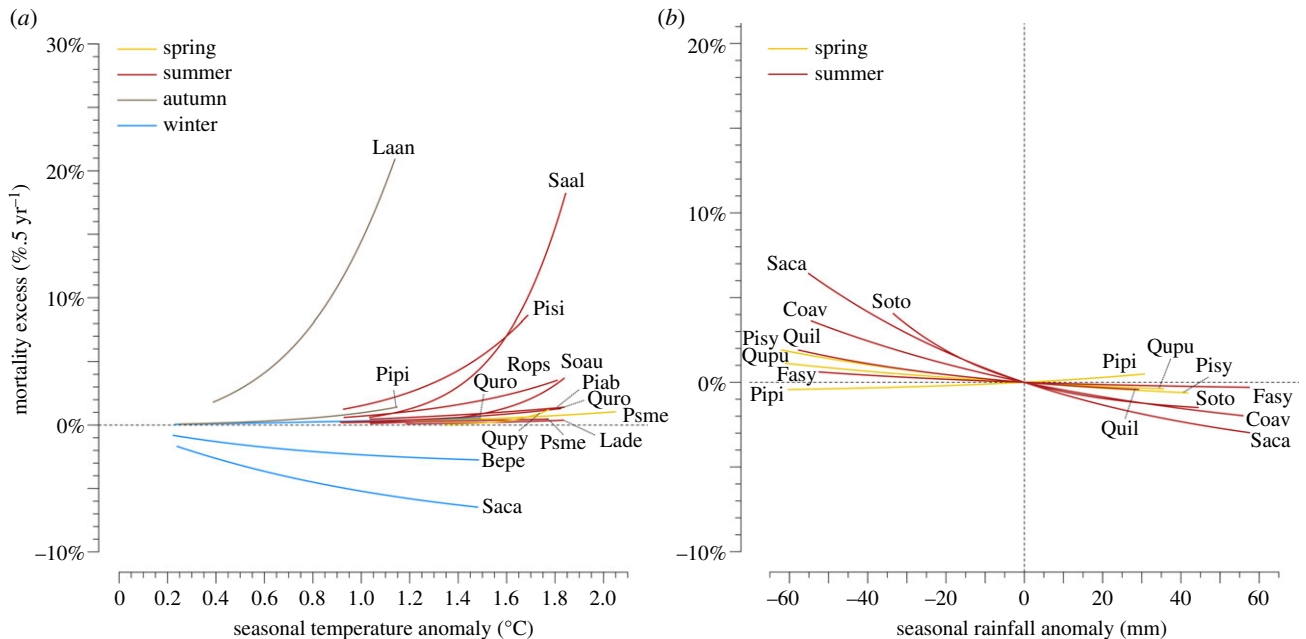


Figure 5. Excess probability of mortality along temperature (*(a)*, $n = 13$ species) and rainfall (*(b)*, $n = 8$ species) anomaly gradients for the species with significant climate change effects. For each species sensitive to climate change, we calculated the response curve corresponding to the climate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

4. Discussion

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

We found that the RI of factors related to the tree status and the stand characteristics was on average more than 10 times higher than that of climate change variables. The tree population on which we calibrated our models was composed of trees of all sizes and ages. According to the self-thinning rule [39], the smallest trees are expected to die as a result of competition and selection with stand ageing. For example, in pure and even-aged stands, self-thinning relationships among 11 temperate forest species showed that up to 90% of small trees naturally died with stand ageing [40]. Therefore, the high importance of tree and stand

characteristic variables highlighted in our models was expected. Contrary to previous studies attributing tree mortality solely to climate variability [5], recent climate change [11,16], or competition intensity [17], we emphasize that all these explanatory factors are potential confounding factors that have to be studied jointly to properly predict tree mortality. Without using temporal correlations that can be biased by changes in stand structure and composition [12,17], we found that when other causes of mortality are taken into account, a climate change effect remains visible on 45% of the studied species. By removing the trees and plots affected by forest fires, storms, avalanches, floods, wind events, and the species affected by the most important health issues from our analysis, we removed major sources of catastrophe-related mortality and ensured that the effects we highlighted could be confidently attributed to long-term trends of climate change on background tree mortality.

From a physiological viewpoint, hydraulic failure has been identified as the main process responsible for drought-related mortality, highly connected with trees' carbon balances [41]. This phenomenon results from xylem dysfunctioning due to cavitation, when water loss from transpiration is higher than water uptake by roots [42]. Embolism thresholds leading to hydraulic failure were measured experimentally on a variety of tree species and turned out to be highly species dependent [43,44]. We found that the effects of increased temperature on mortality were twice as frequent as those of rainfall decrease. Heat stress alone can diminish photosynthetic activity and damage tree leaves, but only at extremely high temperatures uncommon in temperate forests, and is unlikely to lead to tree death when not associated with water shortage [45]. However, when high temperatures are combined with low soil water availability, the effects of drought can be exacerbated because of increased evapotranspiration, and rapid tree death can occur [46]. Additionally, as the soil water-holding capacity greatly varied across the study area, rainfall intensity could be only weakly correlated to the actual soil water content [47]. Therefore, the effects of temperature increase on mortality could be direct effects on the physiological functioning of trees, but they could also be proxies for water stress effects. Thus, we suggest that future research further investigate the links between mortality and the evolution of the soil water balance. Finally, the higher importance of temperature effects over rainfall effects could also result from important differences in spatial patterns of climate change across the French territory. While temperatures significantly and differently increased across the whole study area, changes in rainfall regimes were more heterogeneous, with decreases in summer rainfall only in a limited part of the study area. Therefore, our models could have been more efficient at detecting widespread temperature increase effects rather than rarer rainfall decrease effects. The detection of the sole effects of rainfall decrease can be improved in future studies by studying broader geographical ranges, for example, by combining forest inventories from several European countries [48], provided that the levels of accuracy, the survey protocols of the stand characteristics, and environmental conditions are similar.

Extreme events such as abnormal droughts or heatwaves are important drivers of tree mortality [49], and they are expected to increase in frequency and intensity with climate change [1]. The extent to which they affect tree functioning

depends on their intensity, duration, frequency, and timing. For example, the adverse effects of the 2003 drought on *Pinus sylvestris* in Europe were amplified by repeated droughts in the following years [50]. Under the same heat sum, *Quercus rubra* seedlings were more vulnerable under short and intense stress than under longer and lower intensity stress [51]. We studied trees that died in the 5 years preceding their survey, limiting the study of the relationships between the timing of extreme events and tree death. Intense droughts and heatwaves were indirectly taken into account as averaged values over 15-year periods characterizing contemporary climate. Further studies using specific methods to disentangle the effects of long-term changes from extreme events, including drought frequencies and intensities, coupled with the use of data from annually surveyed permanent plots would allow better understanding of the respective effects of extreme events and long-term tendencies on tree mortality.

Our study probably undervalued the effects of climate change on tree mortality. Management effects were accounted for in our models but probably poorly evaluated, because many dying or dead trees were preferentially cut during salvage loggings, clear or selective cuts and were not recorded in the forest inventory database. To avoid confusion with mortality events unrelated with long-term changes in temperature and rainfall, we calibrated our models on a tree population cleaned from trees that died from abrupt disturbances and from species with the most important health issues. However, as climate change also likely increases fire and windstorm frequency as well as outbreaks of insect or pathogenic disturbances [52], the death of many trees removed from our analysis due to disturbances could be linked to climate change. Therefore, our models of background tree mortality tended to underestimate rather than overestimate the total effects of climate change on tree mortality.

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

5. Conclusion

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

further explored to adapt forests to future climatic conditions.

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

Competing interests. We declare we have no competing interests.

Funding. This study was funded through a PhD grant to A. Taccoen from the French National Forest Office and the Regional Council of Grand-Est (Formerly Lorraine).

Acknowledgements. We are grateful to the numerous friends and colleagues from SILVA and AgroParisTech for their support. Particularly, we thank Émilien Kuhn for help with scripts and programming under R, Nathalie Bréda, Myriam Legay, and Marta Benito Garzón for helpful comments. We would like to thank the two anonymous reviewers for their suggestions and comments that greatly improved the manuscript.

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