Received: 26 January 2023 | Accepted: 13 July 2023
DOI: 10.1111/1365-2745.14184

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Competition-induced tree mortality across Europe is driven by shade tolerance, proportion of conspecifics and drought

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Funding information
Academy of Finland, Grant/Award Number: 344722; Agence Nationale de la Recherche, Grant/Award Number: ANR-20-EBI5-0005-03; BiodivClim ERA-net Cofund (joint BiodivERsA call); Bundesministerium für Bildung und Forschung, Grant/Award Number: 16LC2021A; HORIZON EUROPE European Innovation Ecosystems, Grant/Award Number: 101000574

Handling Editor: Giovanna Battipaglia

Abstract

1. Forest stand densities are increasing in the boreal and temperate biomes, suggesting that tree-tree competition is intensifying. Anticipating the consequences of this intensified competition is difficult because competition-induced mortality may depend not only on the occurrence of extreme climatic events such as drought, but also on stand composition, since tree species differ in their ability to compete and tolerate competition. A better understanding of the effects of stand composition and drought on competition-induced mortality would help to anticipate future changes in forest ecosystems.
2. We studied the tree-level probability of competition-induced mortality using National Forest Inventory data from three European countries (Finland, France and Germany), covering a latitudinal gradient from the Mediterranean to the Arctic. We investigated how (i) the proportion of conspecifics, (ii) the shade tolerance (ST) of the focal tree and its competitors and (iii) drought events modify the effect of competition on tree mortality. We used a generalized linear mixed model on a dataset of 461,109 trees representing 39 species on 48,088 individual plots.
3. Competition, measured as the basal area of larger trees, was a stronger driver of background mortality (BM) than tree size and climate. A higher proportion of conspecifics increased the competition effect on mortality, showing that conspecific individuals had a higher competitive effect compared to heterospecific individuals. The competition effect on mortality also increased as a function of the ST of neighbouring trees, suggesting an increased shading effect. A higher ST of a focal tree decreased the competition effect on mortality. Drought anomalies increased the competition effect, resulting in a higher mortality probability for the most suppressed trees.

4. *Synthesis*. Competition was the main driver of background mortality. Increasing stand density increased competition-induced tree mortality in both monospecific and mixed stands, but to different extents depending on the proportion of conspecifics and tree species shade tolerance (ST). Drought periods increase mortality, especially among the most suppressed trees, suggesting an interaction between competitive status and drought. Incorporating more detailed information on stand composition and tree species ST into tree mortality models will improve our understanding of forest dynamics in a changing climate.

KEYWORDS
background mortality, climate change, competition, functional ecology, plant–climate interactions, plant–plant interactions, shade tolerance, tree mortality

1 | INTRODUCTION

Tree mortality is a key process that affects forest composition, structure and dynamics (McDowell et al., 2020), influences ecosystem processes and services such as carbon cycling and storage (Thom & Seidl, 2016) and biodiversity (Gao et al., 2014). Recent evidence from Europe (Taccoen et al., 2019, 2021) and elsewhere (Bauman et al., 2022; van Mantgem et al., 2009) suggests that the baseline of tree mortality is changing in forest ecosystems. The observed changes in tree mortality rates are not only caused by the increase in the occurrence of severe disturbances (Senf et al., 2018), but also derive from changes in the rate of background mortality (BM) (Archambeau et al., 2020; Taccoen et al., 2019)—that is, tree mortality that occurs in the absence of severe disturbances (Das et al., 2016). The observed changes in forest structure, such as increased stand density and wood volume (Korhonen et al., 2020; Kuusela, 1994; Pretzsch et al., 2014), that are partly driven by climate change may—in part—explain the changing rates of BM by altering inter-tree competition (Lines et al., 2010). In the face of global change, safeguarding forest functionality and ecosystem service provisioning, promoting resilience to climate change and developing sustainable forest management practices demand a better understanding of BM.

In temperate and boreal biomes, competition among trees is one of the most important drivers of BM (Luo & Chen, 2011, 2015; Zhang et al., 2015), especially in the early successional stages and for suppressed and/or otherwise stressed trees (Franklin & Van Pelt, 2004; Oliver & Larson, 1996). Competition causes a reduction in resource availability for a tree, which may lead to a reduction in photosynthesis and ultimately tree death if the tree's respiratory needs are not met (regular mortality sensu Oliver & Larson, 1996). Competition may also drive tree mortality by weakening the ability of trees to defend themselves against disturbance agents such as insect pests (Franklin et al., 1987). Trees compete for both above-ground and below-ground resources. While trees compete primarily for light, in infertile or arid sites where light availability is not the main factor limiting tree growth, competition for soil resources may also drive tree mortality (Coomes & Grubb, 2000; Pretzsch & Biber, 2010). In all cases, trees that are relatively small and in a suppressed position experience increased competitive pressure due to limited light availability (Kulha et al., 2023; Peltoniemi & Mäkipää, 2011). This size-asymmetric competition results in higher mortality rates for suppressed trees than for dominant trees (Gendreau-Berthiaume et al., 2016; Kweon & Comeau, 2019; Luo & Chen, 2011).

Due to variation in morphological and physiological traits, tree species tolerate competition differently (Niinemets, 2010). For example, for trees of similar size, the probability of mortality due to size-asymmetric competition may vary depending on the shade tolerance (ST) of tree species (Kobe et al., 1995). In addition to being able to persist in suppression, shade-tolerant trees can build a deep, multilayered crown because they can sustain self-shading (Petrovska et al., 2021). Consequently, shade-tolerant species also intercept more solar radiation than shade-intolerant species with translucent crowns (Canham & Burbank, 1994; Leverenz & Hinckley, 1990; Petrovska et al., 2021). Due to the increased shading effect, shade-tolerant trees exert greater competitive pressure on neighbouring trees than shade-intolerant species. This may lead to increased size-asymmetric competition (Searle & Chen, 2020) and increased mortality in stands dominated by shade-tolerant species (Kobe et al., 1995).

The processes that influence the probability of competition-driven BM may be broadly divided into three categories. First, at the individual level, the largest trees are in the best position to harvest light (Kulha et al., 2023) and—in certain cases—water and nutrient resources (Forrester et al., 2022). Thus, the competitive pressure they exert increases with increasing tree size (i.e. size-asymmetric competition). Second, species-level competitive hierarchies, where species are ranked according to their competitive effects or responses, influence the probability of BM (Keddy, 2001). However, the competitive effect that dominant trees exert on neighbours may vary within and between tree species, depending on the ability of tree individuals to harvest above-ground and below-ground resources. This differential competitive effect may cause variability in mortality probabilities among relatively smaller neighbours. Third, according to the theory of limiting similarity, a tree may be less affected by heterospecific neighbours than by conspecific neighbours (Abrams, 1983). The limiting similarity arises, for example, from similarity in species-level traits and growth strategies (i.e. niche overlap; Yachi & Loreau, 2007) and negative density-dependent effects such as the occurrence of host-specific pests (Grossman et al., 2019; Jakuš et al., 2011) and herbivores (Connell et al., 1984; Janzen, 1970). Consequently, for the same level of competitive intensity, the probability of competition-induced mortality may be higher in monospecific stands than in mixed stands, as shown in several empirical studies (e.g. Changenet et al., 2021; Luo & Chen, 2011, 2015). Although the mechanisms of BM are understood at a general level, how stand composition and tree species growth strategies in relation to light availability influence the probability of BM remains unknown. Understanding these causalities is key to understanding future changes in BM, considering that changing tree species composition could lead to changes in the level of BM even if the rate of competition among trees remains constant.

The rate of competition-induced BM may vary due to the occurrence of adverse events such as droughts (Andrus et al., 2021; Franklin et al., 1987). In addition to causing catastrophic mortality over broad spatial scales (Neumann et al., 2017; Senf et al., 2020), drought events may contribute to BM directly (Aakala & Kuuluvainen, 2011; Cailleret et al., 2017) or indirectly by predisposing trees to abiotic (Csilléry et al., 2017) and biotic (Grossman et al., 2019) disturbances and stresses. Competition may amplify the negative effects of drought on tree survival, as trees experiencing both drought and suppression show reduced growth (Bottero et al., 2017; Gleason et al., 2017) and increased mortality rates (Taccoen et al., 2021; Young et al., 2017). Such interactive effects between competition and drought could explain the non-stationary effect of drought on tree demography (Astigarraga et al., 2020). However, the importance of the interaction between drought and competition on BM probability relative to their direct effects is not known. Given the predicted future increase in the severity and/or frequency of droughts in Europe (Spinoni et al., 2018), understanding the interaction between drought and competition in driving tree mortality is critical.

We investigated competition-induced BM along a latitudinal gradient spanning from the Mediterranean to the Arctic. To understand how stand composition and tree species growth strategy influence the probability of BM and to elucidate the importance of climate-competition interactions, we examined the importance of competition type, tree species ST, and the occurrence of drought events as drivers of BM. Specifically, we asked whether the tree-level probability of BM due to size-asymmetric competition varies as a function of (1) the proportion of conspecific competition, (2) the ST of both the focal tree and of its competitors and (3) drought events.

2 | MATERIALS AND METHODS

2.1 | Forest inventory data

We used National Forest Inventory (NFI) data from three European countries (Finland, France and Germany) to examine the probability of BM (Table 1). We excluded plots that were measured only once and plots in which any of the trees were harvested between the censuses. To be able to disentangle the drivers of BM from severe disturbances, we also removed plots where >20% of the plot basal area (France, Finland) or >20% of trees within the plot (Germany) died between the censuses. We used different criteria for Germany because of the different sampling methods used there (Table 1). We excluded trees that were dead at the first census and used the information about whether a tree was dead ($d = 1$) or alive ($d = 0$) at the time of the second census as a dependent variable. We removed all trees with a diameter at breast height (DBH) less than 7.5 cm to harmonize the datasets. We included species with <500 observations in the quantification of the competition indices but did not estimate their BM probability due to an insufficient sample size per species. With this criteria, the data contained samples from 461,109 trees representing 38 species on 48,088 plots. As is typical of European forests in general (Sabatini et al., 2018), the studied stands mostly represent stands managed for timber production.

The protocols for collecting the NFI data examined in this study varied between the three countries (Table 1). Importantly, the French NFI is based on nested subplots with fixed radii that have different DBH thresholds, whereas the Finnish NFI combines two subplots with fixed radii and different DBH thresholds. The German NFI is conducted with an angle-count sampling (ACS) method using a basal area factor of 4 m^2/ha. The different sampling methods determine, for example, the diameter distributions of the sampled trees, with ACS targeting large trees at the expense of small trees (Figure S1) (Lorimer, 1983). While the timing of sampling also differs between the countries, most notably that the German observations were collected earlier than the French and Finnish observations, the country-specific sampling periods also overlap (Figure S2).

2.2 | Tree species shade and drought tolerance

We used species-level ST as a proxy for both the competitive pressure exerted by trees of that species and the ability of the species to tolerate competition. We assumed that shade-tolerant species not only tolerate light competition but also intercept more solar radiation, thereby exerting stronger competitive pressure on neighbouring trees compared to shade-intolerant species (Canham & Burbank, 1994). We quantified ST by using the ST index of Niinemets and Valladares (2006). For European tree species, which make up the majority of the tree species in the data analysed here, the index is based on indicator values that—for light—characterize the natural distribution of species along habitats of varying light availability. These indicator values are determined for the seedling and sapling stages of plant development. The ST index ranges from 1 to 5, with low values indicating low ST and vice versa. In our data, *Pinus halepensis* Miller had the lowest ST (1.35) and *Abies alba* Mill the highest (4.60).

To investigate how the occurrence of drought modulates competition-driven tree mortality, we used the drought tolerance

TABLE 1 Summary of the National Forest Inventory data used in this study.

	France	Germany	Finland
Year of first survey	2010–2014	2002	2014–2017
Year of second survey	2015–2019	2012	2019–2020
Average census length (year)	5	10	5
Number of plots	20,215	19,830	8043
Number of trees	208,108	128,110	124,891
Number of dead trees	5928	3373	2522
Average number of trees per plot	10	7	16
Average BA per plot (m^2/ha)	21.4	25.8	14.7
Sampling plot placement design	Systematic 1 km^2 grid in forested areas	Cluster design with four subplots. Standard grid size 16 km^2 but the size varies regionally	Cluster design, number of plots in cluster depends on plot type. Cluster density varies regionally
Sample tree survey design	Nested circular subplots with radii of 6, 9 and 15 m. Trees with a minimum DBH of 7.5, 22.5 and 37.5 cm are measured on the subplots, respectively	Angle-count sampling with basal area factor 4 m^2/ha. Trees are recorded with maximum plot radius of 10 m	Nested circular subplots with fixed or varying radius. The fixed plot radii are 5.64 and 9 m. The DBH thresholds are 4.5 and 9.5 cm, respectively. Trees with DBH < 4.5 cm are measured on an angle-count sampling subplot with basal area factor 1.5 m^2/ha
Maximum plot size (m^2)[a]	707	314	255
Reference	IGN—French National Forest Inventory (2005)	Thünen Institut (2015) and Riedel et al. (2017)	Korhonen et al. (2021)

[a] Size of the largest subplot for France and Finland.

index of Niinemets and Valladares (2006) to control for the different drought tolerances at species level. The drought tolerance index varies between 1 and 5, with low values indicating low drought tolerance and vice versa. In our data, *Betula pubescens* (Ehrh.) had the lowest drought tolerance (1.27) and *P. halepensis* the highest (4.97). See appendix B in Niinemets and Valladares (2006) for full details of the quantification of the indices and further references.

2.3 | Climate data

We used observations of temperature and moisture availability to characterize the general growth conditions and test whether the probability of BM changed with changing moisture availability. We obtained monthly mean air temperature (MMT), precipitation (MMP) and potential evapotranspiration (PET) data for each NFI plot from the CHELSA database (Karger et al., 2017, 2020). The CHELSA data have a spatial resolution of 30 arc seconds and cover the years 1901–2016. For each NFI plot, we used the MMP and PET to calculate the water availability index (WAI) for each month between the years 1985 and 2015. We first calculated the WAI for each month over the entire interval as:

$$\mathrm{WAI} = \frac{(\mathrm{MMP} - \mathrm{PET})}{\mathrm{PET}}, \quad (1)$$

and then calculated the arithmetic mean of the monthly values to characterize the general climatic water availability on each study plot. High values of WAI indicate high climatic water availability, and vice versa.

In this study, we define a drought event as a temporary meteorological moisture deficit relative to the mean conditions at a site. To quantify the occurrence of drought events and to test whether the probability of BM is a function of climatic drought anomalies, we used the standardized precipitation evapotranspiration index (SPEI). Briefly, the SPEI is a multi-scale drought index based on monthly PET and precipitation, the former being derived from the Penman–Monteith equation (Vicente-Serrano et al., 2010). The SPEI is expressed as a standardized index relative to the drought history of a site, with negative values indicating more intense drought anomalies and positive values indicating higher than average water availability. Here, the SPEI describes the drought intensity of a given period compared to site conditions between 1901 and 2018. We obtained the lowest 3-, 12- and 24-month SPEI values centred between May and September during the period from 2 years before the 1st census to the 2nd census. We chose to include the 2 years before the 1st census to account for the potential lag effect in drought-related mortality (Greenwood et al., 2017). We used AIC to determine which SPEI value gave the best fit in modelling BM. We extracted SPEI at the plot level using gridded data at 0.5-degree resolution in R version 4.2.2 (Beguería & Vicente-Serrano, 2023).

We chose to use both WAI and SPEI because the indices are complementary. WAI is a non-standardized index that is a general representation of the variation in moisture conditions, whereas SPEI is a relative measure of the temporal variation in moisture availability at the site during a given time interval. Therefore, we consider MMT and WAI to be characterizations of typical climatic conditions at a site, whereas SPEI indicates an anomaly in moisture availability at the site.

2.4 | Statistical modelling

Using the package glmmTMB (Brooks et al., 2017) in R, we fitted a generalized linear mixed model (glmm) with a *cloglog* link function to model the probability of death of individual trees. We refer to this model as the BM model. The BM model was based on two sub-equations: a control sub-equation, which accounts for the effect of competition-independent processes, and a competition sub-equation, which accounts for the various competition-dependent processes that we want to test:

$$\eta\left(M_{ip}\right) = \text{control} + \text{competition} + \varepsilon_s + \ln\left(t_{x_p}\right), \tag{2}$$

where $\eta(M_{ip})$ is the cloglog of the probability of death of the *i*th focal tree ($i=1, \ldots, 461{,}109$) in the *p*th plot ($p=1, \ldots, 48{,}088$), ε_s is the random intercept for species and $\ln(t_{xp})$ is natural logarithm-transformed time between the censuses at plot *p*, which we used as an offset term to correct for variability in census lengths within and between countries. The control sub-equation for tree *i* in plot *p* was:

$$\begin{aligned} \text{control} = {} & \tau_{0,\text{country}} + \tau_1 DBH_i + \tau_2 \ln\left(DBH_i\right) + \tau_3 MMT_p \\ & + \tau_4 WAI_p + \tau_5 DT_i + \tau_6 SPEI_p, \end{aligned} \tag{3}$$

where $\tau_{0,\text{country}}$ is a country specific intercept and τ_{0-7} are parameters to be estimated. DBH_i is the DBH of tree *i* at the time of the first census, MMT_p is the mean monthly air temperature in plot *p*, WAI_p is the mean water availability index in plot *p*, DT_i is the species-specific drought tolerance value of tree *i*, and $SPEI_p$ is the minimum of the 3-month SPEI—that had the lowest AIC among the three SPEI variables tested (Table S1)—recorded in the plot *p*. We also included an effect of $\ln(DBH_i)$ in the model, to account for the fact that the effect of tree size on BM may be non-linear (e.g. U-shaped), as observed in other studies (Lines et al., 2010).

The sub-equation for competition was constructed using the basal area of all trees larger than the focal tree *i* in plot *p* (BAL). Based on Kunstler et al. (2016), the sub-equation for competition includes five parameters that allow us to test our research hypotheses:

$$competition_{ip} = \sum_{j=1}^{N_{ip}} \left(\alpha_T + \alpha_C C_{ij} + \alpha_R ST_i + \alpha_E SE_j + \alpha_{BS} SPEI_p\right) BA_j, \tag{4}$$

where N_{ip} is the number of competitors of tree *i* in plot *p* (i.e. the number of trees with a DBH larger than that of the focal tree *i*), C_{ij} is a binary variable equal to 1 if focal tree *i* and competitor tree *j* are of the same species and 0 otherwise, ST_i is the species-specific ST of tree *i*, and SE_j is the species-specific ST of competitor tree *j*, which we used as a proxy for competitor trees' shading effect. $SPEI_p$ is the minimum of the 3-month SPEI recorded between the two censuses and the two preceding years. The parameter α_T is the species-independent competition. More specifically, α_T corresponds to the effect of the basal area of larger trees ($BAL_{ip} = \sum_{j=1}^{N_{ip}} BA_j$), independent of their species, which is classically used to quantify size-asymmetric competition. α_C quantifies how conspecific competition differs from this species-independent competition. α_R and α_E are trait-related competition parameters that account for how the ST of a focal tree and the shading effect of its competitors, respectively, affect competition. α_{BS} quantifies how the effect of competition varies with drought anomaly. We also tested a competition sub-equation that included the competitive effect of trees smaller than the target tree (i.e. all trees except the focal tree), but this model was rejected based on AIC comparison (Table S1).

We paid particular attention to accounting for differences in sampling protocols between countries. First, we included a country-specific intercept in the BM model to account for the difference between countries. Second, to account for the differences in plot structure between countries (nested sub-plots with different DBH thresholds or ACS) and undersampling of small trees, we used the inverse of the sampling area as a statistical weight for the trees in the model. Finally, the BAL used in the competition sub-equation was calculated as m^2 per hectare to account for differences in sampling protocols between the countries.

As the BM model response is binary and the predicted values are mortality probabilities, we could not evaluate the BM model predictions by directly comparing them to the observed values. Instead, we evaluated the model predictions by dividing the data into classes of predicted mortality probability from the BM model and comparing the mean prediction of each class with the mean observed mortality probability in each class. We filtered out classes with fewer than 30 trees and fitted a null glmm separately for each of the 54 classes to estimate the annual probability of mortality observed in each class, accounting for census length. The null model used country as a predictor, ln-transformed census length as an offset term, and the same statistical weights as the BM model. This gave us an observed annual mortality probability for each country and each class.

We used the area under the receiver operating characteristic curve, calculated with the performance package (Lüdecke et al., 2021), to assess the performance of the model. The area under the curve of the BM model, quantified with fivefolds and 1000 bootstrap samples, was 0.76. We used the DHARMa package (Hartig, 2022) to examine partial residual plots of each explanatory variable to examine their relationship with tree mortality, and the correlation matrix and variance inflation factor to test for multicollinearity among the explanatory variables (Table S2). The independent variables did not show multicollinearity (Table S2). To examine the influence of the different sampling protocols between countries, we fitted country-specific BM models and compared the ranking of their parameter estimates with that of the BM model. We also compared the predictions of the country-specific models to the BM model predictions. Further, due to the different sampling protocol in Germany compared to France and Finland, we removed the German observations from the full data, refitted the BM model to the trimmed data and compared the country-specific predictions of this trimmed model to those of the BM model.

3 | RESULTS

Among the competition-related covariates, species-independent competition had the highest contribution to the BM probability (α_T=0.62), followed by ST of a focal tree (α_R=−0.42) and ST of neighbouring trees (α_E=0.21) (Figure 1). Among the control covariates, the three variables with the highest contribution to BM probability were ln-transformed DBH (τ_2=−0.45), drought tolerance (τ_5=0.31) and temperature (τ_3=0.28) (Figure 1). Here, positive parameter estimates imply that the variable increased the probability of mortality, and vice versa.

The annual probability of mortality increased with increasing species-independent competition, but the increase was more pronounced as a function of conspecific competition than as a function of species-independent competition (Figures 1c and 2a; Figure S3). For example, the annual mortality probability of a tree with BAL 15 m^2/ha was 0.24% in species-independent and 0.27% in conspecific competition, but for a tree with BAL 35 m^2/ha, the mortality probability was 0.61% in species-independent and 0.78% in conspecific competition (Figure 2a), with the other variables set to their arithmetic means and the country set to France.

While the probability of mortality of a focal tree increased with increasing BAL, increasing ST of the focal tree slowed down the increase (Figures 1e and 2b). For example, for a focal tree with a BAL of 15 m^2/ha, the annual probability of mortality was 0.37% if the focal tree was shade-intolerant and 0.07% if the focal tree was shade-tolerant (Figure 2b). For a focal tree with a BAL of 35 m^2/ha, the annual probability of mortality was 0.92% if the focal tree was shade-intolerant and 0.17% if the focal tree was shade-tolerant (Figure 2b). In contrast to this effect, increasing the ST of neighbouring trees increased the mortality probability of a focal tree (Figures 1d and 2c). For example, a tree with a BAL of 15 m^2/ha had an annual mortality probability of 0.23% if its neighbours were shade-intolerant and 0.59% if its neighbours were shade-tolerant (Figure 2c). A tree with a BAL of 35 m^2/ha had an annual mortality probability of 0.56% if its neighbours were shade-intolerant and 1.45% if its neighbours were shade-tolerant (Figure 2c).

The occurrence of drought periods amplified the effect of increasing mortality probability due to inter-tree competition

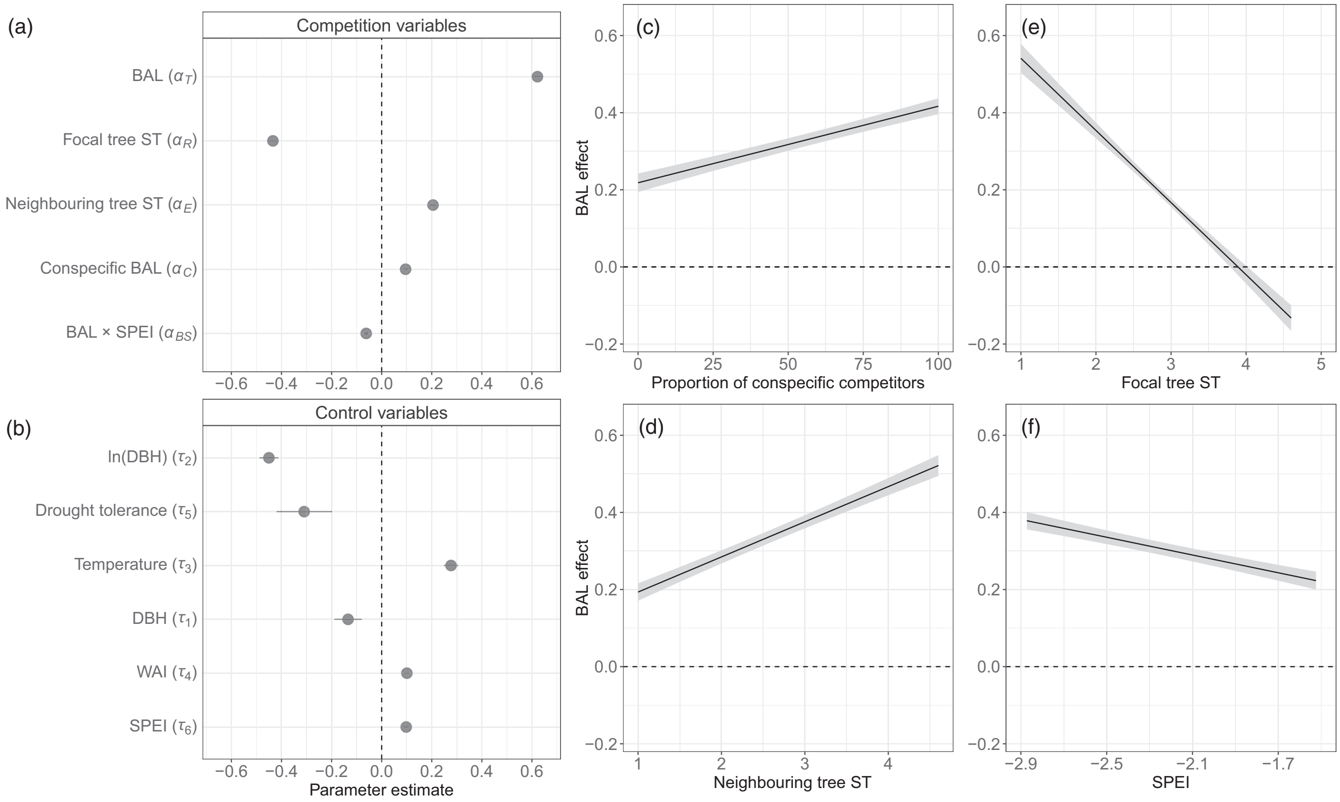

FIGURE 1 Regression model parameter estimates for the scaled and centred competition-related (a) and control (b) covariates, and the effect of BAL on background mortality at different proportions of conspecific competition (c), neighbouring tree shade tolerance (ST) (d), focal tree ST (e) and the standardized precipitation evapotranspiration index (f). In panels (a) and (b), the covariates are ranked from top to bottom in the order of the magnitude of their contribution to the tree mortality probability. The error bars indicate 95% confidence intervals for the estimates. The symbols in parentheses refer to those used in Equations (3) and (4). Numerical model parameter estimates are given in Table S3.

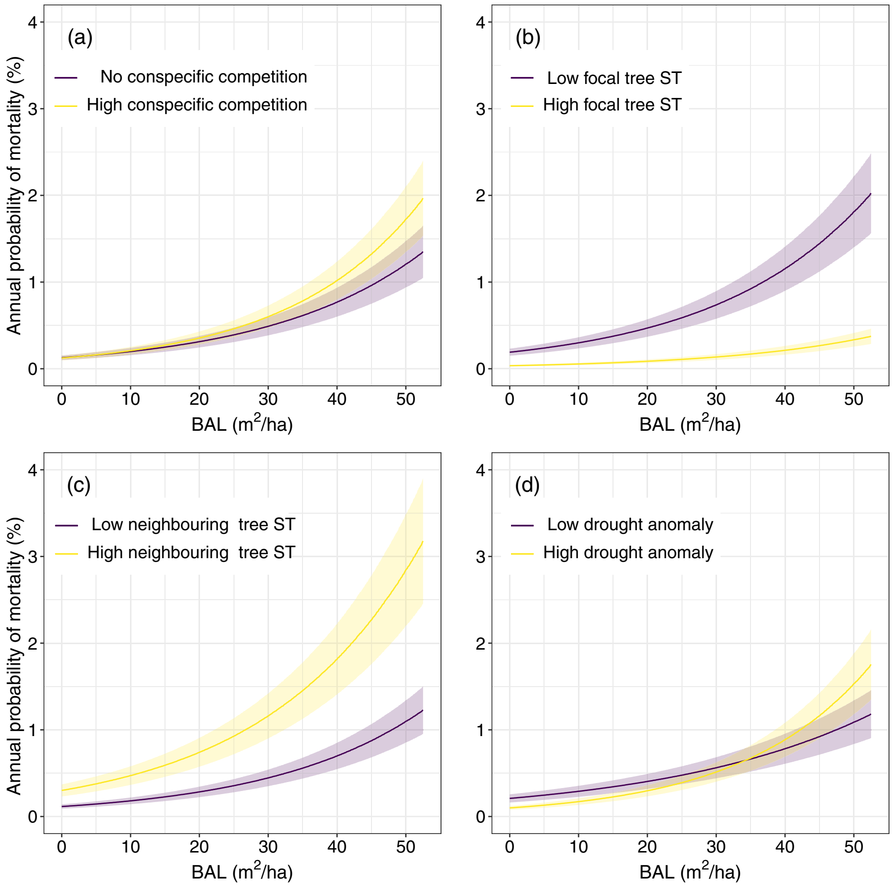

FIGURE 2 Predicted mortality probabilities as a function of BAL for different levels of conspecific competition (a), different levels of focal tree shade tolerance (ST) (b), different levels of neighbouring tree ST (c) and for different drought anomalies (d). For each panel, the variables other than the one used in the prediction were set to their arithmetic mean, and the country was set to France. Mortality probabilities were predicted with BAL values <99th quantile (53 m/ha^2) to exclude outlier BAL values. Mortality probabilities plotted over the full range of BAL are shown in Figure S3.

(Figures 1f and 2d). For example, a tree with a BAL of 15 m^2/ha had a mortality probability of 0.34% if it experienced a mild drought and a mortality probability of 0.23% if it experienced a severe drought (Figure 2d). However, a tree with a BAL of 45 m^2/ha had a mortality probability of 0.92% if it experienced a mild drought and a mortality probability of 1.16% if it experienced a severe drought (Figure 2d).

Increasing tree diameter and species-level drought tolerance decreased the probability of focal tree mortality (Figure 1b). For example, the probability of mortality was 0.76% for a tree with a 7.5 cm DBH, 0.30% for a tree with a 20 cm DBH, 0.11% for a tree with a 50 cm DBH, and 0.07% for a tree with a 70 cm DBH (Figure S4A). A tree with low drought tolerance (1.26) had a mortality probability of 0.44%, while a tree with high drought tolerance had a mortality probability of 0.16% (Figure S4B). Temperature and WAI both increased the mortality probability of a focal tree (Figure 1b). For example, the probability of mortality was 0.17% when the mean annual temperature was 0°C, 0.34% when the mean temperature was 10°C and 0.49% when the mean temperature was 15°C (Figure S4C). Mortality probabilities were 0.26%, 0.29% and 0.38% when WAI was −0.5, 0.5 and 1.5, respectively (Figure S4D).

In general, the predictions of the BM model agreed with the observed probability of death in the 54 classes of predicted probability of death that we estimated with the null model. Predictions were closest for small mortality probabilities, with dispersion increasing as mortality probabilities increased (Figure 3). Partial residual plots showed no trends between simulated residuals and model covariates (Figure S5), and similar trends in mortality probabilities were predicted for the three countries (Figure S6). However, the mortality probabilities predicted with the BM model were consistently lower in Finland than in France and Germany (Figure S6). Parameter estimate rankings and model predictions were consistent in the BM model and the country-specific BM models (Figures S6 and S7). Removing the German observations—obtained with a different sampling strategy compared to Finland and France—resulted in slightly higher predicted mortality probabilities for the competition-related variables compared to the mortality probability predictions obtained with the full data (Figure S8).

4 | DISCUSSION

4.1 | The influence of competition-related variables on tree mortality

Competition was the main driver of BM, with the probability of tree mortality increasing as competition increased. However, the increase was faster when the proportion of conspecific competition was high compared to heterospecific competition. Consistent with our results, conspecific competition has been shown to increase mortality probability more than interspecific competition (Archambeau et al., 2020; Changenet et al., 2021; Luo & Chen, 2011). Furthermore, greater reductions in tree growth rates—a pattern

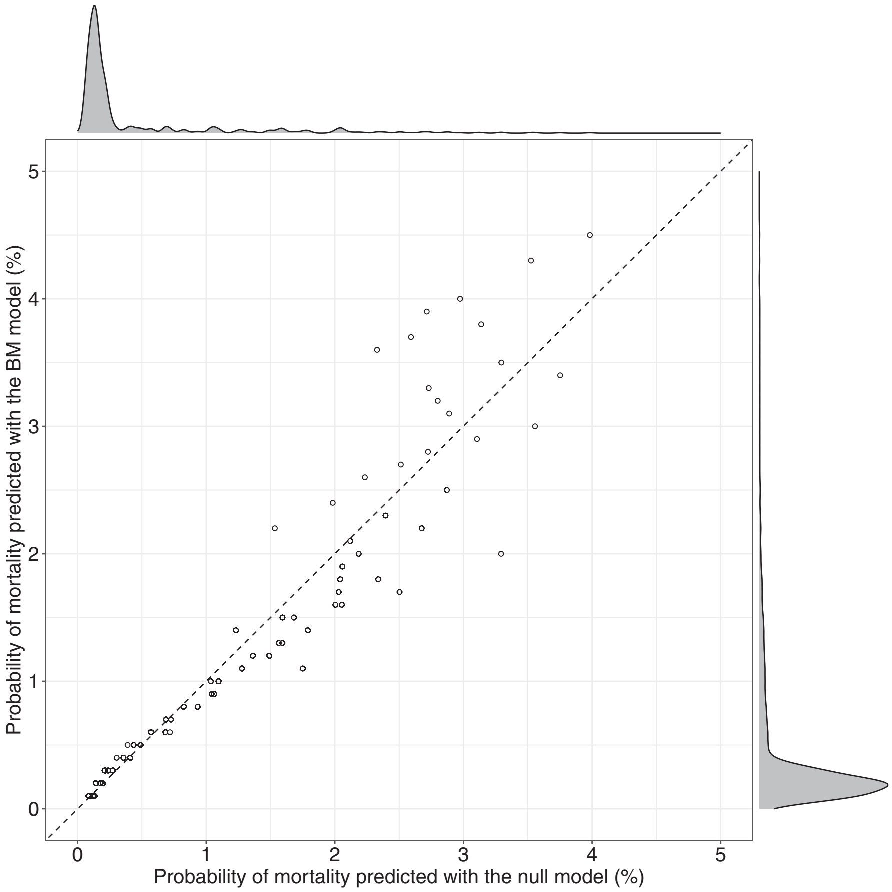

FIGURE 3 The relationship between the annual mortality probability predicted by the background mortality (BM) model and the observed annual mortality in each class and all countries. Observed annual mortality was estimated with a null model to account for different census lengths (see details in Section 2). The density distributions show the number of trees in each point class.

that often precedes competition-induced tree mortality (Cailleret et al., 2017)—have been reported due to conspecific rather than interspecific competition (Aussenac et al., 2019; Kunstler et al., 2016; Ramage et al., 2017). In our results, the divergence in survival probabilities between conspecific and heterospecific competition began to emerge when BAL exceeded approximately 20 m^2/ha and increased with increasing BAL. This indicates that the negative effect of conspecific competition on tree survival is mainly manifested in moderately to extremely suppressed trees, suggesting a difference in survival probability between monospecific and mixed stands. In contrast to monospecific stands, species-level variability in functional traits and growth strategies may promote the survival of suppressed trees in heterospecific stands (Searle & Chen, 2020). Negative density-dependent effects, such as the increased occurrence of biotic disturbances, may also explain the higher mortality rates in monospecific than mixed stands (Grossman et al., 2019; Jactel & Brockerhoff, 2007). This is particularly the case for *Picea abies* (L.), which is the most sensitive to bark beetles—a currently dominant biotic disturbance agent in Central Europe (Kautz et al., 2017)—and other species susceptible to biotic disturbances, such as *Betula* spp. (Barrere et al., 2023). Trees already under stress due to suppression are most susceptible to the influence of these processes, which may ultimately lead to tree death (Franklin et al., 1987).

Increasing the ST of neighbouring trees increased the mortality probability of a focal tree, while increasing the ST of the focal tree decreased its mortality probability. This suggests that in addition to the ability to tolerate shade, shade-tolerant trees exert a stronger competitive effect on their neighbours than shade-intolerant trees (Canham & Burbank, 1994; Leverenz & Hinckley, 1990; Niinemets, 2010). Light availability is one of the most important factors limiting tree survival (Bianchi et al., 2021; Harcombe, 1987; Niinemets & Valladares, 2006). As a result, high mortality rates are often observed among suppressed trees (Gendreau-Berthiaume et al., 2016; Vanoni et al., 2019). For suppressed trees, low light availability means reduced resource acquisition capacity, leading to reduced photosynthate production and its allocation to primary and secondary metabolism. This may lead to tree death from carbon starvation (Oliver & Larson, 1996) or weaken the ability of a tree to recover from a disturbance or stress (Kunstler et al., 2005; Pedersen, 1998). In addition to light competition, below-ground competition for water and nutrients also affects tree growth and survival (Coates et al., 2009). Due to the variability in, for example, soil characteristics and consequently in the intensity of below-ground competition, the mortality rate of a species may vary within forest stands, independent of its ST (Kobe et al., 1995).

Drought events amplified the effect of competition-induced mortality, especially for the most suppressed trees in sites with the strongest drought anomalies, while drought had a weak direct effect on BM. In contrast to the drought–competition interaction, increasing drought tolerance at the species level decreased the probability of BM. In general, our result is consistent with previous studies from drought-prone regions in southern Europe and eastern North America showing that drought amplified the effect of competition between trees by increasing mortality (Ruiz-Benito et al., 2013; Young et al., 2017) and aligns with the observation that climate effects may increase mortality, especially among suppressed trees (Taccoen et al., 2021). Drought may increase the cumulative stress effects on trees and predispose them to other processes that may eventually lead to mortality, such as biotic disturbances (Aakala & Kuuluvainen, 2011; Trugman et al., 2021) or competition (Das et al., 2016; Franklin et al., 1987). This may be particularly true in high-density areas where competition is the most intense (Ruiz-Benito et al., 2013). Among trees with similar drought tolerance, the largest trees typically have deeper coarse roots and a greater fine root biomass, which allow for better water uptake compared to suppressed trees (Pretzsch et al., 2013). Therefore, despite their high respiration costs, dominant trees may survive a 3-month drought better than suppressed trees, and the drought–competition interaction may partially reflect this size effect on drought tolerance. Recent droughts have caused severe tree mortality events across Europe (Senf et al., 2020), with co-occurring biotic disturbances increasing the severity of these events (Trugman et al., 2021). Given that we removed plots where mortality was >20% of the plot basal area, this suggests that we removed plots where severe drought-related mortality events occurred, potentially explaining the weak direct effect of drought on BM probability.

4.2 | The influence of control variables on tree mortality

Among the control covariates, tree size had the largest contribution to BM. However, the effect of tree size was smaller than that of competition. Our observation of the size dependence of tree mortality probability is consistent with the well-documented high mortality rate for small trees, driven mostly by competition (e.g. Bianchi et al., 2021; Gendreau-Berthiaume et al., 2016; Vanoni et al., 2019). Other studies have also found an increasing probability of mortality for large trees, mainly due to senescence (Holzwarth et al., 2013; Vieilledent et al., 2010) and certain natural disturbances such as high winds (Barrere et al., 2023). Mortality due to senescence occurs in stands that have avoided natural or anthropogenic disturbances long enough for the trees to reach the end of their life span (Luo & Chen, 2011). The fact that we mostly examined managed forests with harvest rotation cycles well below the natural longevity of trees and filtered out plots where mortality exceeded 20% of the plot basal area may explain the negligible increase in mortality probability for large trees observed here.

Increasing temperature and water availability increased the probability of tree mortality, suggesting increased productivity and consequently competition in warm and humid climates (Astigarraga et al., 2020; Gendreau-Berthiaume et al., 2016; Stephenson et al., 2011). Our data also support this line of reasoning, as plots with high water availability and a moderate mean temperature had the highest plot-level basal area (Figure S9A,B). High temperatures may also reduce tree survival by directly damaging tree leaves and causing trees to close stomata to prevent xylem cavitation. In our study area, such direct effects are most likely limited to the Mediterranean region, where the mean annual temperature is the highest, while disruptions to tree physiology may be more common, especially at the warm edge of their range (Taccoen et al., 2022). In cold regions, trees are generally smaller and, therefore, less susceptible to abiotic disturbances compared to warmer regions (Di Filippo et al., 2015). Due to the slower growth of trees in cold regions, the natural longevity of trees in these regions may be higher than in regions with higher temperatures (Brienen et al., 2020; Di Filippo et al., 2012).

Our data from Finland indicate that WAI was generally higher in stands on organic soils than in stands on mineral soils (Figure S9C). Therefore, it is also possible that in the northernmost sites, the probability of mortality increases with increasing water availability on organic soils, where waterlogging sometimes occurs (Rouvinen et al., 2002). However, this could not be tested with the full set of data examined here, as we lacked information on both exact plot locations (France) and soils (Germany). For this reason, and due to the lack of soil information of consistent quality across the study area, we also could not include soil quality as a control variable in the BM model. A third plausible explanation for the positive relationship between mortality probability and WAI is that the highest WAI occurs in high-altitude areas, where frost damage and winter desiccation are more frequent than in low-altitude areas (Barbeito et al., 2012; Germino et al., 2002). Our data from France and Finland, where we have information on plot elevation, supports this reasoning (Figure S9D).

4.3 | Analytical challenges

Shade tolerance at the species level results from multiple functional traits (Valladares & Niinemets, 2008). However, defining a species' ST remains a challenge, despite the rigorous attempts to construct global measures and definitions of ST (e.g. Niinemets & Valladares, 2006; Valladares & Niinemets, 2008). As an example of the difficulties in classifying species' ST, ST at the individual level generally decreases with increasing tree size (Kneeshaw et al., 2006; Kunstler et al., 2009). Despite these difficulties, the ST index of Niinemets and Valladares (2006) used in this study was an effective proxy for both ST and shading effect. However, we believe that future research, model development and forest management could benefit from bridging measurable functional traits that capture species responses to competition and drought to better understand and quantify tree mortality.

The predicted mortality probabilities were consistently lower in Finland than in France and Germany. This may be due to decreasing productivity and hence stand density with increasing latitude in Europe (Kuusela, 1994), as indicated also by our data. Removing the German observations—collected with the ACS method—resulted in a slightly higher predicted mortality probability due to inter-tree competition in Finland and France (where data were collected from fixed-radius plots). However, the direction of the effect of competition on BM probability remained unchanged despite the data filtering. Due to its sampling design, ACS gives preference to large trees (Lorimer, 1983). For this reason, observations from ACS plots typically contain fewer small trees than data collected from fixed-radius plots. Consequently, ACS may be a suboptimal sampling method for competition-driven mortality analyses, as this type of mortality is highest among the smallest and most suppressed trees (Luo & Chen, 2011). Together with the harvesting of dead trees before they were inventoried as dead (i.e. salvage logging), ACS may have reduced the estimated mortality probabilities for the German data.

5 | CONCLUSIONS

Our examination of more than 460,000 individual trees showed that the intensity of competition between trees is a stronger driver of BM than tree size or climatic variables. Increasing the proportion of conspecifics and the occurrence of drought events amplify the effect of competition on tree mortality. Increasing ST reduces the probability of trees dying from competition but also increases the mortality of their neighbours due to increased shading. Taken together, these results suggest that current increases in stand density in temperate and boreal biomes may accelerate tree mortality rates and promote the dominance of shade-tolerant species. Increasing severity and/or frequency of adverse events—such as drought—may act in concert with competition to render suppressed trees particularly vulnerable to competition-induced mortality. This will have long-term consequences for forest regeneration and dynamics.

AUTHOR CONTRIBUTIONS

Mikko Peltoniemi, Georges Kunstler and Juha Honkaniemi developed the original research idea, and Mikko Peltoniemi, Georges Kunstler and Carola Paul acquired research funding. Niko Kulha, Juha Honkaniemi, Julien Barrere, Susanne Brandl, Thomas Cordonnier, Georges Kunstler, Carola Paul, Björn Reineking and Mikko Peltoniemi refined the study approach. Julien Barrere and Georges Kunstler harvested the climate data. Niko Kulha harmonized the NFI data with support from Julien Barrere, Carola Paul and Susanne Brandl. Niko Kulha performed the analyses with support from all authors. Niko Kulha wrote the first draft of the manuscript. All authors contributed to the drafting of the manuscript and gave the final approval for publication.

ACKNOWLEDGEMENTS

We thank Juha Heikkinen (Natural Resources Institute Finland, Luke), Kai Husmann (University of Göttingen), Matthias Neumair (Technical University of Munich), Ville Pietilä (Luke) and Leena Ruha (Luke) for their help in data analysis and model fitting.

This research was funded through the BiodivClim ERA-Net Cofund (joint BiodivERsA Call on 'Biodiversity and Climate Change', 2019–2020) with national co–funding through the Academy of Finland (decision no. 344722), ANR (France, project ANR-20-EBI5-0005-03) and the Federal Ministry of Education and Research (Germany, grant no. 16LC2021A). This study has also received funding from the European Union's Horizon 2020, grant no. 101000574.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest associated with this work.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14184.

DATA AVAILABILITY STATEMENT

The French and German NFI data used in this study are openly available, respectively, at https://inventaire-forestier.ign.fr/dataifn/ (IGN—French National Forest Inventory, 2005) and https://bwi.info/Download/de/BWI-Basisdaten/ (Thünen Institut, 2015) (both sites accessed latest on 23 January 2023). Due to data disclosure, the Finnish NFI data used in this study cannot be made openly available. The inquiries about the use of the Finnish NFI data should be directed to the head of the Forest Inventory and Planning group at the Natural Resources Institute of Finland.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Country-wise diameter distributions of the trees examined in this study.

Figure S2. The time period covered by the data used in this study. German observations were collected in years 2002 (first census) and 2012 (second census).

Table S1. BM model selection using AIC. The AIC values of the models are compared to 145 116 that is the AIC of the BM model presented in the Section 2.4 of the main text of this study.

Figure S3. Predicted mortality probabilities for the competition-related covariates plotted over the full range of BAL. Uncentered and unscaled variables were used in the predictions. For each panel, the other variables than the one used in the prediction were set to their arithmetic mean values, and country to France. In the panel legends, ST means shade tolerance.

Figure S4. Mortality probabilities predicted over the control covariates of the BM model. Uncentered and unscaled variables were used in the predictions. For each panel, the other variables than the one used in the prediction were set to their arithmetic mean values, and country to France.

Table S2. Correlation matrix of the continuous BM model covariates. The covariate acronyms are: BAL, basal area of trees with larger DBH than focal tree; BAL_c, basal area of conspecific trees with larger DBH than focal tree; DBH, diameter at breast height; DT, drought tolerance; Focal ST, shade tolerance of the focal tree; MMT, mean monthly temperature; Neighbor ST, shade tolerance of the neighboring trees; SPEI, standardized precipitation evapotranspiration index; WAI, climatic water availability. VIF is the variance inflation factor. N.B. that the focal ST and neighbor ST are interactions with BAL, quantified as $\sum_{j=1}^{N_{ip}} ST_j BA_j$ and $\sum_{j=1}^{N_{ip}} SE_j BA_j$, respectively.

Table S3. Parameter estimates of the background mortality model for the scaled and centered covariates. The covariates are ranked from top to bottom in the order of the magnitude of their contribution to tree mortality probability.

Figure S5. Simulated partial residuals of the BM model plotted against the scaled and centered model covariates.

Figure S6. Predictions of mortality probabilities for France, Germany and Finland derived from the BM model (i.e., the model that includes data from all three countries) and country-specific BM models. Country-specific predictions from the BM model are shown as solid lines, while dashed lines represent predictions from country-specific BM models. To facilitate comparison, the solid grey lines show the BM model prediction for the full data set used in this study. In this prediction, the variables not being predicted were set to their arithmetic means and the country was set to France. The line colors are consistent across the panels. Panels (A)–(D) show the effect of BAL on BM probability at moderate level of conspecific competition (A), when the trees neighboring a focal tree have high shade tolerance (B), when the focal tree has low shade tolerance (C) and during a severe drought (D). In predictions, the other variables are set to their arithmetic means. Prediction confidence intervals are omitted for clarity.

Figure S7. Comparison of the ranking of regression model parameter estimates between the BM model fitted with all data used in the study (A), data from France (B), Germany (C), and Finland (D). The variables were scaled and centered before fitting the models. To facilitate comparison with the BM model, the covariates are ranked from top to bottom in the order of the magnitude of their contribution to the tree mortality probability in the BM model. The error bars indicate 95% confidence intervals for the estimates. The symbols in parentheses refer to those used in Equations (3) and (4) presented in the main text.

Figure S8. Country-specific predictions for the mortality probability in Finland and France when the German data—produced with different sampling design than the Finnish and French data—are removed from the dataset over which tree mortality is predicted. These predictions are shown with dashed lines, the line colors separating the two countries. To facilitate comparison, the panels also show the predictions derived from the BM model (i.e., the model fitted with the data that also includes the German observations) with solid lines. In the panel titles, ST means shade tolerance.

Figure S9. Plot basal area in plots grouped to 10th and 90th quantiles according to their WAI value (A), plot basal area in plots grouped to 10th, 10th–90th, and 90th quantiles according to their mean annual temperature (B), WAI in plots on mineral and organic soils in the Finnish data (C), and WAI in plots grouped to 10th and 90th quantiles according to their elevation (D).

How to cite this article: Kulha, N., Honkaniemi, J., Barrere, J., Brandl, S., Cordonnier, T., Korhonen, K. T., Kunstler, G., Paul, C., Reineking, B., & Peltoniemi, M. (2023). Competition-induced tree mortality across Europe is driven by shade tolerance, proportion of conspecifics and drought. *Journal of Ecology*, *00*, 1–14. https://doi.org/10.1111/1365-2745.14184