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# **Climate change impact on tree mortality differs with tree social status**

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## **Abstract**

Changes in temperature and rainfall linked to recent climate change increase the mortality rates of European temperate tree species. The economic importance of trees and the ecosystem services they provide differ according to their social status (dominant or suppressed trees) and their size. The extent to which climate change impacts these different categories in different ways remains little explored.

Ecophysiological differences between tree size and status suggest different sensitivities to climate change. Dominant trees are exposed to more evapotranspiration than suppressed trees that benefit from buffered climatic conditions. Large trees are able to develop a network of fine roots that allow deeper water and nutrient uptake during water shortage periods, but that have higher water requirements and more physical constraints than small trees due to the fact that they must lift water to greater heights.

We used 207,100 trees from the French forest inventory data (including 3,514 dead trees), representing eight common European tree species. For each species, we separated the tree population into three subsets of suppressed, small dominant and large dominant trees. For each subset, we modelled the mortality observed in a stand in the absence of disturbances (background mortality), with a focus on the differences in sensitivity to recent changes in temperature and rainfall.

After having taken the main mortality drivers related to competition into account, as well as stand characteristics including logging intensity effect, we assessed the over-mortality linked to the recent changes in temperature and rainfall for each of the three subsets.

When considering both changes in temperature and rainfall, the climate change related to over-mortality was greater for suppressed than for small or large dominant trees, for all the species. Over-mortality of suppressed trees was related to temperature increase, whereas a maximum vulnerability related to rainfall decrease was observed for large dominant trees.

Over-mortality driven by climate change not only concerns large and dominant trees, but small and especially suppressed ones as well. These results suggest that in addition to wood production, forest renewal and ecosystem services associated with understorey vegetation are threatened by the recent changes in temperature and rainfall in European temperate forests.

**Keywords:** global change ecology, climate change, temperature, rainfall, tree species, mortality, temperate forest, tree circumference, tree social status.

# 1 Introduction

According to their social status and size, trees provide different ecological, economic and social services. An extensive review by Lindenmayer and Laurance (2017) listed the known ecological roles of large trees. This includes influences on nutrient cycles (Lindo and Whiteley 2011), mobilization of deep groundwater (Nepstad et al. 1994), climate regulation (Dean et al. 1999), and provision of wildlife habitat (Remm and Löhmus 2011). Large trees are also of utmost importance for carbon sequestration and wood production as the 1% largest trees represent around 50% of the worldwide mature forest biomass (Lutz et al. 2018). Additionally, they also play some important social and cultural roles (Blicharska and Mikusinski 2014). For their part, small and suppressed trees are of great importance from a demographic viewpoint because their survival and development is critical to ensure forest renewal. They provide numerous ecosystem functions and services (Ampoorter et al. 2016), influencing both litter composition and seed germination. Small trees are more diversified than large trees (Memiaghe et al. 2016), increasing overall functional diversity and promoting a better resilience of ecosystems to disturbances. In addition, they contribute to carbon storage (Vincent et al. 2015), have an effect on hydrological processes (Gonzalez-Martinez et al. 2017), soil nutrient availability and local microclimate (Turrell and Austin 1965), and provide food and habitat for many animals.

The increase in human pressure combined with recent climate change is a threat to forests in many parts of the world. Numerous studies have reported an increase in tree mortality and massive forest dieback in different biomes (Neumann et al. 2017, Klein and Hartmann 2018). Senf et al. (2018) showed that the area affected by tree mortality has doubled in the past 30 years in Europe, whereas van Mantgem et al. (2009) observed a doubling of mortality in the western United States. A decline in the number of trees was reported at a global scale in boreal, temperate and tropical forests (Lindenmayer et al. 2014). In mid-boreal Swedish forests, the proportion of large trees decreased by 90% between the early 19<sup>th</sup> century and the late 20<sup>th</sup> century (Linder and Östlund 1998).

The causes of dieback are extremely varied and include light availability, targeted logging, forest clearing, pest outbreaks, wildfires, drought, grazing, agriculture intensification, diseases and air pollution. These different sources of mortality are difficult to disentangle. Different studies have highlighted the importance of climate on tree mortality, with recognized direct effects of temperature (McDowell et al. 2016, Senf et al. 2018) and water availability (Greenwood et al. 2017), or indirectly as a result of biotic factors (Marini et al. 2017, Pureswaran et al. 2018, Jaime et al. 2019). Extreme events like severe or recurrent drought episodes or heat waves have increased tree vulnerability to pests and diseases and led to forest decline (Breda et al. 2006, Allen et al. 2015). However, most of the studies have focused on the effects of extreme events on tree mortality to the detriment of long-term trend studies. Consequently, the long-term effects of changes in temperature and rainfall due to recent climate change is poorly known. In addition, these effects can be confused with changes in stand characteristics, tree ageing and competition, which are the primary causes of mortality. Despite these difficulties, recent research focused on past mortality trends revealed an over-mortality attributed to recent climate change (Luo and Chen 2015, Hember et al. 2017, Taccoen et al. 2019).

Large trees are considered more vulnerable to drought than small trees. For instance, in tropical forests, higher mortality rates were found for many species of large trees following natural or experimental water shortage (Nepstad et al. 2007, Phillips et al. 2009, da Costa et al. 2010). More recently, a global-scale meta-analysis of the size-dependence vulnerability of trees to drought, performed on 40 drought events at 38 locations worldwide, concluded that the effects of drought events on tree growth and mortality were significantly greater for large than for small trees (Bennett et al. 2015). Stovall et al. (2019) demonstrated in California that large trees die at twice the rate of small trees during extreme drought events. This trend was highlighted in many biomes including tropical, sub-tropical, arid and temperate forests. Additionally, some studies focusing on small understorey trees in tropical forests found that they were generally less exposed to radiation, vapour pressure deficit and temperature than large dominant trees (Bennett et al. 2015).

Recent climate change is characterised both by hotter temperatures and more intense droughts. Grote et al. (2016) listed the main ecophysiological differences between small and large trees that can affect their exposure and response to water deficit and temperature. This includes greater hydraulic constraints for large than for small trees due to the physical resistance to lifting water to greater heights, as well as differences in stomatal control mechanisms and in fine and coarse root biomass and vertical distribution. Due to their height, large trees have an increased risk of cavitation and carbon deficits that can lead to death (Ryan et al. 2006). The greater vulnerability of large trees could also be related to biotic factors because trees are not affected by the same risks according to their size. For example, bark beetles preferentially attack large trees because they have thicker bark and phloem for digging their breeding galleries and for feeding than small trees (Pfeifer et al. 2011), with an exacerbated tree vulnerability during drought periods (McDowell et al. 2011). In well-watered areas, hotter temperatures can increase tree growth (Charru et al. 2017), but in more continental areas with drought events, growth is impaired due to the interaction between high temperatures, potential evaporation and, finally, increased soil water deficit. Depending on the stomatal behaviour of the species, drought-induced tree mortality may be triggered if the ambient temperature is warmer, as demonstrated in an experimental study on two gymnosperm species (Duan et al. 2015).

Despite the fact that big or old trees are considered to be more vulnerable to drought, decline was also reported for small or young trees. For example, Peng et al. (2011), van Mantgem et al. (2009) and Shenkin et al. (2018) observed an increase in mortality in Canada, the western United States and the Amazonian forest for small trees in response to climate warming and drought intensity, with higher mortality rates compared to large trees. Similar results can also be found in tree radial growth studies based on data collected in different stands and from a long-term experimental network. They showed a greater growth decrease of small and understorey trees compared to large trees during extreme drought events in temperate forests, hypothesized as the result of a shallower root system, leading to a more limited access to deep water content (Pichler and Oberhuber 2007, Trouvé et al. 2014). This discrepancy between past drought-induced mortality studies was sometimes attributed to limitations in the spatial extent or sample size for retrospective analysis (Stovall et al. 2019). Understanding the effects of the recent temperature and rainfall changes on different categories of trees is a difficult task as they are submitted to contrasting environmental condition and competition

intensity, and because a confusion exists between tree size and social status, that can be both correlated with age.

In this study, we analysed the effects of recent changes in climate on the observed mortality in a stand without disturbance (i.e. background mortality). We tested the hypothesis that long-term effects of changes in temperature and rainfall due to recent climate change can differently impact background tree mortality according to the tree size and social status. For eight of the most common European species and 207,100 available trees scattered over the whole France, we determined three subsets of suppressed, small dominant and large dominant trees. Using French Forest Inventory data collected between 2009 and 2015 and historic climatic data, we modelled background mortality for each species' subset. We accounted for effects related to competition, stand attributes and logging intensity within the plot. In addition, we added the recent changes in temperature and rainfall in order to evaluate their importance in the background tree mortality models, and to calculate and map the associated over-mortality.

## 2 Material and methods

### 2.1 Database description and plot selection

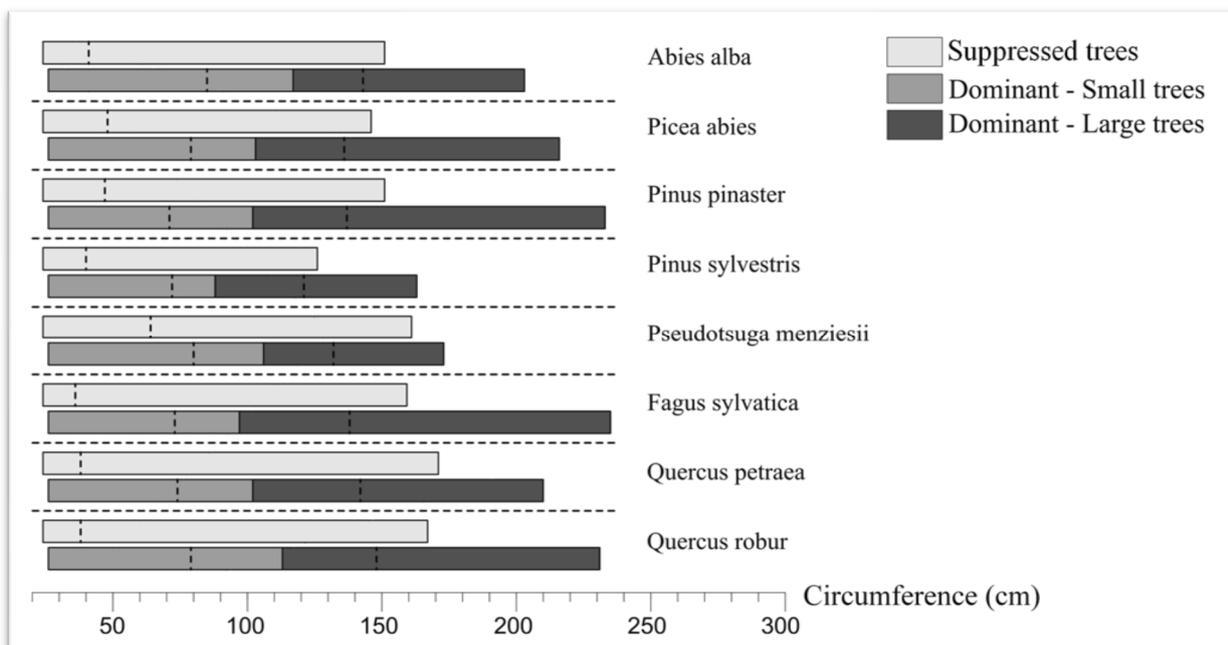
We used data from the French Forest Inventory of the National Geographic Institute (NGI), collected between 2009 and 2015 for France. Approximately 6,500 plots were inventoried per year on a quasi-systematic grid, corresponding to 41,692 plots and 554,133 inventoried trees, including 37,767 dead trees. Only trees with a diameter at breast height (1.30 meters,  $dbh$ )  $> 7.5$  cm were counted. On each plot, trees were surveyed in concentric subplots of 6, 9 and 15 m in radius for trees of  $7.5 < dbh < 22.5$  cm,  $22.5 \leq dbh < 37.5$  cm, and  $37.5 \text{ cm} \leq dbh$ , respectively, and the tree and stand characteristics were calculated for a same surface unit (per hectare of forest land). According to the protocol, a dead tree was recorded when it had a  $dbh > 7.5$  cm, had no living part above 1.3 m height, and was presumed dead within the five years prior to the inventory.

Standing dead trees, felled trees and broken dead trees were individually recorded. Perturbations of soil conditions and vegetation cover were also systematically recorded in the field, including forest fires, storms, waterlogging, flooding, landslides, avalanches and potential anthropogenic disturbances. In order to avoid confusion between mortality factors related to abrupt disturbances not necessarily related to climate change and those related to gradual changes in temperature and rainfall regimes, all plots with evidence of such perturbations were removed from the analysis. For the same reasons, felled and broken individual trees were discarded. When a plot was composed of less than 10% of trees with a diameter  $> 7.5$  cm, it was removed from the analysis due to the impossibility to calculate reliable synthetic indices such as basal area ( $BA$ ). To focus on homogeneous stands only, plots including forest edges and small groves were also removed. The proximity of forest edges modifies light availability, increases wind-related disturbances, and induces different growth conditions from closed forest. In total, 207,100 trees, including 3,514 dead trees, distributed on 25,209 plots, were used for the eight studied species.

### 2.2 Species selection and data partitioning

We selected species based on the list of the 20 most important species in Europe in terms of forest coverage (Brus et al. 2012). In order to compare climate change effects on tree mortality in relation to tree development stage and social status, we separated the tree

population into three subsets for each species: suppressed trees, dominant small trees and dominant large trees. Because individual tree height is not measured, the separation between suppressed and dominant trees was based on tree relative size, i.e. the circumference ratio of each tree over the mean circumference of all the trees in the plot (*RelCirc*), irrespective of species composition, developmental stage, or stand density. If this ratio was  $\geq 1$ , the tree was considered dominant, and if it was  $< 1$ , the tree was considered suppressed. The effects of climate change between small and large trees were focused on the dominant tree population (live and dead trees) to avoid bias related to tree social rank. Two subsets of small and large dominant trees were defined according to the median circumference value of set of dead trees. We only kept species for which we had at least 20 dead individuals in each of the three subsets. We obtained a list of eight species, including five gymnosperms and three angiosperms (**Figure 1**). The location and the exact number of live and dead trees for suppressed, small dominant and large dominant tree subsets is available in **Appendix A**. The number of live and dead trees for suppressed, small and large dominant trees per species is available in **Appendix B**. Because competition between trees during the early stages of their development is the principal determinant of tree mortality (Charru et al. 2012), and because declining large trees are preferentially harvested, dead trees are mainly suppressed trees.



**Figure 1.** Circumference of the suppressed tree subset (light grey boxes), the small and dominant tree subset (medium grey boxes) and the large and dominant tree subset (dark grey boxes). The separation between the two dominant tree subsets represents the median circumference value of dominant dead trees. For each subset, the dotted line represents the median circumference value of all the trees. The upper limit of the light grey and dark grey boxes represents the 1<sup>st</sup> and 99<sup>th</sup> percentile of the distribution.

## 2.3 Mortality models

We modelled the status of each tree (alive or dead) using logistic regression, a method that makes it possible to model a binary dependent variable (Cox 1958) and that was widely used in previous tree mortality models (Monserud and Sterba 1999, Hülsmann et al. 2018). We will first explain the choice of the variables used to model background mortality, based on previous literature, before describing the modelling approach.

## 2.4 Characterising the effects of competition and stand characteristics

Based on previous models that assess the drivers of background tree mortality in European temperate forests (Ruiz-Benito et al. 2013, Hülsmann et al. 2018, Taccoen et al. 2019), we calculated five variables that characterise tree and stand characteristics on the basis of information from NGI plots. Tree relative circumference at 1.3 m in height; (*Relcirc*), stand development stage (plot basal area; *BA*), circumference distribution of trees within the plot (Gini coefficient; *Gini*), stand species composition (proportion of the total plot basal area occupied by the tree species of interest; *PropBA*), and stand management intensity (presence of skid trails, *Trails*) are presented in **Table 1**. By considering *Relcirc* and *BA*, we accounted for the effects of competition, which were identified as the main determinant of background mortality, particularly affecting small trees (Das et al. 2016, Hülsmann et al. 2018). The *Gini* index of inequality (Latham et al. 1998) is calculated on the tree diameter distribution in the plot and ranges between 0 and 1. It provides an indication of the type of silviculture practiced on the plot (irregular or regular). *PropBA* reflects the tree species composition on the plot. These two variables have shown themselves to be strong predictors of tree mortality in a previous study in the same biome (Taccoen et al. 2019). Finally, *Trails* is an indirect indicator of stand management intensity. It is important to take into account because silvicultural practices in Europe generally imply the removal of dead or declining trees (Schelhaas et al. 2018). Therefore, the presence of dead trees can be strongly influenced by logging intensity.

## 2.5 Climate change variables

To assess the potential effects of recent climate change on background tree mortality, we considered two variables that describe changes in temperature and rainfall during the vegetation period (March to August included). We used the interaction between climatic conditions and climate evolution because previous research highlighted its better efficiency to assess background tree mortality than average climate or climate evolution considered alone (Taccoen et al. 2019).

We first averaged monthly temperature and rainfall values over a reference period before climate warming in the studied area, spanning the 1961-1987 period. We selected this period because in France temperatures rose continuously as of 1988, while no important changes were recorded for rainfall between 1961 and 2015 (**Appendix C**). These variables were modelled and mapped using 237 and 435 meteorological stations for temperature and rainfall, respectively (Piedallu et al. 2016). Secondly, we calculated changes in temperature and rainfall compared to the reference period using homogenised temperature and rainfall series provided by Météo-France (Gibelin et al. 2014). We used 200 and 1,119 meteorological stations for temperature and rainfall, respectively. For each of them, we calculated the difference between the reference period and periods contemporary to the NGI sample plots recorded each year between 2009 and 2015. According to the NGI protocol, trees were assumed to have died during the five years before the survey. Additionally, trees may die long after climatic disturbances (Das et al. 2013). Therefore, to fully capture the effects of delayed mortality, we considered 15-year shifting time periods before the survey date for each plot in order to define periods contemporary to the NGI sample plots. For the 15-year period before each of the seven yearly

NGI datasets surveyed, changes in climate conditions were calculated monthly for each meteorological station, interpolated with ordinary kriging using Arcgis 10.5, and averaged for the whole period.

Finally, for each of 15-year period shifting time periods, we calculated monthly interactions between the reference climate period and changes in temperature and rainfall.  $T^{\circ}Evo$  were calculated as the product of reference temperatures and their changes.  $RfEvo$  was calculated as the quotient of rainfall changes over the reference rainfall values.  $RfEvo$  values were then cumulated over the vegetation period (from April to August), while  $T^{\circ}Evo$  values were averaged over the same period (**Table 1**).

## 2.6 Modelling approach and quality assessment

A model was run with the same procedure for each of the eight species and the three subsets (suppressed trees, dominant small trees and dominant large trees). The seven candidate variables were used together to calibrate each model. To assess the commonly observed U-shaped and bell-shaped response curves to tree size and competition intensity (Holzwarth et al. 2013), we tested tree stand attribute variables (*RelCirc*, *BA*, *Gini*, *PropBA*) in their quadratic forms in addition to the monotonic one (Ter Braak and Looman 1986), and kept the best performance. To validate each model with an independent dataset, we used a k-fold cross-validation method [with  $k = 1000$  (Friedman et al. 2001)]. For each iteration, we calibrated the model on 80% of the trees randomly selected from the full sample, and validated with the 20% remaining trees. We calculated the final coefficients for each selected variable by averaging the 1000 iterations of the calibration dataset. We then compared these coefficients for the three subsets. The more the  $T^{\circ}Evo$  coefficient is positive or the  $RfEvo$  coefficient is negative, the more the recent temperature increase or rainfall decrease will lead to tree mortality, particularly in hot or dry areas, respectively. Model quality was assessed with the mean Area Under the Curve calculated with the 1000 iterations of the independent validation dataset [AUC, (Fielding and Bell 1997)].

We estimated and mapped the over-mortality driven by  $T^{\circ}Evo$  and  $RfEvo$  for each tree species. For each plot, we calculated the difference between the probabilities of mortality predicted from the model with all the variables, and a model where the two climate change-related variables were set to 0. In order to map only the effects of climate change on tree mortality and to remove the stand effect, all the non-climatic variables were set to their mean value (Muller and MacLehose 2014). For a representative stand, we obtained a value in %, corresponding to the changes in the probability of finding a tree that died in the last five years as a consequence of temperature and rainfall changes. For each species and subset, we interpolated these values with ordinary kriging using ArcGIS 10.5 to map the excess probability of mortality for the entire area studied.

<b>Effect considered</b>	<b>Variable description</b>	<b>Abb.</b>	<b>Unit</b>	<b>Source</b>
Tree social status	Ratio of the circumference (c13) of the tree over the mean c13 of all the trees in the plot	RelCirc	%	Calc.
Stand development stage	Sum of the tree basal areas in the plot	BA	m <sup>2</sup>	Calc.
Circumference distribution within the plot	Gini coefficient of the tree circumferences in each plot	Gini	/	Calc.
Stand species composition	Percent of basal area occupied by the species in each plot	PropBA	%	Calc.
Stand management intensity	Indicator of the presence of previously existing skid trails and of the possibility of creating new ones	Trails	/	Field
Intensity of climate change	Interaction between temperature evolution and the reference period temperature calculated as a product of these two values from April to August	<i>T°Evo</i>	/	Mod.
	Relative rainfall evolution calculated as the ratio of rainfall evolution over the reference period rainfall from April to August.	<i>RfEvo</i>	mm	Mod.

**Table 1: Description of the seven explanatory variables used in the models.** Abb = abbreviation. The Source column indicates the origin of the data: (1) collected by the NGI (Field); (2) calculated using NGI information (Calc); or (3) extracted using Geographic Information System from digital models (Mod.).

### 3 Results

#### 3.1 Performance of background mortality models for the three studied subsets

Average AUC values were greater than 0.82 for each subset for gymnosperms and greater than 0.74 for angiosperms (**Table 2**). According to Hosmer Jr et al. (2013), AUC indicates acceptable ( $0.7 \leq AUC < 0.8$ ) to excellent ( $0.9 > AUC$ ) performances. Model quality was significantly greater for the suppressed tree subset ( $0.83 \pm 0.01$ ) than for the small tree subset ( $0.80 \pm 0.02$ ) and the large dominant tree subset ( $0.79 \pm 0.02$ ). The best model performances were obtained for the suppressed tree subset of *Pinus pinaster*, with an AUC of 0.91. The lowest performances were obtained for the large dominant tree subsets of *Quercus petraea* and *Quercus robur*, both with an average AUC of 0.71.

<b>Gymnosperms</b>	Suppressed trees	Dominant small trees	Dominant Large trees
<i>Abies alba</i>	$0.82 \pm 0.01$	$0.84 \pm 0.03$	$0.81 \pm 0.02$
<i>Picea abies</i>	$0.80 \pm 0.01$	$0.82 \pm 0.01$	$0.77 \pm 0.02$
<i>Pinus pinaster</i>	$0.91 \pm 0.00$	$0.84 \pm 0.02$	$0.86 \pm 0.01$
<i>Pinus sylvestris</i>	$0.77 \pm 0.01$	$0.81 \pm 0.01$	$0.79 \pm 0.01$
<i>Pseudotsuga menziesii</i>	$0.89 \pm 0.01$	$0.82 \pm 0.02$	$0.86 \pm 0.03$
<b>Average</b>	<b><math>0.84 \pm 0.01</math></b>	<b><math>0.82 \pm 0.02</math></b>	<b><math>0.82 \pm 0.02</math></b>

<b>Angiosperms</b>	Suppressed trees	Dominant small trees	Dominant Large trees
<i>Fagus sylvatica</i>	$0.79 \pm 0.01$	$0.83 \pm 0.03$	$0.80 \pm 0.03$
<i>Quercus petraea</i>	$0.83 \pm 0.00$	$0.72 \pm 0.03$	$0.71 \pm 0.03$
<i>Quercus robur</i>	$0.80 \pm 0.00$	$0.72 \pm 0.02$	$0.71 \pm 0.01$
<b>Average</b>	<b><math>0.81 \pm 0.01</math></b>	<b><math>0.76 \pm 0.02</math></b>	<b><math>0.74 \pm 0.02</math></b>

**Table 2.** Performance of background mortality models for the eight studied species: average AUC and standard errors for suppressed, small and large dominant tree subsets calculated from a  $k$ -fold bootstrap ( $k = 1000$ ).

### 3.2 Non-climate effects on background mortality

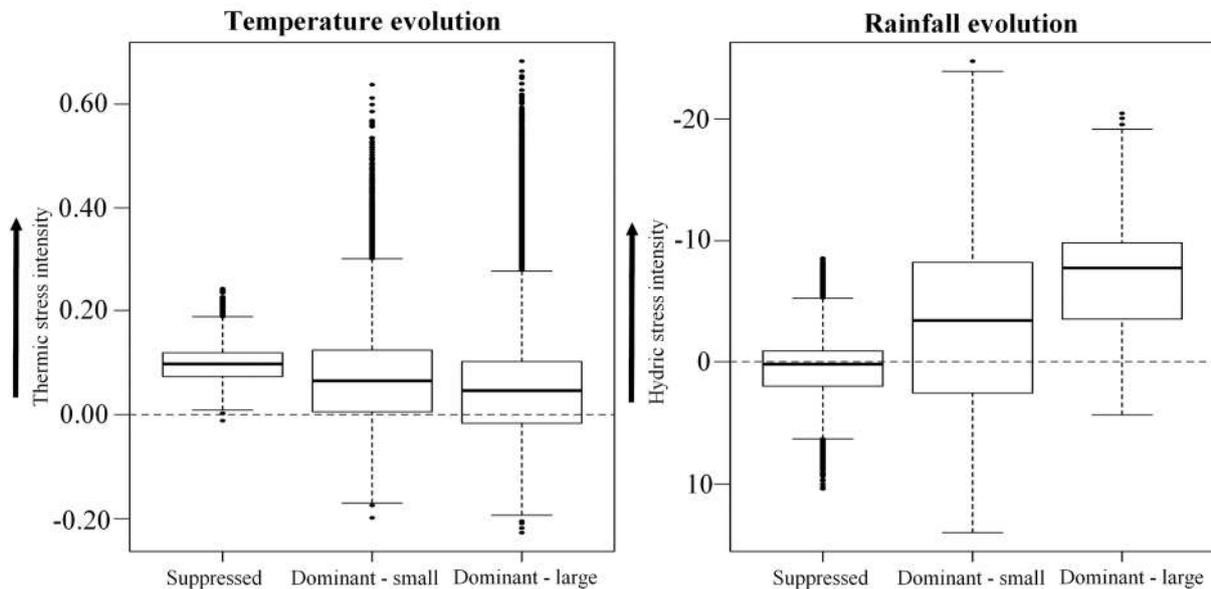
For all the species, the *RelCirc* and *BA* variables indicate considerable competition-related effects on the suppressed tree subsets. The decreasing response curves to *RelCirc* showed higher probabilities of background mortality for the most suppressed trees, ranging between 10% (*Fagus sylvatica*) and 48% (*Pseudotsuga menziesii*, *Quercus robur*, **Appendix D**). The probabilities of mortality strongly decreased for all the species when *RelCirc* is close to one. Effects of *BA* were also important on suppressed trees, increasing curves indicating higher probabilities of mortality with large plot basal area (**Appendix E**). For the dominant tree subsets, these competition-related effects were of low intensity ( $p < 0.05$ ).

*Gini* (**Appendix F**) and *PropBA* (**Appendix G**) had effects both on suppressed and dominant trees, with a lesser importance for the latter. The trends vary depending on species, showing globally lower probabilities of mortality with pure stands. Coefficient values for all the variables and each species are available in **Appendix J**.

### 33 Climate change-related effects

For the three subsets, the trends of  $T^{\circ}Evo$  coefficients were clearly positive, with higher values for the suppressed tree subset (**Figure 2**, average value of  $0.10 \pm 0.03$ , and **Appendix H** for the responses curves).  $T^{\circ}Evo$  coefficients were lower for dominant small trees, (average value of  $0.08 \pm 0.08$ ) and reached their minimum value for dominant large trees (average value of  $0.07 \pm 0.10$ ; **Figure 2**). This indicates an increasing probability of mortality in areas with higher average temperatures that have experienced the most warming.

$RfEvo$  coefficients were mainly negative, indicating increasing probabilities of mortality in areas with lower reference rainfall that have recently experienced rainfall decreases (**Figure 2** and **Appendix I** for the response curves). This is particularly true for large dominant trees (average value of  $-7.02 \pm 3.20$ ) and, to a lesser extent, for small dominant trees (average value of  $-3.72 \pm 5.65$ ), whereas no clear trends were visible for suppressed trees (average value of  $0.34 \pm 2.38$ ).

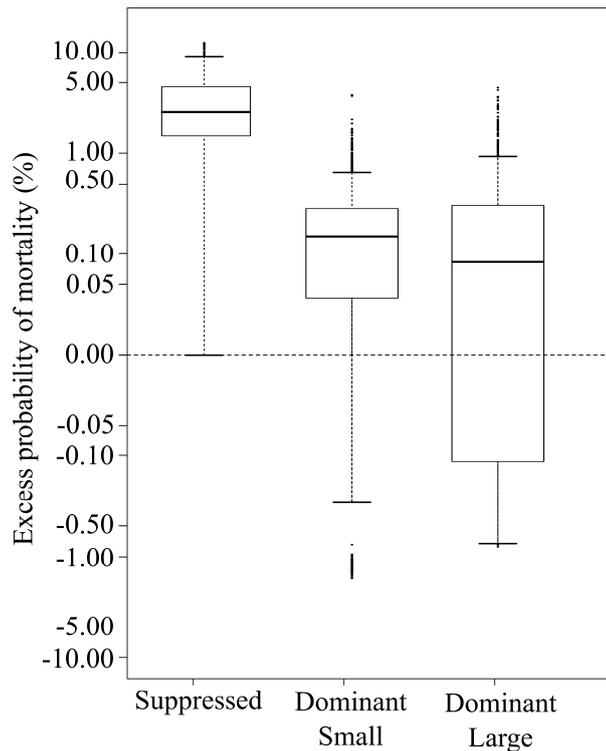


**Figure 2.** Coefficient values of  $T^{\circ}Evo$  and  $RfEvo$  for the eight species and the suppressed, small dominant and large dominant tree subsets. Each boxplot is composed of 8000 coefficient values obtained with a  $k$ -fold bootstrap on each of the eight species ( $k = 1000$ ). The per species version of this figure is available in **Appendix K and L**, and the variable coefficients in **Appendix J**.

### 34 Climate change-related excess probability of mortality

In order to evaluate the combined effects of changes in temperature and rainfall, we calculated the excess probability of mortality for each species compared to a climate change-free context for the suppressed, small dominant and large dominant tree subsets. The excess probability of mortality linked to recent climate change for suppressed trees (median = +2.56%; mean = +3.22% [ $\pm 2.14\%$ ]) was generally greater than for dominant small (median = +0.15%; mean = +0.07% [ $\pm 0.53\%$ ]) and large trees (median = +0.08%; mean = +0.12% [ $\pm 0.39\%$ ]) (**Figure 3**, values for each species are available in **Appendix M**).

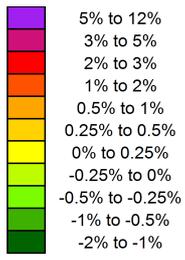
To ensure that the differences in mortality between suppressed and dominant trees were not related to tree size differences but rather to social status differences, we selected two subsets of suppressed and dominant trees with equal average circumference (**Appendix N and O**). We used the suppressed tree subset developed for the previous analysis and we sampled a dominant tree subset with an average circumference equal to that of suppressed trees (**Appendix N**). We obtained comparable results [median = +2.56% for suppressed trees, and +0.03% ( $\pm 0.83\%$ ) for dominant trees, **Appendix O**], demonstrating that the difference in modelled excess probability of mortality between suppressed and dominant trees can be attributed to social status effects and not to size effects.



**Figure 3. Over-mortality linked to climate change: combined temperature and rainfall changes related to the excess of probability of mortality for the suppressed, small dominant and large dominant tree subsets.** It is calculated as the difference between predicted values for the full model and a partial model where climate change-related effects have been set to 0. For each model, all non-climate change-related variables were set to their mean value for all the trees of the considered species, while qualitative variables were set to their most frequent value.

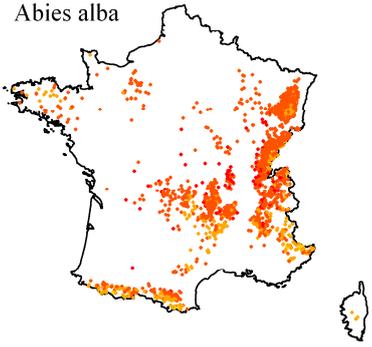
For each species, we mapped the climate change-related excess probability of mortality for suppressed, small dominant and large dominant tree subsets (**Figure 4**). With the exception of *Abies alba*, *Picea abies* and *Pinus pinaster*, for which the north-south gradient is greater for dominant trees, mortality patterns of suppressed, small and large dominant trees were globally similar, with a maximum excess probability of mortality at low altitudes or latitudes. Consistent with the trends illustrated in **Figure 3**, maps of suppressed trees showed higher mortality rates driven by climate change than those for either small or large dominant trees. While climate change impact systematically leads to an increase in tree mortality for suppressed trees, it can locally lead to a decrease for dominant trees in the coldest part of their distribution area.

Mortality excess rate

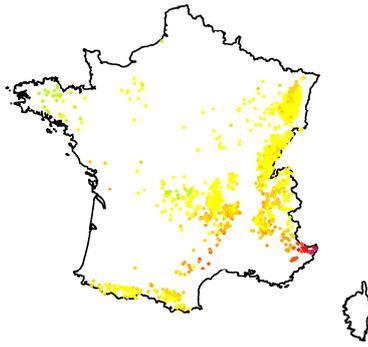


**Suppressed**

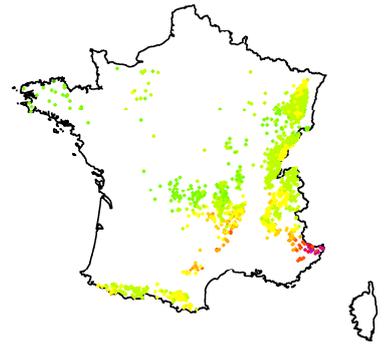
*Abies alba*



**Dominant - small**

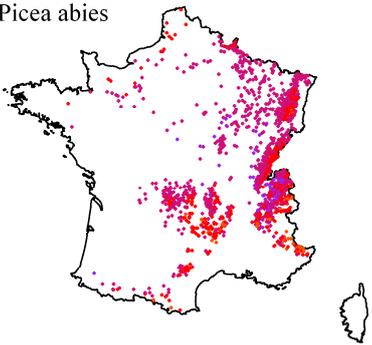


**Dominant - large**

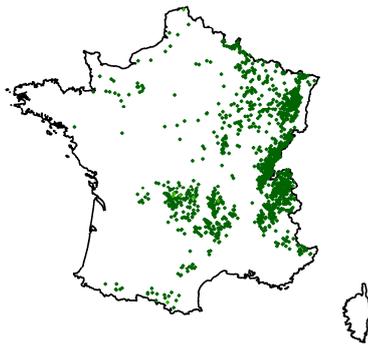


**Suppressed**

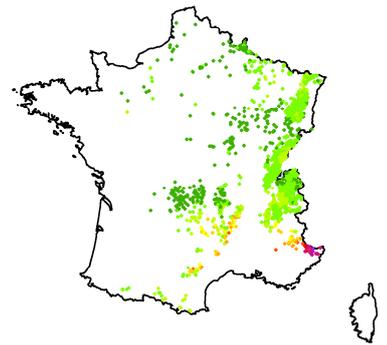
*Picea abies*



**Dominant - small**

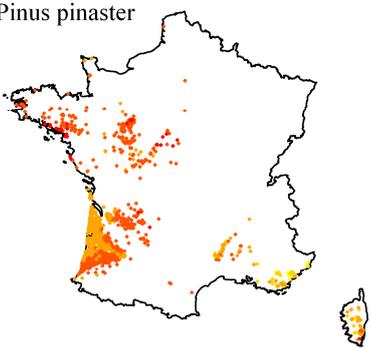


**Dominant - large**

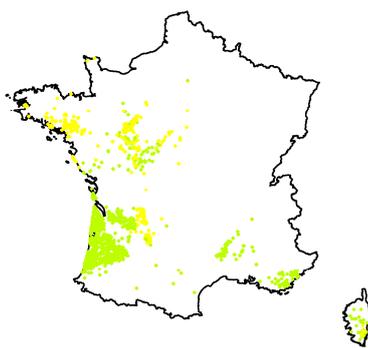


**Suppressed**

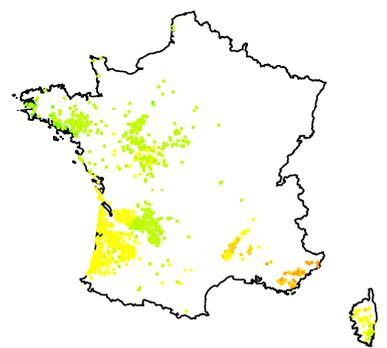
*Pinus pinaster*



**Dominant - small**

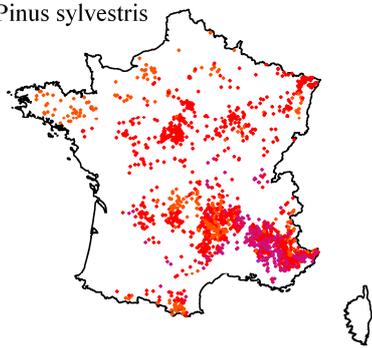


**Dominant - large**

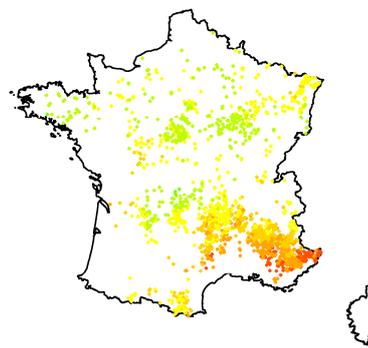


**Suppressed**

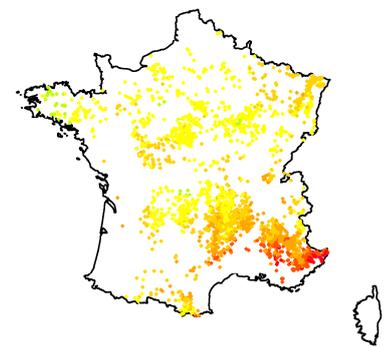
*Pinus sylvestris*

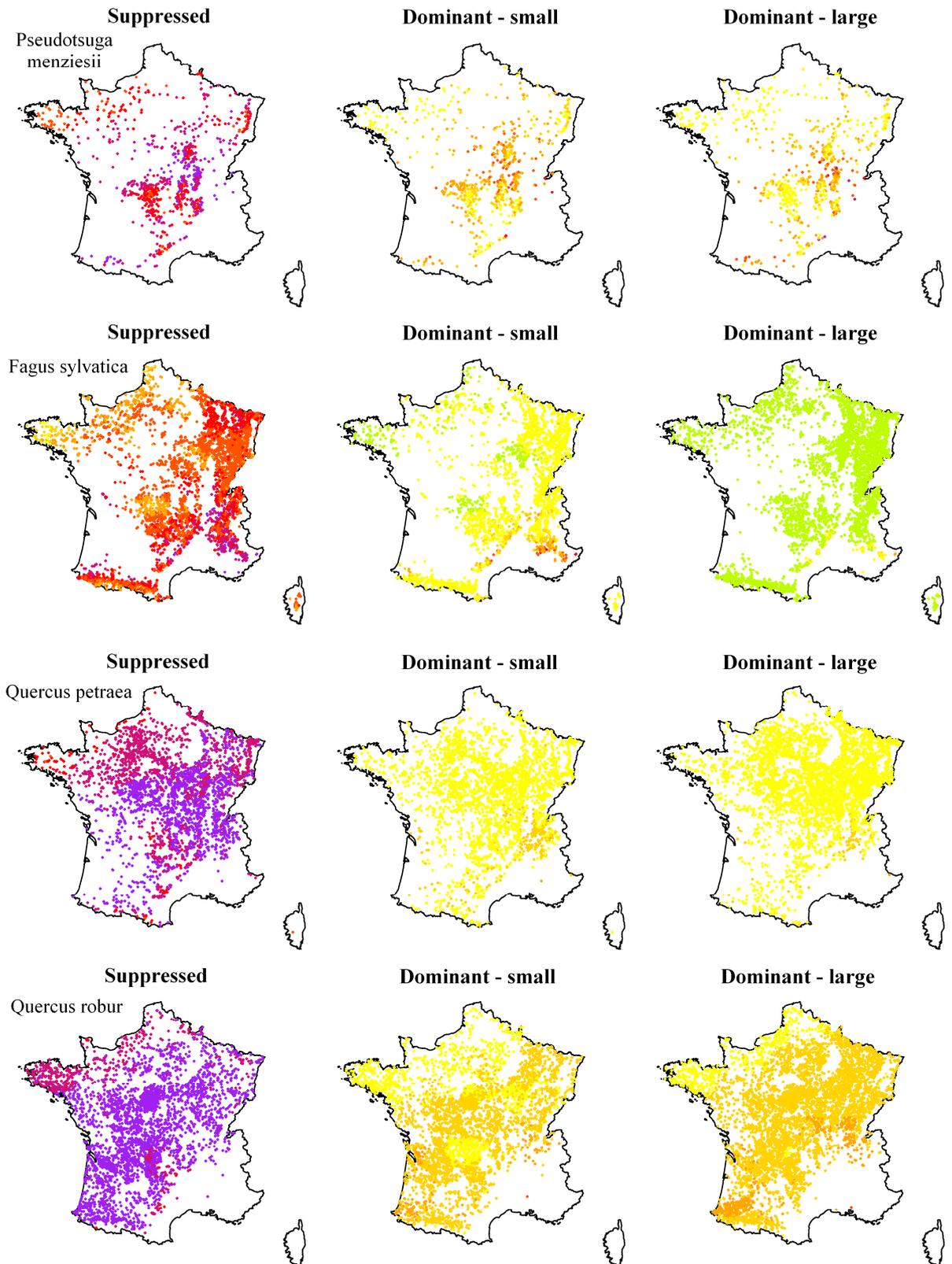


**Dominant - small**



**Dominant - large**





**Figure 4.** Excess probability of mortality resulted from combined effects of changes in temperature and rainfall for the suppressed, small dominant and large dominant tree subsets. When changes in temperature and rainfall lead to higher mortality, the excess mortality rate is represented by warm colours, and by cold colours when they lead to lower mortality.

## 4 Discussion

We demonstrated that long-term changes in temperature and rainfall due to the recent climate change increase background tree mortality for all the studied species, even if there are different responses according to tree size and social status. As main results, we found a significant over-mortality for suppressed trees mainly related to temperature increase, while rainfall decrease impairs the dominant trees. These results emphasize that despite different social status or size and although the trees were not exposed to the same water stress, they all respond to climate change.

### 4.1 Combined effects of temperature and rainfall changes lead to over-mortality for all of the species studied

After taking drivers related to competition and stand characteristics, including the logging intensity effect, into account, we identified a statistically significant impact of recent temperature and rainfall changes on background mortality for the eight studied species, leading to an over-mortality for at least one of the studied subsets for each of them. The model performances and the consistency of the response curves among the species suggest that, despite the low number of dead trees for some subsets, the most important drivers were taken into account. In agreement with existing knowledge, the over-mortality was attributed to increasing temperatures and decreasing rainfall (McDowell et al. 2016). Some of the species, like *Abies alba* and *Quercus petraea*, showed no climate change-related effects in previous studies carried out in the same ecological context, but that considered all the tree sizes and social statuses together (Taccoen et al. 2019). These results highlight the advantage of separating the different tree statuses to assess forest vulnerability to climate change since some effects cannot be seen when considering all the trees together. They were consistent with existing studies that show high mortality rate increases in European Mediterranean and temperate forests (Carnicer et al. 2011, Senf et al. 2018), strongly correlated with temperature warming or droughts.

### 4.2 Over-mortality is especially severe in the case of suppressed trees

We found that the recent temperature and rainfall changes related to over-mortality were greater for suppressed than for dominant trees. This result is in contrast with most of the existing research that highlights more drought-induced mortality for large trees than for small ones (Bennett et al. 2015, Stovall et al. 2019). However, suppressed trees were generally not inventoried or not studied in these cases, which mainly focused on extreme drought event effects instead of long-term evolutions of climate over many decades. The differences in the stand characteristics, data collection and processing between studies also probably contribute to explaining these differences (van Mantgem et al. 2009, Shenkin et al. 2018). Indeed, the causes of observed mortality are manifold (stand evolution, climate warming, extreme drought events, storm, wildfire, pests and diseases, etc.), and they can interact at different time and spatial scales (Thorpe and Daniels 2012).

When excluding extreme events by focusing on background mortality only, and removing mortality attributed to stand evolution, we demonstrated that suppressed trees are more impaired than large ones for all of the studied species, whereas there is no great difference in vulnerability between small and large dominant trees. Similar results were found in boreal forests by Luo and Chen (2011) on permanent sampling plots covering a wide range of development stages. These findings highlight the importance of disentangling the effects of tree size and social status in tree mortality studies. They complement existing studies showing that large trees were impacted by extreme drought events, demonstrating that small and particularly suppressed ones were also affected by recent climate change effects, with potential impacts on ecosystem services and forest regeneration.

Whereas few studies have focused on the impact of temperature or rainfall changes on tree mortality according to stand structure, several studies have identified a reduction of tree radial growth as a function of water stress that is greater for suppressed trees compared to dominant ones. In the Alps, growth reductions consecutive to extreme drought episodes and heat waves were greater for suppressed than for dominant *Pinus sylvestris* trees (Pichler and Oberhuber 2007). In lowland French forests, growth reductions were also the greatest for suppressed *Quercus petraea* trees in response to high summer soil water deficits (Trouvé et al. 2014). Similar results were also found for *Pinus strobus* and *Picea abies* (Martin-Benito et al. 2010). Most of the ecophysiological differences between suppressed and dominant trees, including rooting depth, hydraulic constraints, xylem conductivity and gas exchange mechanisms, appear to be mostly related to differences in tree height and circumference rather than to social status. On the contrary, the canopy structured by dominant trees strongly controls microclimate in the understorey, including temperature, rainfall, vapour deficit and light availability (Aussenac 2000, Grote et al. 2016). Our results suggest that suppressed trees suffer more from lack of water (shallower root systems), even if their crowns are exposed to lower transpiration (Bréda et al. 1993). This was consistent with the similar hydraulic conductance observed, regardless of the crown class, among *Picea abies* trees when they were well-watered, but that underwent severe changes when submitted to rainfall exclusion (Granier et al. 1989).

We probably underestimated the temperature and rainfall changes related to tree mortality due to logging intensity and the period concerned by this study. Because they were preferentially harvested when mortality occurred, the proportion of dead dominant trees is probably more underestimated in the inventory databases compared to suppressed trees. Even if management intensity is taken into account in our models, the probability of mortality that we calculated for the dominant and large trees is probably lower than the reality. Also, the temperature and rainfall changes that induced over-mortality of dominant *Picea abies*, *Abies alba* and *Fagus sylvatica* trees were of low magnitude. This result may come as a surprise since *Picea abies* and *Abies alba* have experienced massive mortality due to bark beetle outbreaks in recent years (Marini et al. 2017). However, the trees used for modelling here were collected between the years 2009 and 2015, which corresponds to a period without an extreme drought event and, consequently, a period of reprieve for bark beetle outbreaks in France (Gillette 2017). Concerning *Fagus sylvatica*, while important range contractions were forecasted from species distribution models for the coming decades (Dyderski et al. 2018), experimental studies showed that this species was particularly resilient to severe water shortage and was able to sustain its survival metabolism through allocation changes, even when exposed to two years of total water deprivation (Chuste et al. 2019).

### **4.3 Climatic drivers of tree mortality differ according to tree size and social status**

We found that for each studied species, temperature increase led to more over-mortality for suppressed rather than for dominant trees. Among dominant trees, we did not highlight any major differences between small and large trees. The effect of rainfall decrease was the greatest for dominant trees and, particularly, for the large ones, whereas lesser effects were visible for the suppressed ones. These differences illustrate that trees are not exposed to the same water deficit according to their size and their social status.

Rainfall and temperature both contribute to determining available water for trees through the water balance, with a pronounced water shortage leading to tree mortality through hydraulic failure or carbon starvation (Adams et al. 1995, Allen et al. 2015). Suppressed and dominant trees are not exposed to the same environmental conditions. Dominant trees are usually higher and have deeper coarse roots and a greater fine root biomass than understorey trees, allowing access to higher water content and potentially delaying the date of water shortage (Pretzsch et al. 2013, Grote et al. 2016). However, the sun-exposed crowns of large trees with high leaf areas are exposed to higher potential evapotranspiration than suppressed ones. Suppressed trees benefit from lower radiation, vapour pressure deficit, less wind and buffered temperatures (Davis et al. 2019). For example, the analysis of paired temperature measurements on five continents under canopy and in open areas showed differences that can reach 5 or 10°C for maximal temperatures (De Frenne et al. 2019). Consequently, the canopies of suppressed trees, which have limited total leaf area, are exposed to lower evapotranspiration, and their transpiration is considerably lower than that of dominant ones (Bréda et al., 1993). Granier et al. (1989) and Lu et al. (1996) reported that few differences in tree transpiration and hydraulic conductance exist among tree statuses for several coniferous species and oaks under well-watered conditions, whereas inter-tree variability sharply increases in the event of water shortage.

For a similar stand, we demonstrated higher over-mortality when temperature increases for suppressed trees compared to small or dominant ones. Higher temperatures reduce water availability by increasing evaporation and transpiration. A major effect of temperature rather than rainfall has already been demonstrated for radial growth in a similar ecological context (Lebourgeois et al. 2014). The higher sensitivity to temperatures of suppressed trees compared to small dominant ones suggests that for trees with a shallow root system, the canopy plays an important role in a climate change context. This could be explained, for example, by differences in adaptation in a context of rapid changes. Dominant trees experienced greater temperature variations and can be more resistant to the recent warming than suppressed trees that benefit from buffered temperatures. Local adaptation is considered to be able to counteract the effects of extreme conditions (Lazaro-Nogal et al. 2016). The temperature increase for suppressed trees can be exacerbated by a sudden increase in light availability if dominant trees are declining and lose their leaves or their needles (Laurance and Williamson 2001).

The higher vulnerability to rainfall decrease of large dominant trees strengthens the previous results in terms of growth reduction and over-mortality following extreme drought events (Bennett et al. 2015). Since root biomass is correlated with tree height, leaf biomass and

light exposure (Cheng et al. 2005, Wutzler et al. 2008), it is difficult to disentangle it from the effects related to tree size and social status. Our results suggest that the deeper and more developed root system of large trees, which allows a better water uptake under water shortage, does not compensate for their greater water need for transpiration due to large leaf area and exposure to high potential evapotranspiration. With ongoing climate change, this impact of the soil water deficit is expected to increase as a result of both increased evapotranspiration due to warming and decreased rainfall, mainly in mid-latitude and subtropical dry regions (IPCC 2014). A study based on the physical modelling of water transfer in trees showed that tall trees with specific functional traits (isohydric stomatal control, low hydraulic conductance, high leaf area) are most likely to die from severe drought in the coming decades (McDowell and Allen 2015). These theoretical forecasts seem to be confirmed by the rapid increase of forest diebacks observed worldwide in recent years (Crockett and Westerling 2018, Hirayama et al. 2019).

#### **4.4 Conclusion**

An increase in tree mortality has been observed in these last decades in different biomes. Consequently, in a context where rising temperatures and the increased frequency and intensity of droughts are expected, it is urgent to improve our understanding of the causes and the mechanisms of these forest diebacks. The impact of climate change on tree mortality has been demonstrated, but many questions about the intensity of changes in forest ecosystems and how to cope with a drier and hotter climate remain answered. We showed that temperature and rainfall change-related mortality does not concern only large trees but small dominant and suppressed ones as well. The vulnerability of suppressed trees that suffer from shallow root system could be exacerbated by transpiration increase due to large tree removal during harvesting. Our results suggest that climate change could not only affects wood production, but also has an influence on forest renewal, a key parameter for anticipating changes in tree species composition, with possible cascading implications on the ecosystem services provided.

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#### **Authors' contributions**

A.T., J.C.G. and C.P. developed the ideas and designed the methodology; A.T. and I.S. organised the database; AT and A.G.P. contributed to the statistical analyses; A.T. and C.P. wrote the manuscript. All of the authors discussed and commented on the methods and the results, read and corrected the paper, and gave their final approval for publication.

## References

- Adams, J. B., D. E. Sabol, V. Kapos, R. Almeida Filho, D. A. Roberts, M. O. Smith, and A. R. Gillespie. 1995. Classification of multispectral images based on fractions of endmembers: application to land-cover change in the Brazilian Amazon. *Remote Sensing of Environment* **52**:137-154.
- Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**.
- Ampoorter, E., F. Selvi, H. Auge, L. Baeten, S. Berger, E. Carrari, A. Coppi, M. Fotelli, K. Radoglou, N. N. Setiawan, M. Vanhellemont, and K. Verheyen. 2016. Driving mechanisms of overstorey-understorey diversity relationships in European forests. *Perspectives in Plant Ecology Evolution and Systematics* **19**:21-29.
- Aussenac, G. 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Annals of Forest Science* **57**:287-301.
- Bennett, A. C., N. G. McDowell, C. D. Allen, and K. J. Anderson-Teixeira. 2015. Larger trees suffer most during drought in forests worldwide. *Nature Plants* **1**:15139.
- Blicharska, M., and G. Mikusinski. 2014. Incorporating Social and Cultural Significance of Large Old Trees in Conservation Policy. *Conservation Biology* **28**:1558-1567.
- Bréda, N., H. Cochard, E. Dreyer, and A. Granier. 1993. Water transfer in a mature oak stand (*Quercus petraea*): seasonal evolution and effects of a severe drought. *Canadian Journal of Forest Research* **23**:1136-1143.
- Breda, N., R. Huc, A. Granier, and E. Dreyer. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science* **63**:625-644.
- Brus, D., G. Hengeveld, D. Walvoort, P. Goedhart, A. Heidema, G. Nabuurs, and K. Gunia. 2012. Statistical mapping of tree species over Europe. *European Journal of Forest Research* **131**:145-157.
- Carnicer, J., M. Coll, M. Ninyerola, X. Pons, G. Sanchez, and J. Penuelas. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences of the United States of America* **108**:1474-1478.
- Charru, M., I. Seynave, J. C. Herve, R. Bertrand, and J. D. Bontemps. 2017. Recent growth changes in Western European forests are driven by climate warming and structured across tree species climatic habitats. *Annals of Forest Science* **74**:1-34.
- Charru, M., I. Seynave, F. Morneau, M. Rivoire, and J.-D. Bontemps. 2012. Significant differences and curvilinearity in the self-thinning relationships of 11 temperate tree species assessed from forest inventory data. *Annals of Forest Science* **69**:195-205.
- Cheng, S., P. Widden, and C. Messier. 2005. Light and tree size influence belowground development in yellow birch and sugar maple. *Plant and Soil* **270**:321-330.
- Chuste, P.-A., C. Massonnet, D. Gérant, B. Zeller, J. Levillain, C. Hossann, N. Angeli, R. Wortemann, N. Bréda, and P. Maillard. 2019. Short-term nitrogen dynamics are impacted by defoliation and drought in *Fagus sylvatica* L. branches. *Tree Physiology*.
- Cox, D. R. 1958. The regression analysis of binary sequences. *Journal of the Royal Statistical Society. Series B (Methodological)*:215-242.
- Crockett, J. L., and A. L. Westerling. 2018. Greater Temperature and Precipitation Extremes Intensify Western US Droughts, Wildfire Severity, and Sierra Nevada Tree Mortality. *Journal of Climate* **31**:341-354.
- da Costa, A. C. L., D. Galbraith, S. Almeida, B. T. T. Portela, M. da Costa, J. D. Silva, A. P. Braga, P. H. L. de Goncalves, A. A. R. de Oliveira, R. Fisher, O. L. Phillips, D. B. Metcalfe, P. Levy, and P. Meir. 2010. Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytologist* **187**:579-591.

- Das, A. J., N. L. Stephenson, and K. P. Davis. 2016. Why do trees die? Characterizing the drivers of background tree mortality. *Ecology* **97**:2616-2627.
- Das, A. J., N. L. Stephenson, A. Flint, T. Das, and P. J. van Mantgem. 2013. Climatic Correlates of Tree Mortality in Water- and Energy-Limited Forests. *Plos ONE* **8**:e69917.
- Davis, K. T., S. Z. Dobrowski, Z. A. Holden, P. E. Higuera, and J. T. Abatzoglou. 2019. Microclimatic buffering in forests of the future: the role of local water balance. *ECOGRAPHY* **42**:1-11.
- De Frenne, P., F. Zellweger, F. Rodríguez-Sánchez, B. R. Scheffers, K. Hylander, M. Luoto, M. Vellend, K. Verheyen, and J. Lenoir. 2019. Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution* **3**:744-749.
- Dean, W., S. Milton, and F. Jeltsch. 1999. Large trees, fertile islands, and birds in arid savanna. *Journal of Arid Environments* **41**:61-78.
- Duan, H. L., A. P. O'Grady, R. A. Duursma, B. Choat, G. M. Huang, R. A. Smith, Y. A. Jiang, and D. T. Tissue. 2015. Drought responses of two gymnosperm species with contrasting stomatal regulation strategies under elevated CO<sub>2</sub> and temperature. *Tree Physiology* **35**:756-770.
- Dyderski, M. K., S. Paź, L. E. Frelich, and A. M. Jagodziński. 2018. How much does climate change threaten European forest tree species distributions? *Global Change Biology* **24**:1150-1163.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**:38-49.
- Friedman, J., T. Hastie, and R. Tibshirani. 2001. The elements of statistical learning. Springer series in statistics New York.
- Gibelin, A.-L., B. Dubuisson, L. Corre, N. Deaux, S. Jourdain, L. Laval, J.-M. Piquemal, O. Mestre, D. Denettière, and S. Desmidt. 2014. Evolution de la température en France depuis les années 1950: Constitution d'un nouveau jeu de séries homogénéisées de référence. Rubrique: Climatologie.
- Gillette, M. 2017. Point d'actualité sur le typographe. Département de Santé des Forêts, Paris.
- Gonzalez-Martinez, T. M., G. Williams-Linera, and F. Holwerda. 2017. Understory and small trees contribute importantly to stemflow of a lower montane cloud forest. *Hydrological Processes* **31**:1174-1183.
- Granier, A., N. Bréda, J. P. Claustres, and F. Colin. 1989. Variation of hydraulic conductance of some adult conifers under natural conditions. *Annales Des Sciences Forestieres* **46 (suppl)**:357-360.
- Greenwood, S., P. Ruiz-Benito, J. Martínez-Vilalta, F. Lloret, T. Kitzberger, C. D. Allen, R. Fensham, D. C. Laughlin, J. Kattge, G. Bönisch, N. J. B. Kraft, and A. S. Jump. 2017. Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters*:n/a-n/a.
- Grote, R., A. Gessler, R. Hommel, W. Poschenrieder, and E. Priesack. 2016. Importance of tree height and social position for drought-related stress on tree growth and mortality. *Trees* **30**:1467-1482.
- Hember, R. A., W. A. Kurz, and N. C. Coops. 2017. Relationships between individual-tree mortality and water-balance variables indicate positive trends in water stress-induced tree mortality across North America. *Global Change Biology* **23**:1691-1710.
- Hirayama, D., K. Ito, K. Yamamoto, and S. Fujii. 2019. Forest dieback proceeds rapidly around the coastal lake Sugari-oike in Owase City, Japan. *Journal of Forest Research*.
- Holzwarth, F., A. Kahl, J. Bauhus, and C. Wirth. 2013. Many ways to die - partitioning tree mortality dynamics in a near-natural mixed deciduous forest. *Journal of Ecology* **101**:220-230.
- Hosmer Jr, D. W., S. Lemeshow, and R. X. Sturdivant. 2013. Applied logistic regression. John Wiley & Sons.
- Hülsmann, L., H. Bugmann, M. Cailleret, and P. Brang. 2018. How to kill a tree: empirical mortality models for 18 species and their performance in a dynamic forest model. *Ecological Applications* **28**:522-540.
- IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

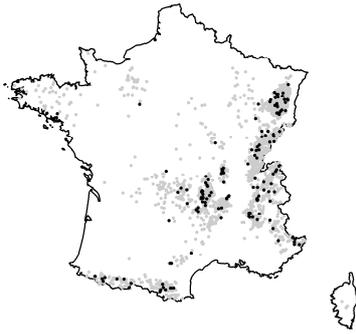
- Jaime, L., E. Batllori, J. Margalef-Marrase, M. Á. Pérez Navarro, and F. Lloret. 2019. Scots pine (*Pinus sylvestris* L.) mortality is explained by the climatic suitability of both host tree and bark beetle populations. *Forest Ecology and Management* **448**:119-129.
- Klein, T., and H. Hartmann. 2018. Climate change drives tree mortality. *Science* **362**:758-758.
- Latham, P. A., H. R. Zuuring, and D. W. Coble. 1998. A method for quantifying vertical forest structure. *Forest Ecology and Management* **104**:157-170.
- Laurance, W. F., and G. B. Williamson. 2001. Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. *Conservation Biology* **15**:1529-1535.
- Lazaro-Nogal, A., S. Matesanz, L. Hallik, A. Krasnova, A. Traveset, and F. Valladares. 2016. Population differentiation in a Mediterranean relict shrub: the potential role of local adaptation for coping with climate change. *Oecologia* **180**:1075-1090.
- Lebourgeois, F., P. Eberle, P. Merian, and I. Seynave. 2014. Social status-mediated tree-ring responses to climate of *Abies alba* and *Fagus sylvatica* shift in importance with increasing stand basal area. *Forest Ecology and Management* **328**:209-218.
- Lindenmayer, D. B., and W. F. Laurance. 2017. The ecology, distribution, conservation and management of large old trees. *Biological Reviews* **92**:1434-1458.
- Lindenmayer, D. B., W. F. Laurance, J. F. Franklin, G. E. Likens, S. C. Banks, W. Blanchard, P. Gibbons, K. Ikin, D. Blair, L. McBurney, A. D. Manning, and J. A. R. Stein. 2014. New Policies for Old Trees: Averting a Global Crisis in a Keystone Ecological Structure. *Conservation Letters* **7**:61-69.
- Linder, P., and L. Östlund. 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. *Biological Conservation* **85**:9-19.
- Lindo, Z., and J. A. Whiteley. 2011. Old trees contribute bio-available nitrogen through canopy bryophytes. *Plant and Soil* **342**:141-148.
- Luo, Y., and H. Y. H. Chen. 2011. Competition, species interaction and ageing control tree mortality in boreal forests. *Journal of Ecology* **99**:1470-1480.
- Luo, Y., and H. Y. H. Chen. 2015. Climate change-associated tree mortality increases without decreasing water availability. *Ecology Letters* **18**:1207-1215.
- Lutz, J. A., T. J. Furniss, D. J. Johnson, S. J. Davies, D. Allen, A. Alonso, K. J. Anderson-Teixeira, A. Andrade, J. Baltzer, K. M. L. Becker, E. M. Blomdahl, N. A. Bourg, S. Bunyavejchewin, D. F. R. P. Burslem, C. A. Cansler, K. Cao, M. Cao, D. Cárdenas, L.-W. Chang, K.-J. Chao, W.-C. Chao, J.-M. Chiang, C. Chu, G. B. Chuyong, K. Clay, R. Condit, S. Cordell, H. S. Dattaraja, A. Duque, C. E. N. Ewango, G. A. Fischer, C. Fletcher, J. A. Freund, C. Giardina, S. J. Germain, G. S. Gilbert, Z. Hao, T. Hart, B. C. H. Hau, F. He, A. Hector, R. W. Howe, C.-F. Hsieh, Y.-H. Hu, S. P. Hubbell, F. M. Inman-Narahari, A. Itoh, D. Janík, A. R. Kassim, D. Kenfack, L. Korte, K. Král, A. J. Larson, Y. Li, Y. Lin, S. Liu, S. Lum, K. Ma, J.-R. Makana, Y. Malhi, S. M. McMahon, W. J. McShea, H. R. Memiaghe, X. Mi, M. Morecroft, P. M. Musili, J. A. Myers, V. Novotny, A. de Oliveira, P. Ong, D. A. Orwig, R. Ostertag, G. G. Parker, R. Patankar, R. P. Phillips, G. Reynolds, L. Sack, G.-Z. M. Song, S.-H. Su, R. Sukumar, I.-F. Sun, H. S. Suresh, M. E. Swanson, S. Tan, D. W. Thomas, J. Thompson, M. Uriarte, R. Valencia, A. Vicentini, T. Vrška, X. Wang, G. D. Weiblen, A. Wolf, S.-H. Wu, H. Xu, T. Yamakura, S. Yap, and J. K. Zimmerman. 2018. Global importance of large-diameter trees. *Global Ecology And Biogeography* **27**:849-864.
- Marini, L., B. Økland, A. M. Jönsson, B. Bentz, A. Carroll, B. Forster, J.-C. Grégoire, R. Hurling, L. M. Nageleisen, S. Netherer, H. P. Ravn, A. Weed, and M. Schroeder. 2017. Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. *ECOGRAPHY* **40**:1426-1435.
- Martin-Benito, D., P. Cherubini, M. del Rio, and I. Canellas. 2010. Growth response to climate and drought in *Pinus nigra* Arn. trees of different crown classes (vol 22, pg 363, 2008). *Trees-Structure and Function* **24**:195-197.
- McDowell, N. G., and C. D. Allen. 2015. Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change* **5**:669.

- McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution* **26**:523-532.
- McDowell, N. G., A. P. Williams, C. Xu, W. T. Pockman, L. T. Dickman, S. Sevanto, R. Pangle, J. Limousin, J. Plaut, D. S. Mackay, J. Ogee, J. C. Domec, C. D. Allen, R. A. Fisher, X. Jiang, J. D. Muss, D. D. Breshears, S. A. Rauscher, and C. Koven. 2016. Multi-scale predictions of massive conifer mortality due to chronic temperature rise. *Nature Climate Change* **6**:295-300.
- Memiaghe, H. R., J. A. Lutz, L. Korte, A. Alonso, and D. Kenfack. 2016. Ecological Importance of Small-Diameter Trees to the Structure, Diversity and Biomass of a Tropical Evergreen Forest at Rabi, Gabon. *Plos ONE* **11**.
- Monserud, R. A., and H. Sterba. 1999. Modeling individual tree mortality for Austrian forest species. *Forest Ecology and Management* **113**:109-123.
- Muller, C. J., and R. F. MacLehose. 2014. Estimating predicted probabilities from logistic regression: different methods correspond to different target populations. *International Journal of Epidemiology* **43**:962-970.
- Nepstad, D. C., C. R. de Carvalho, E. A. Davidson, P. H. Jipp, P. A. Lefebvre, G. H. Negreiros, E. D. da Silva, T. A. Stone, S. E. Trumbore, and S. Vieira. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* **372**:666.
- Nepstad, D. C., I. M. Tohver, D. Ray, P. Moutinho, and G. Cardinot. 2007. Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology* **88**:2259-2269.
- Neumann, M., V. Mues, A. Moreno, H. Hasenauer, and R. Seidl. 2017. Climate variability drives recent tree mortality in Europe. *Global Change Biology* **23**:4788-4797.
- Peng, C. H., Z. H. Ma, X. D. Lei, Q. Zhu, H. Chen, W. F. Wang, S. R. Liu, W. Z. Li, X. Q. Fang, and X. L. Zhou. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change* **1**:467-471.
- Pfeifer, E. M., J. A. Hicke, and A. J. Meddens. 2011. Observations and modeling of aboveground tree carbon stocks and fluxes following a bark beetle outbreak in the western United States. *Global Change Biology* **17**:339-350.
- Phillips, O. L., L. E. Aragão, S. L. Lewis, J. B. Fisher, J. Lloyd, G. López-González, Y. Malhi, A. Monteagudo, J. Peacock, and C. A. Quesada. 2009. Drought sensitivity of the Amazon rainforest. *Science* **323**:1344-1347.
- Pichler, P., and W. Oberhuber. 2007. Radial growth response of coniferous forest trees in an inner Alpine environment to heat-wave in 2003. *Forest Ecology and Management* **242**:688-699.
- Piedallu, C., J.-C. Gégout, F. Lebourgeois, and I. Seynave. 2016. Soil aeration, water deficit, nitrogen availability, acidity and temperature all contribute to shaping tree species distribution in temperate forests. *Journal of Vegetation Science* **27**:387-399.
- Pretzsch, H., G. Schütze, and E. Uhl. 2013. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biology* **15**:483-495.
- Pureswaran, D. S., A. Roques, and A. Battisti. 2018. Forest Insects and Climate Change. *Current Forestry Reports* **4**:35-50.
- Remm, J., and A. Löhmus. 2011. Tree cavities in forests—the broad distribution pattern of a keystone structure for biodiversity. *Forest Ecology and Management* **262**:579-585.
- Ruiz-Benito, P., E. R. Lines, L. Gomez-Aparicio, M. A. Zavala, and D. A. Coomes. 2013. Patterns and Drivers of Tree Mortality in Iberian Forests: Climatic Effects Are Modified by Competition. *Plos ONE* **8**.
- Ryan, M. G., N. Phillips, and B. J. Bond. 2006. The hydraulic limitation hypothesis revisited. *Plant, Cell & Environment* **29**:367-381.
- Schelhaas, M.-J., J. Fridman, G. M. Hengeveld, H. M. Henttonen, A. Lehtonen, U. Kies, N. Krajnc, B. Lerink, Á. N. Dhuháin, and H. Polley. 2018. Actual European forest management by region, tree species and owner based on 714,000 re-measured trees in national forest inventories. *Plos ONE* **13**:e0207151.

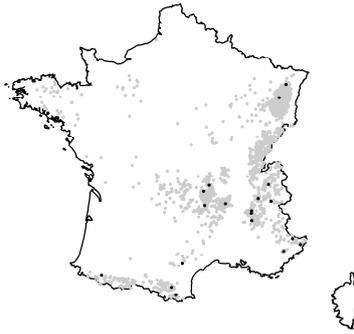
- Senf, C., D. Pflugmacher, Z. Q. Yang, J. Sebold, J. Knorn, M. Neumann, P. Hostert, and R. Seidl. 2018. Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nature Communications* **9**.
- Shenkin, A., B. Bolker, M. Pena-Claros, J. C. Licona, N. Ascarrunz, and F. E. Putz. 2018. Interactive effects of tree size, crown exposure and logging on drought-induced mortality. *Philosophical Transactions of the Royal Society B-Biological Sciences* **373**.
- Stovall, A. E. L., H. Shugart, and X. Yang. 2019. Tree height explains mortality risk during an intense drought. *Nature Communications* **10**.
- Taccoen, A., C. Piedallu, I. Seynave, V. Perez, A. Gegout-Petit, L. M. Nageleisen, J. D. Bontemps, and J. C. Gegout. 2019. Background mortality drivers of European tree species: climate change matters. *Proceedings of the Royal Society B-Biological Sciences* **286**.
- Ter Braak, C. J., and C. W. Looman. 1986. Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio* **65**:3-11.
- Thorpe, H., and L. Daniels. 2012. Long-term trends in tree mortality rates in the Alberta foothills are driven by stand development. *Canadian Journal of Forest Research* **42**:1687-1696.
- Trouvé, R., J.-D. Bontemps, C. Collet, I. Seynave, and F. Lebourgeois. 2014. Growth partitioning in forest stands is affected by stand density and summer drought in sessile oak and Douglas-fir. *Forest Ecology and Management* **334**:358-368.
- Turrell, F. M., and S. W. Austin. 1965. COMPARATIVE NOCTURNAL THERMAL BUDGETS OF LARGE AND SMALL TREES. *Ecology* **46**:25-34.
- van Mantgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fule, M. E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor, and T. T. Veblen. 2009. Widespread Increase of Tree Mortality Rates in the Western United States. *Science* **323**:521-524.
- Vincent, J. B., B. Henning, S. Saulei, G. Sosanika, and G. D. Weiblen. 2015. Forest carbon in lowland Papua New Guinea: Local variation and the importance of small trees. *Austral Ecology* **40**:151-159.
- Wutzler, T., C. Wirth, and J. Schumacher. 2008. Generic biomass functions for Common beech (*Fagus sylvatica*) in Central Europe: predictions and components of uncertainty. *Canadian Journal of Forest Research* **38**:1661-1675.

## APPENDIX

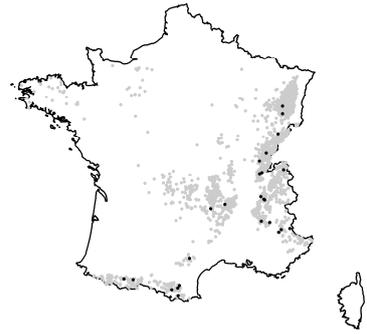
*Abies alba* - Suppressed trees  
24 cm <= Circ < 151



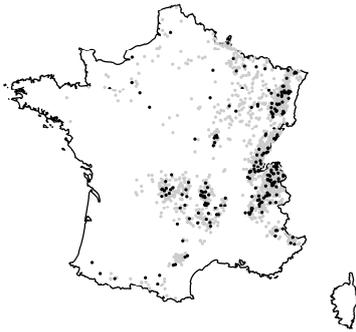
*Abies alba* - Small trees  
26 cm <= Circ < 118



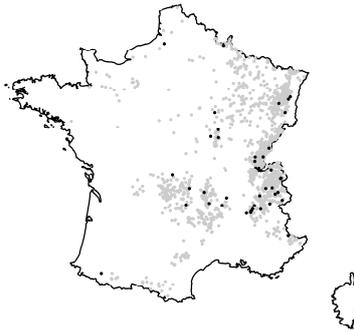
*Abies alba* - Large trees  
118 <= c13 < 207



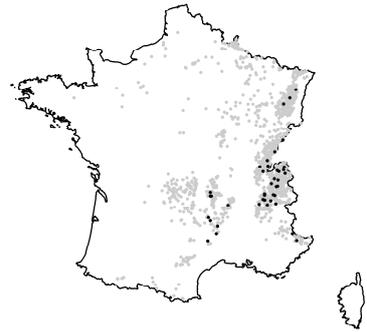
*Picea abies* - Suppressed trees  
24 cm <= Circ < 146



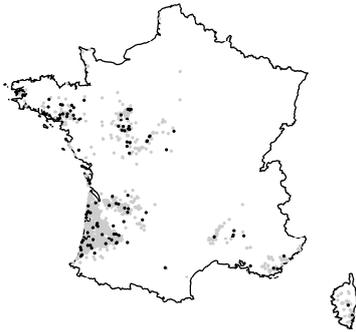
*Picea abies* - Small trees  
26 cm <= Circ < 104



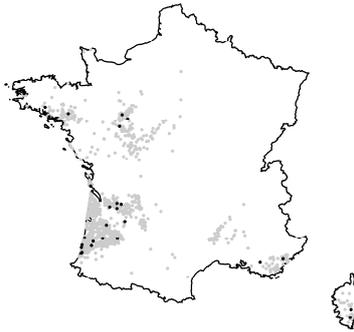
*Picea abies* - Large trees  
104 <= c13 < 223



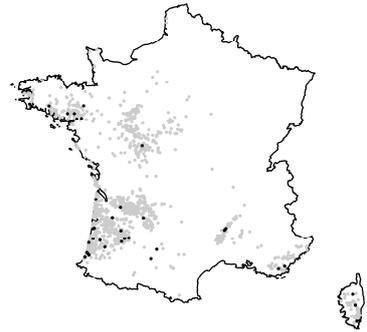
*Pinus pinaster* - Suppressed trees  
24 cm <= Circ < 151



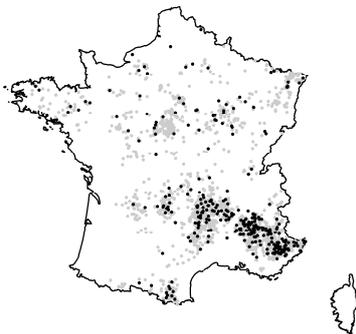
*Pinus pinaster* - Small trees  
26 cm <= Circ < 103



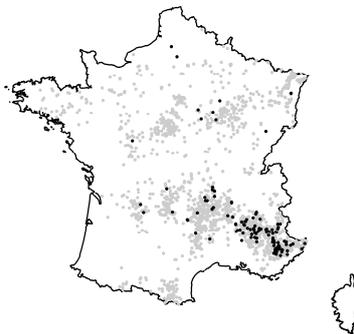
*Pinus pinaster* - Large trees  
103 <= c13 < 262



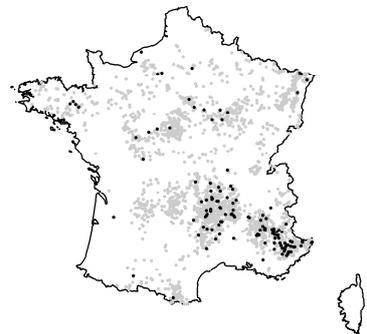
*Pinus sylvestris* - Suppressed trees  
24 cm <= Circ < 126

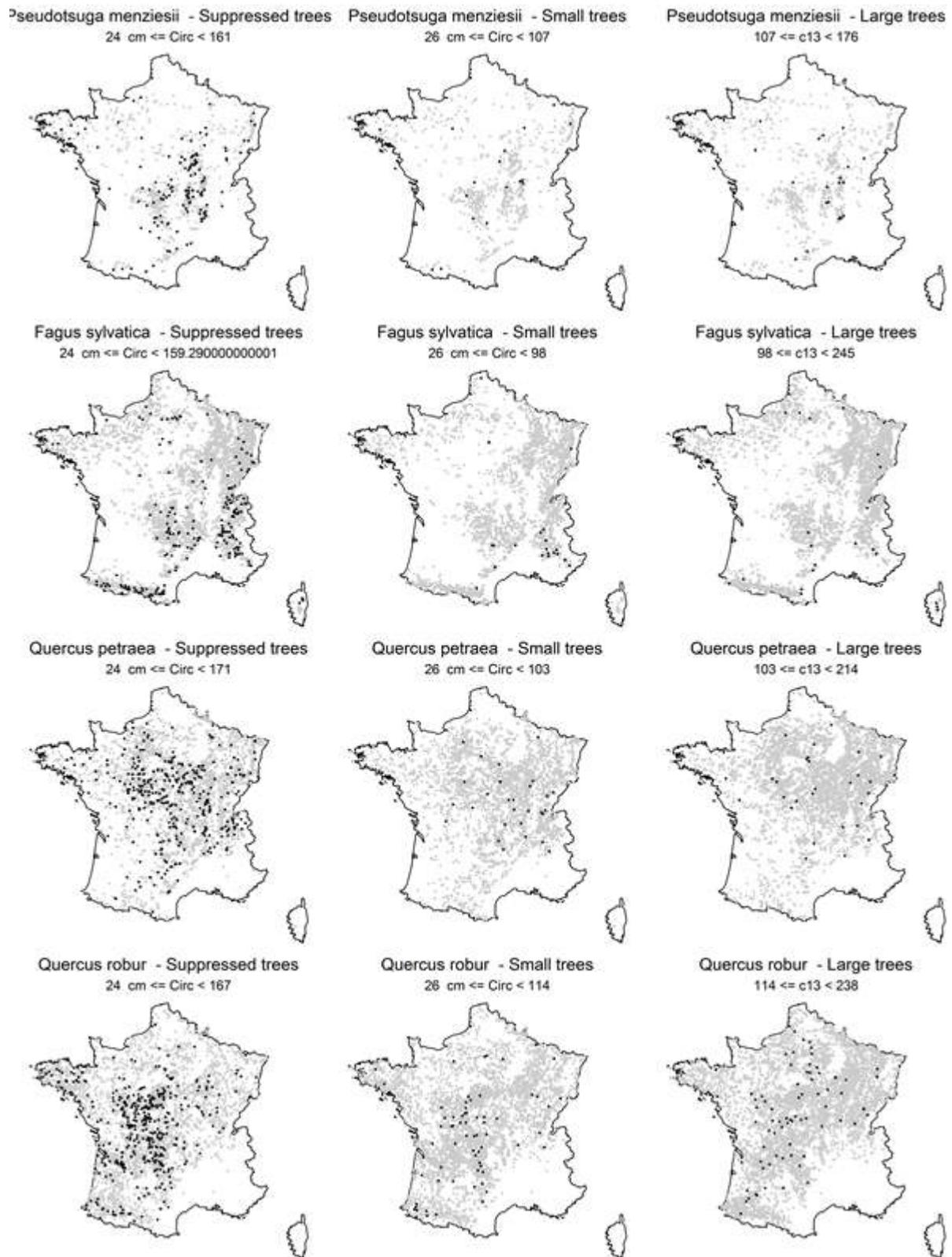


*Pinus sylvestris* - Small trees  
26 cm <= Circ < 88.5



*Pinus sylvestris* - Large trees  
88.5 <= c13 < 166





**Appendix A:** For the eight species studied, location of the plots on which the species is present (grey dots) and with at least one dead tree (black dots), for the suppressed, small and large dominant tree subsets.

Abies alba			
	Suppressed	Dominant - Small	Dominant - Large
Live	7729	5470	7818
Dead	187	26	26

Picea abies			
	Suppressed	Dominant - Small	Dominant - Large
Live	7203	6000	7839
Dead	376	54	56

Pinus pinaster			
	Suppressed	Dominant - Small	Dominant - Large
Live	4818	4691	5698
Dead	170	45	47

Pinus sylvestris			
	Suppressed	Dominant - Small	Dominant - Large
Live	6722	6945	9432
Dead	423	149	148

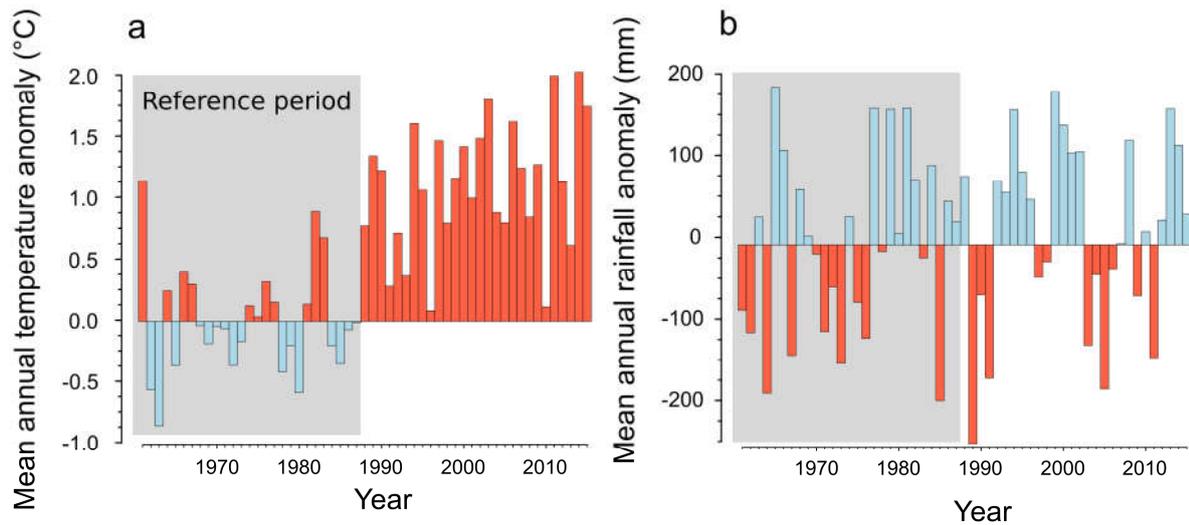
Pseudotsuga menziesii			
	Suppressed	Dominant - Small	Dominant - Large
Live	3468	2972	3611
Dead	191	20	22

Fagus sylvatica			
	Suppressed	Dominant - Small	Dominant - Large
Live	16876	9342	13543
Dead	296	25	24

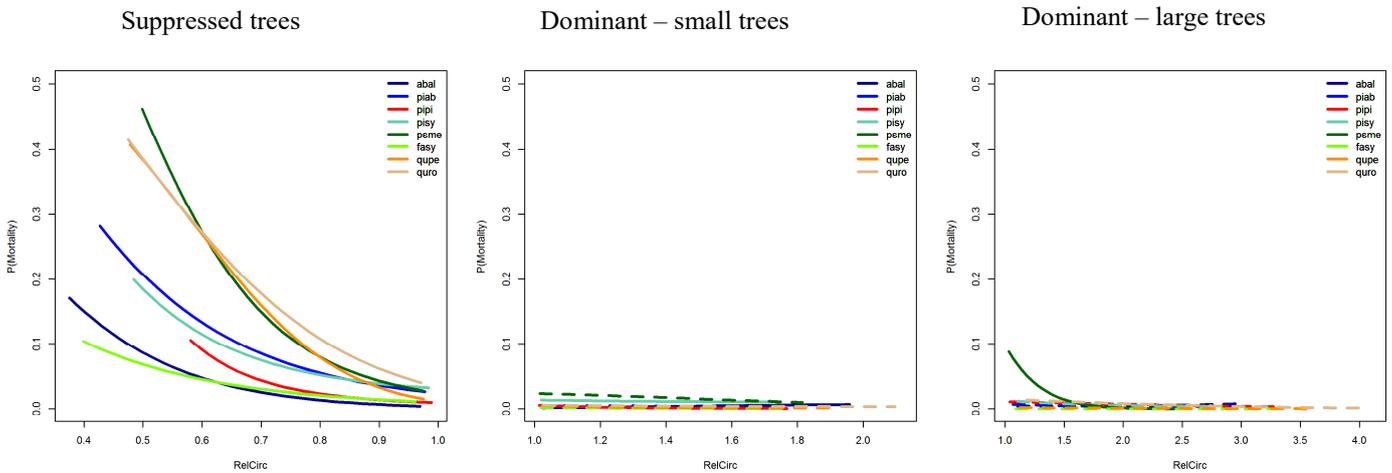
Quercus petraea			
	Suppressed	Dominant - Small	Dominant - Large
Live	10658	11298	15194
Dead	500	30	30

Quercus robur			
	Suppressed	Dominant - Small	Dominant - Large
Live	9467	11258	15524
Dead	547	76	76

**Appendix B:** Number of live and dead trees for suppressed, small and large dominant trees per species.

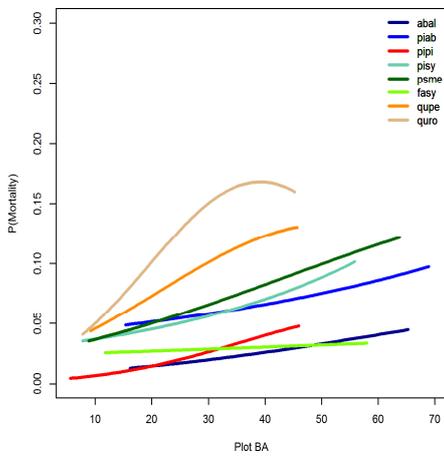


**Appendix C:** Changes between 1961 and 2015. (a) for temperature ( $^{\circ}\text{C}$ ); (b) for rainfall (mm). The period 1961-1987 was considered as the reference period before temperature increase.

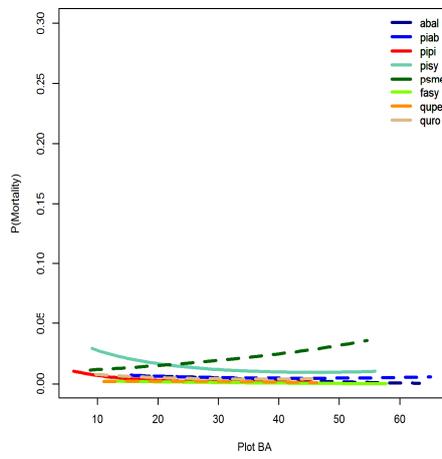


**Appendix D:** Modelled probability of background mortality as a function of relative tree circumference (RelCirc) for the suppressed, small dominant and large dominant tree subsets. We varied the RelCirc variable, whereas the other model variables were set to their average values. Dashed lines are shown when the variable was not significant ( $p > 0.05$ ). abal = *Abies alba*, piab = *Picea abies*, pipi = *Pinus pinaster*, pisy = *Pinus sylvestris*, psme = *Pseudotsuga menziesii*, fasy = *Fagus sylvatica*, qupe = *Quercus petraea*, quro = *Quercus robur*.

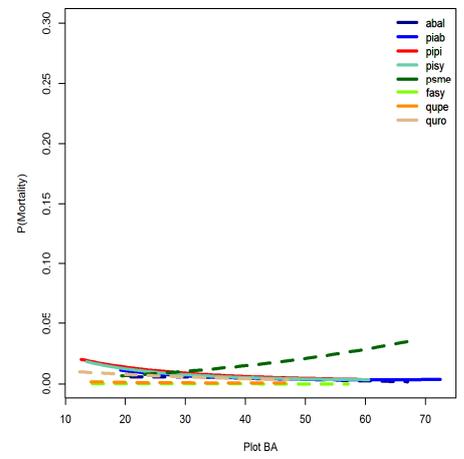
Suppressed trees



Dominant – small trees

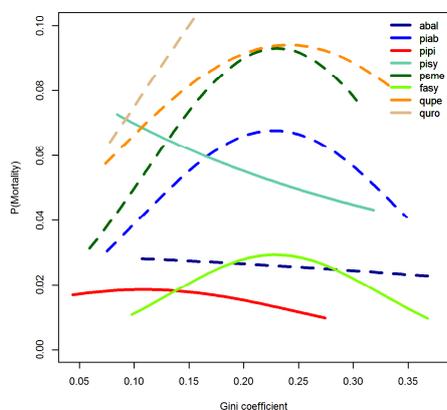


Dominant – large trees

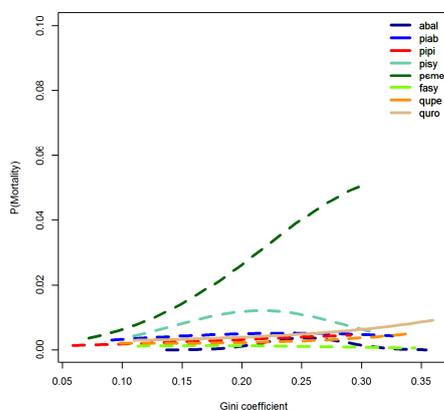


**Appendix E:** Modelled probability of background mortality as a function of plot basal area (BA) for the suppressed, small dominant and large dominant tree subsets. We varied the BA variable, whereas the other model variables were set to their average values. Dashed lines are shown when the variable was not significant ( $p > 0.05$ ). abal = *Abies alba*, piab = *Picea abies*, pipi = *Pinus pinaster*, pisy = *Pinus sylvestris*, psme = *Pseudotsuga menziesii*, fasy = *Fagus sylvatica*, qupe = *Quercus petraea*, quro = *Quercus robur*.

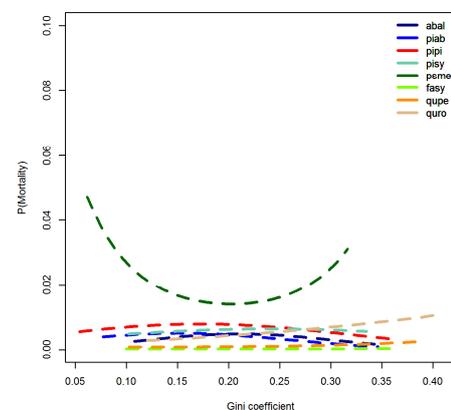
Suppressed trees



Dominant – small trees

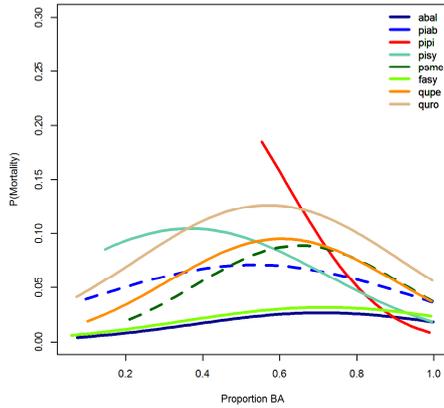


Dominant – large trees

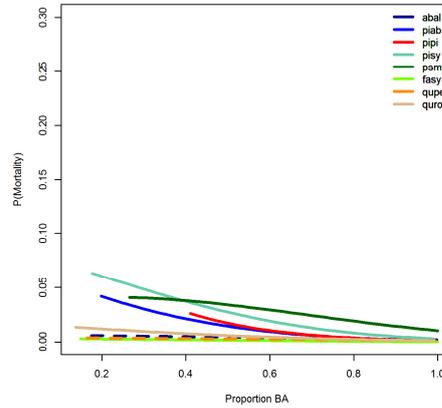


**Appendix F:** Modelled probability of background mortality as a function of the Gini coefficient for the suppressed, small dominant and large dominant tree subsets. We varied the Gini variable, whereas the other model variables were set to their average values. Dashed lines are shown when the variable was not significant ( $p > 0.05$ ). abal = *Abies alba*, piab = *Picea abies*, pipi = *Pinus pinaster*, pisy = *Pinus sylvestris*, psme = *Pseudotsuga menziesii*, fasy = *Fagus sylvatica*, qupe = *Quercus petraea*, quro = *Quercus robur*.

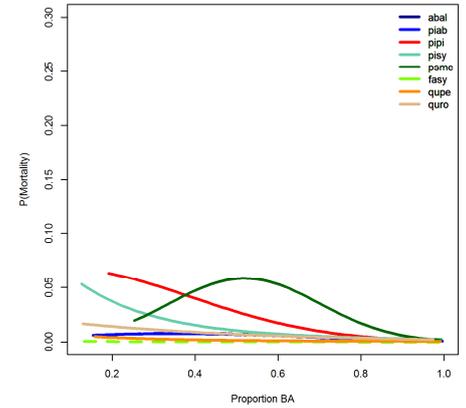
Suppressed trees



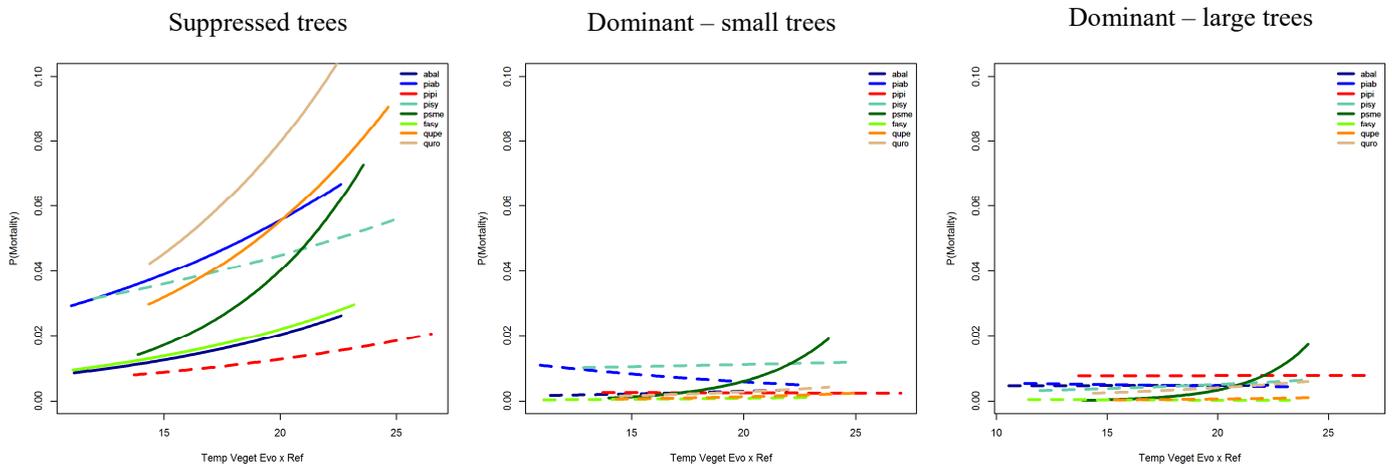
Dominant – small trees



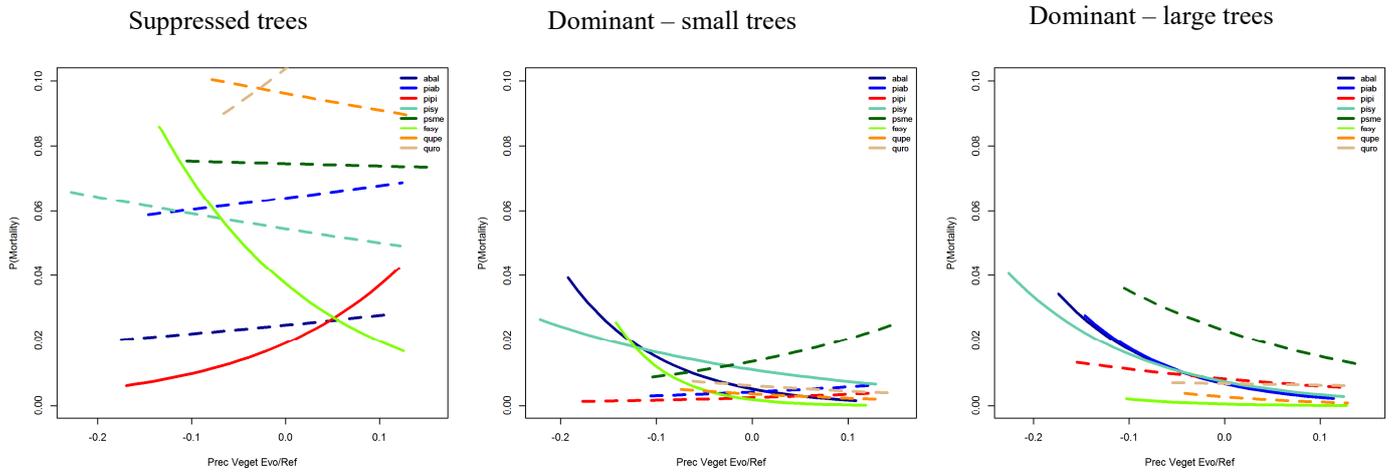
Dominant – large trees



**Appendix G:** Modelled probability of mortality as a function of the proportion of basal area (PropBA) occupied by the species on the plot for the suppressed, small dominant and large dominant tree subsets. We varied the PropBA variable, whereas the other model variables were set to their average values. Dashed lines are shown when the variable was not significant ( $p > 0.05$ ). abal = *Abies alba*, piab = *Picea abies*, pipi = *Pinus pinaster*, pisy = *Pinus sylvestris*, psme = *Pseudotsuga menziesii*, fasy = *Fagus sylvatica*, qupe = *Quercus petraea*, quro = *Quercus robur*.



**Appendix H:** Modelled probability of background mortality as a function of temperature evolution for the vegetation period ( $T^{\circ}\text{Evo}$ ) for the suppressed, small dominant and large dominant tree subsets. We varied the  $T^{\circ}\text{Evo}$  variable, whereas the other model variables were set to their average values. Dashed lines are shown when the variable was not significant ( $p > 0.05$ ). abal = *Abies alba*, piab = *Picea abies*, pipi = *Pinus pinaster*, pisy = *Pinus sylvestris*, psme = *Pseudotsuga menziesii*, fasy = *Fagus sylvatica*, qupe = *Quercus petraea*, quro = *Quercus robur*



**Appendix I:** Modelled probability of background mortality as a function of rainfall evolution for the vegetation period ( $Rf^{\circ}Evo$ ) for the suppressed, small dominant and large dominant tree subsets. We varied the  $Rf^{\circ}Evo$  variable, whereas the other model variables were set to their average values. Dashed lines are shown when the variable was not significant ( $p > 0.05$ ). abal = *Abies alba*, piab = *Picea abies*, pipi = *Pinus pinaster*, pisy = *Pinus sylvestris*, psme = *Pseudotsuga menziesii*, fasy = *Fagus sylvatica*, qupe = *Quercus petraea*, quro = *Quercus robur*

	Abies alba						Picea abies					
	Suppressed		Dominant - small		Dominant - large		Suppressed		Dominant - small		Dominant - large	
	coeffs	pval	coeffs	pval	coeffs	pval	coeffs	pval	coeffs	pval	coeffs	pval
(Intercept)	-4.82	NA	-35.06	NA	-8.62	NA	-3.15	NA	-7.33	NA	-1.57	NA
RelCirc	-5.81	p < 0.0001	4.70	p < 0.05	-0.55	p = 0.26	-6.96	p < 0.0001	9.20	p = 0.46	-1.75	p = 0.66
RelCirc <sup>2</sup>	-0.53	p = 0.63	-1.09	p = 0.34	0.20	p = 0.72	1.50	p = 0.52	-3.89	p = 0.36	0.38	p = 0.08
BA	0.04	p < 0.0001	0.02	p = 0.09	0.03	p = 0.25	0.01	p < 0.0001	-0.04	p = 0.43	-0.08	p < 0.05
BA <sup>2</sup>	0.00	p = 0.4	0.00	p = 0.34	0.00	p = 0.6	0.00	p = 0.73	0.00	p = 0.39	0.00	p = 0.18
Trails	-0.16	p = 0.62	-0.67	p < 0.05	0.88	p = 0.18	0.01	p = 0.21	0.40	p = 0.3	0.14	p = 0.74
Trails_Coeff2	0.08	NA	0.59	NA	-0.01	NA	0.35	NA	0.29	NA	-0.04	NA
PropBA	6.51	p < 0.001	-0.40	p = 0.14	4.35	p = 0.06	3.51	p = 0.28	-2.61	p < 0.0001	3.66	p < 0.001
PropBA <sup>2</sup>	-4.59	p < 0.001	-0.73	p = 0.52	-5.64	p = 0.18	-3.28	p < 0.0001	-1.44	p = 0.46	-5.23	p < 0.05
Gini	-0.29	p = 0.44	204.62	p = 0.36	24.71	p = 0.6	16.46	p = 0.34	11.06	p = 0.7	13.26	p = 0.29
Gini <sup>2</sup>	-1.13	p = 0.69	-404.49	p < 0.001	-58.55	p = 0.2	-36.20	p < 0.001	-23.03	p = 0.49	-43.74	p = 0.17
T°Evo	0.10	p < 0.01	0.06	p = 0.7	0.00	p = 0.63	0.07	p < 0.01	-0.07	p = 0.41	-0.02	p = 0.33
RfEvo	1.16	p = 0.58	-10.75	p < 0.01	-9.54	p < 0.05	0.62	p = 0.64	3.11	p = 0.43	-9.77	p < 0.01

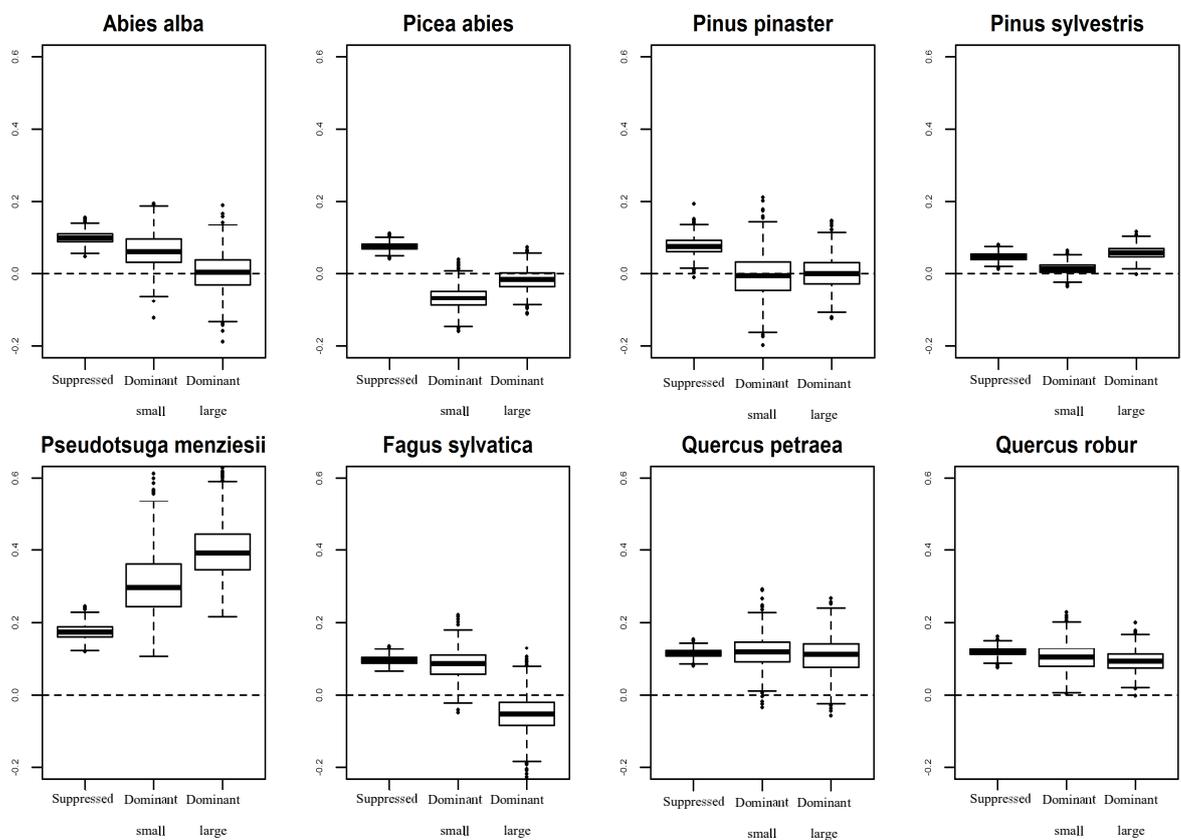
	Pinus pinaster						Pinus sylvestris					
	Suppressed		Dominant - small		Dominant - large		Suppressed		Dominant - small		Dominant - large	
	coeffs	pval	coeffs	pval	coeffs	pval	coeffs	pval	coeffs	pval	coeffs	pval
(Intercept)	3.17	NA	6.22	NA	-1.82	NA	1.43	NA	-4.36	NA	-0.18	NA
RelCirc	-16.48	p < 0.0001	-8.21	p < 0.05	-0.28	p = 0.46	-10.15	p < 0.0001	-1.45	p < 0.01	-1.69	p = 0.07
RelCirc <sup>2</sup>	6.64	p = 0.21	2.05	p < 0.05	-0.05	p = 0.2	4.17	p < 0.05	0.40	p = 0.45	0.27	p = 0.36
BA	0.10	p < 0.0001	-0.13	p < 0.05	-0.07	p < 0.001	0.02	p < 0.0001	-0.08	p < 0.001	-0.08	p < 0.0001
BA <sup>2</sup>	0.00	p = 0.18	0.00	p < 0.01	0.00	p = 0.36	0.00	p = 0.66	0.00	p = 0.17	0.00	p = 0.14
Trails	-0.05	p < 0.05	0.31	p = 0.57	0.94	p = 0.05	-0.11	p = 0.23	0.04	p < 0.0001	0.04	p < 0.05
Trails_Coeff2	-0.99	NA	-0.45	NA	0.05	NA	0.27	NA	0.87	NA	0.44	NA
PropBA	5.69	p < 0.0001	-3.93	p < 0.0001	0.49	p < 0.0001	3.38	p < 0.0001	-1.25	p < 0.0001	-5.65	p < 0.0001
PropBA <sup>2</sup>	-8.50	p < 0.0001	-0.91	p = 0.3	-4.75	p = 0.12	-4.60	p < 0.0001	-2.15	p = 0.1	1.90	p = 0.22
Gini	5.03	p < 0.01	8.15	p = 0.19	8.57	p = 0.51	-2.97	p < 0.05	39.46	p = 0.55	7.10	p = 0.71
Gini <sup>2</sup>	-23.33	p = 0.09	-8.71	p = 0.65	-24.75	p = 0.35	1.53	p = 0.76	-91.25	p < 0.001	-14.72	p = 0.28
T°Evo	0.07	p = 0.48	-0.01	p = 0.47	0.00	p = 0.54	0.05	p = 0.06	0.01	p = 0.69	0.06	p = 0.46
RfEvo	6.76	p < 0.01	3.51	p = 0.41	-3.13	p = 0.41	-0.89	p = 0.31	-4.02	p < 0.01	-7.72	p < 0.0001

	Pseudotsuga menziesii					
	Suppressed		Dominant - small		Dominant - large	
	coeffs	pval	coeffs	pval	coeffs	pval
(Intercept)	-5.34	NA	-14.78	NA	-10.92	NA
RelCirc	-11.08	p < 0.0001	0.72	p = 0.47	-2.64	p < 0.05
RelCirc <sup>2</sup>	2.66	p = 0.72	-0.63	p = 0.66	-0.54	p = 0.54
BA	0.04	p < 0.001	0.02	p = 0.1	0.05	p = 0.13
BA <sup>2</sup>	0.00	p = 0.44	0.00	p = 0.69	0.00	p = 0.72
Trails	-0.15	p = 0.44	-0.11	p = 0.48	0.52	p = 0.38
Trails_Coeff2	0.25	NA	-15.18	NA	-13.79	NA
PropBA	10.15	p = 0.11	0.88	p < 0.05	16.68	p < 0.05
PropBA <sup>2</sup>	-7.78	p < 0.0001	-2.19	p = 0.23	-16.06	p < 0.05
Gini	18.16	p = 0.53	26.21	p = 0.13	-25.45	p = 0.69
Gini <sup>2</sup>	-39.41	p < 0.05	-38.80	p = 0.46	62.75	p = 0.33

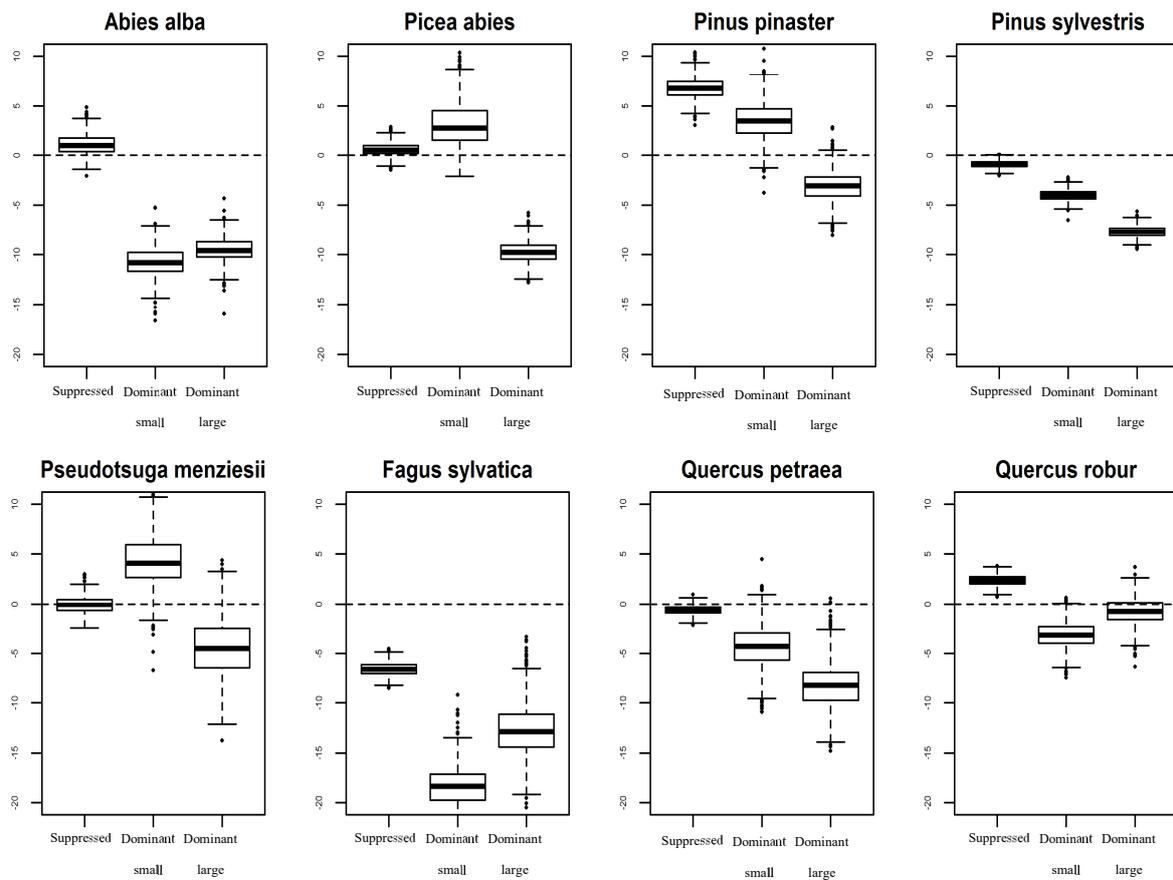
	Fagus sylvatica						Quercus petraea					
	Suppressed		Dominant - small		Dominant - large		Suppressed		Dominant - small		Dominant - large	
	coeffs	pval	coeffs	pval	coeffs	pval	coeffs	pval	coeffs	pval	coeffs	pval
(Intercept)	-7.59	NA	-3.46	NA	-2.42	NA	-7.76	NA	-2.83	NA	-4.33	NA
RelCirc	-5.49	p < 0.0001	-4.05	p = 0.56	-0.84	p = 0.34	2.18	p < 0.0001	-6.74	p = 0.64	-0.38	p = 0.67
RelCirc <sup>2</sup>	1.03	p = 0.72	1.03	p = 0.31	0.14	p = 0.4	-6.77	p < 0.0001	1.91	p = 0.16	-0.06	p = 0.7
BA	0.01	p < 0.05	-0.02	p < 0.05	-0.04	p = 0.65	0.07	p < 0.0001	0.05	p = 0.67	-0.05	p = 0.66
BA <sup>2</sup>	0.00	p = 0.47	0.00	p = 0.57	0.00	p = 0.47	0.00	p < 0.01	0.00	p = 0.43	0.00	p = 0.33
Trails	0.35	p < 0.0001	0.08	p = 0.06	-0.03	p < 0.01	0.27	p < 0.01	-0.07	p = 0.44	0.02	p = 0.76
Trails_Coeff2	0.79	NA	0.64	NA	1.36	NA	0.17	NA	0.48	NA	-0.69	NA
PropBA	5.47	p < 0.0001	-0.10	p < 0.05	-2.15	p = 0.38	8.02	p < 0.05	-0.21	p = 0.1	-4.78	p < 0.01
PropBA <sup>2</sup>	-3.82	p < 0.0001	-2.10	p = 0.51	0.80	p = 0.61	-6.62	p < 0.0001	-0.82	p = 0.62	2.25	p = 0.41
Gini	26.97	p < 0.05	9.50	p = 0.32	-6.47	p = 0.56	9.20	p = 0.69	-4.84	p = 0.18	-4.03	p = 0.34
Gini <sup>2</sup>	-58.85	p < 0.0001	-28.07	p = 0.42	16.86	p = 0.59	-19.09	p < 0.05	19.35	p = 0.5	15.53	p = 0.53
T°Evo	0.10	p < 0.01	0.08	p = 0.54	-0.05	p = 0.38	0.11	p < 0.0001	0.12	p = 0.23	0.11	p = 0.28
RfEvo	-6.57	p < 0.0001	-18.37	p < 0.001	-12.65	p < 0.05	-0.60	p = 0.61	-4.35	p = 0.37	-8.23	p = 0.16

	Quercus robur					
	Suppressed		Dominant - small		Dominant - large	
	coeffs	pval	coeffs	pval	coeffs	pval
(Intercept)	-6.83	NA	-4.21	NA	-5.43	NA
RelCirc	-3.42	p < 0.0001	-1.21	p = 0.46	-0.30	p = 0.19
RelCirc <sup>2</sup>	-1.59	p < 0.05	0.25	p = 0.65	-0.10	p = 0.15
BA	0.12	p < 0.0001	-0.07	p = 0.64	-0.03	p = 0.2
BA <sup>2</sup>	0.00	p < 0.0001	0.00	p = 0.22	0.00	p = 0.73
Trails	0.17	p = 0.24	-0.31	p = 0.65	0.07	p = 0.71
Trails_Coeff2	0.00	NA	-0.24	NA	-0.33	NA
PropBA	5.59	p < 0.05	-1.76	p < 0.0001	-2.31	p < 0.001
PropBA <sup>2</sup>	-4.89	p < 0.0001	-0.86	p = 0.49	-0.01	p = 0.69
Gini	11.29	p = 0.18	0.06	p < 0.05	6.16	p = 0.1
Gini <sup>2</sup>	-20.05	p < 0.05	9.45	p = 0.61	-2.98	p = 0.73
T°Evo	0.12	p < 0.001	0.11	p = 0.08	0.09	p = 0.14
RfEvo	2.37	p = 0.06	-3.14	p = 0.32	-0.76	p = 0.71

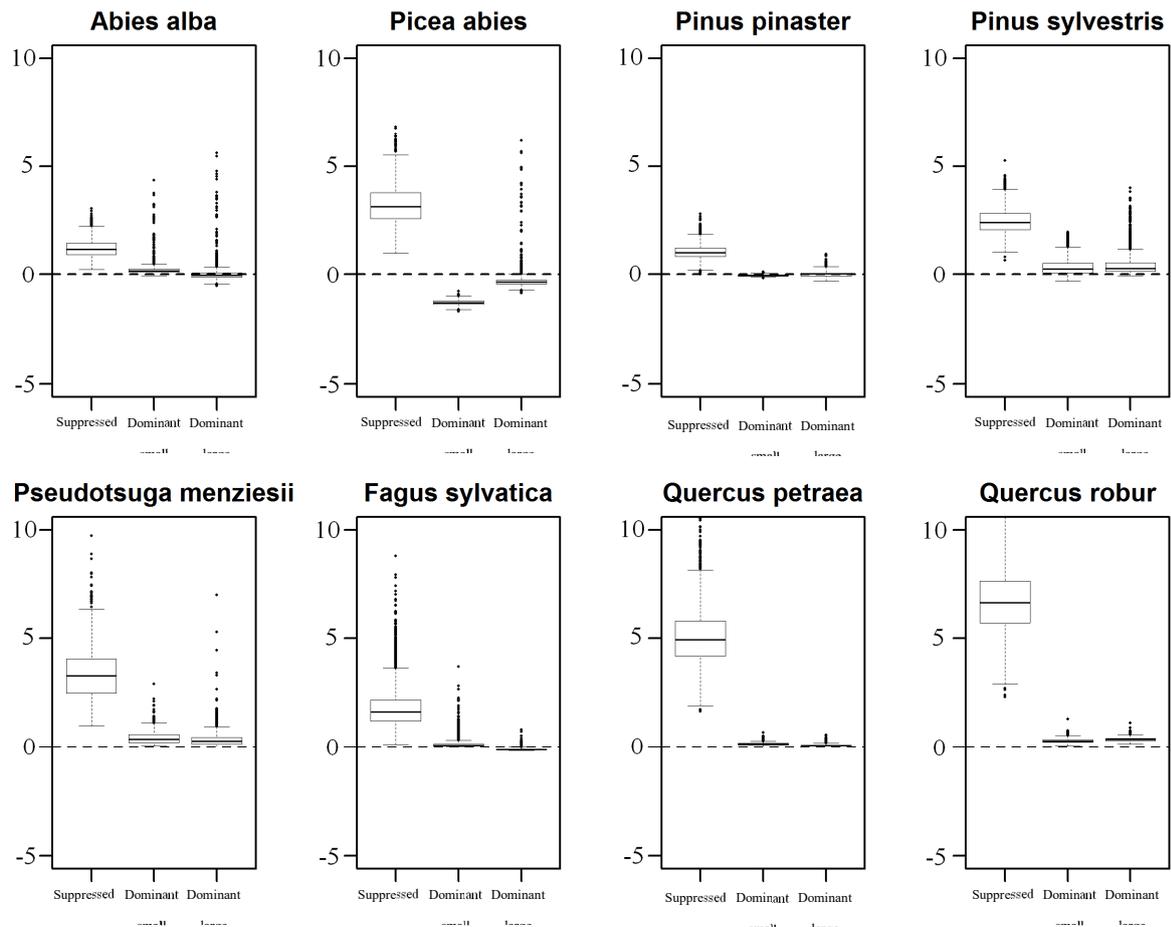
**Appendix J:** Coefficients and p-values for the variables used in the background mortality models for the suppressed, small dominant and large dominant trees subsets. Values were averaged from k-fold bootstraps (k = 1000).



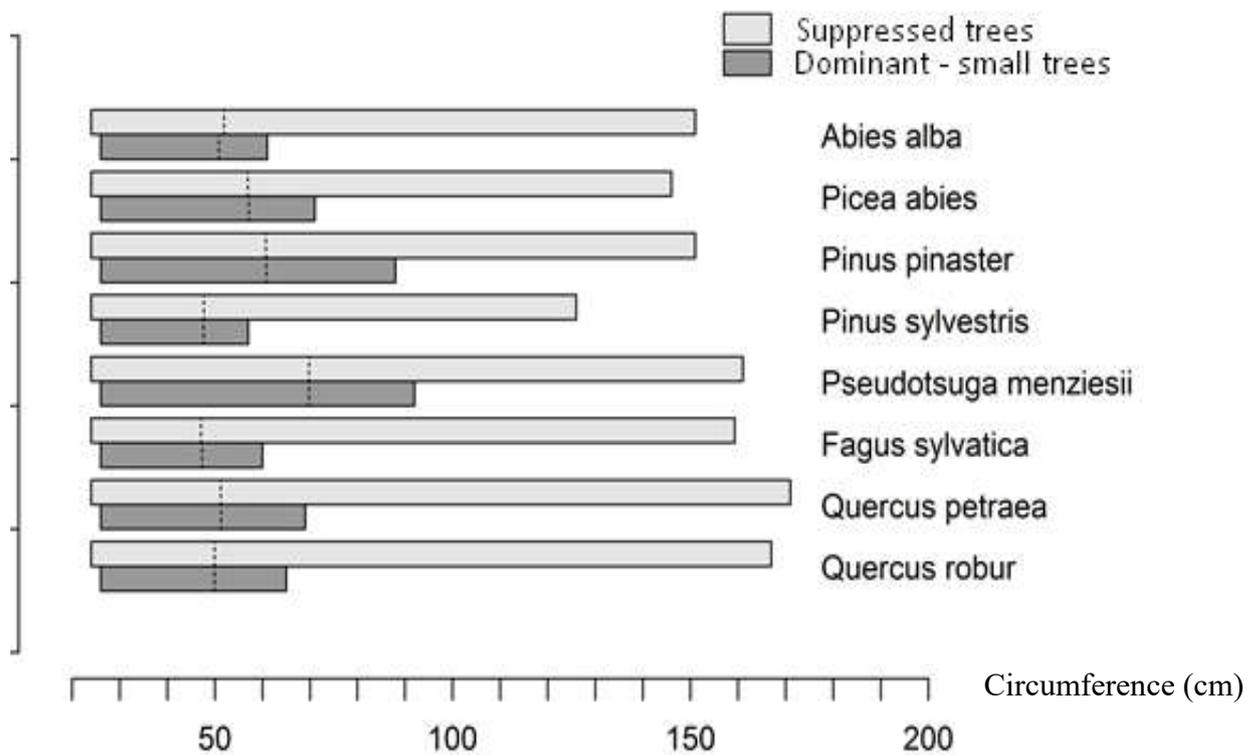
**Appendix K::** Coefficients of temperature evolution for the vegetation period ( $T^{\circ}\text{Evo}$ ) for the eight species and the suppressed, small dominant, and large dominant tree subsets. Each boxplot is composed of 1000 coefficient values obtained with a k-fold bootstrap on each of the eight species ( $k = 1000$ ). A positive value indicates an increasing probability of mortality in areas with warmer average reference temperatures from April to August, and that have experienced the most warming.



**Appendix L:** Coefficients of rainfall evolution for the vegetation period ( $Rf^{\circ}Evo$ ) for the eight species and the suppressed, small dominant, and large dominant tree subsets. Each boxplot is composed of 1000 coefficient values obtained with a k-fold bootstrap on each of the eight species ( $k = 1000$ ). A negative value indicates an increasing probability of mortality in areas with lower reference rainfall from April to August, and that have experienced the most rainfall decreases.

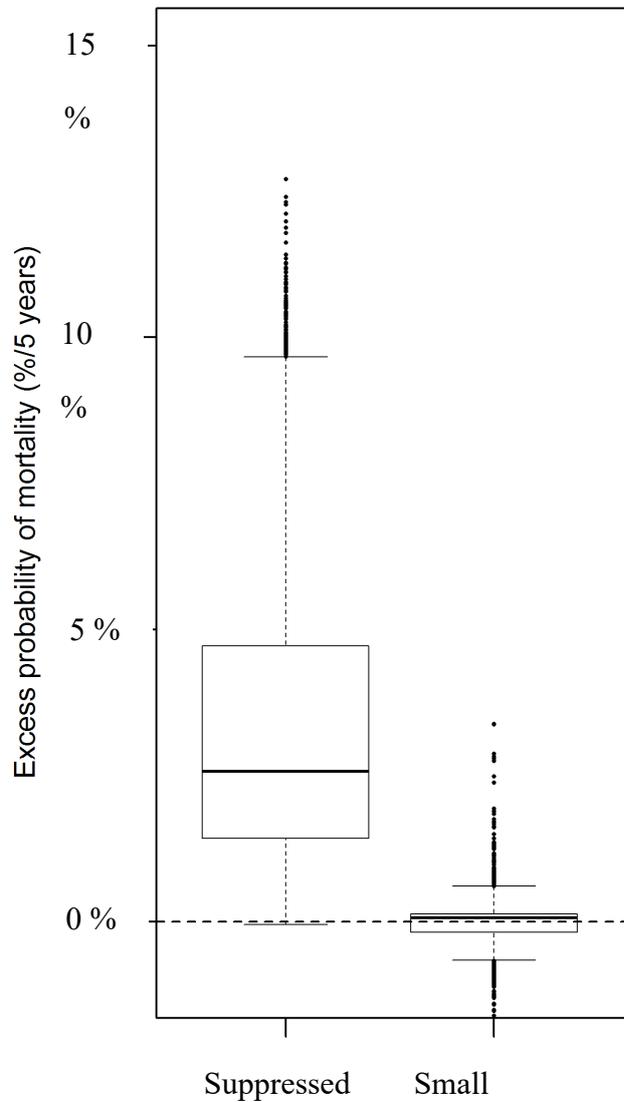


**Appendix M: Excess probability of mortality (%) attributed to combined temperature and rainfall changes for the suppressed, small dominant and large dominant tree subset.** The climate change-related excess probability of mortality is calculated as the difference between predicted values for the full model and a partial model where climate change-related effects have been set to 0. In order to assess the importance of the climate-change effects on tree mortality, all non-climate change-related variables were set to their mean value for all the trees of the considered species, while qualitative variables were set to their most frequent value.



**Appendix N:** Selection of two subsets of suppressed and dominant trees with equal average circumference to ensure that the differences in mortality were related to differences in social status: circumference (in cm) of the suppressed tree subset (light grey boxes), and small dominant tree subset (medium grey boxes). The dotted line represents the mean circumference value of all the trees in the considered box. The upper limit of the light grey and medium grey boxes represents the 1<sup>st</sup> and the 99<sup>th</sup> percentile of the distribution.

### Climate change-related excess probability of mortality



**Appendix O: Excess probability of mortality (%) due to combined temperature and rainfall changes for the suppressed and small dominant tree subsets with equal mean circumference.** It is calculated as the difference between predicted values for the full model and a partial model where climate change-related effects have been set to 0. For each model, all non-climate change-related variables were set to their mean value for all the trees of the considered species, while qualitative variables were set to their most frequent value.