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TITLE

Similar patterns of background mortality across Europe are mostly driven by drought in European beech and a combination of drought and competition in Scots pine.

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1 INTRODUCTION

Tree mortality plays a major role in shaping forest dynamics, structure and composition (Franklin *et al.*, 1987; Ruiz-Benito *et al.*, 2017a), species range shifts (Benito Garzón *et al.*, 2013), ecosystem functioning and services (Millar & Stephenson, 2015), carbon fluxes and feedback to the global climate system (Sitch *et al.*, 2008). Therefore, understanding and predicting tree mortality is a key challenge in ecology, particularly in a changing climate.

Global change is exacerbating drought-induced tree mortality (Allen *et al.*, 2015). Recent forest die-off events have occurred in all major biomes and on every wooded continent (Allen *et al.*, 2015) and background tree mortality also appears to have increased in North America (Mantgem *et al.*, 2009; Hember *et al.*, 2017) and in Spain (Carnicer *et al.*, 2011). Less conspicuous than die-offs events, minor large-scale changes in tree background mortality can have a huge impact on forest ecosystems and dynamic, including changes in productivity rates, functional composition and species turnover (Stephenson & Mantgen, 2005; Ruiz-Benito *et al.*, 2017b). Yet, an empirical quantification of background tree mortality at continental scale is missing and whether or not forest mortality follows an increasing global trend that will keep rising under global change remains unclear (Hartmann *et al.*, 2018). Moreover, mortality is a major process which delimits species range (Gaston, 2009), notably at the driest edge of their distribution (Benito Garzón *et al.*, 2013). Therefore, large scale studies that capture the entire species distribution are essential to determine how climate change induced mortality might affect species distribution.

Understanding and predicting background tree mortality patterns at large scales remains challenging for several reasons (but see Das *et al*. (2016) and Neuman *et al*. (2017) for examples of large-scale studies). First of all, mortality is a stochastic phenomenon (Franklin *et al.*, 1987), which is therefore difficult to predict. Secondly, it is often the result of a complex and gradual process with multiple interacting drivers (Manion, 1981), that act at different spatial and temporal scales (Dietze & Moorcroft, 2011). Thirdly, there may be a lag time between episodic stressful conditions and tree mortality responses (Cailleret *et al.*, 2016; Jump *et al.*, 2017). Lastly, background tree mortality rates are difficult to estimate due to the small sample size of dying trees in local studies, while large samples are needed to understand mortality patterns.

In European forests, background tree mortality is strongly driven by climate variability (Neumann *et al.*, 2017). Among the climatic factors affecting tree mortality, drought plays a major role (McDowell *et al.*, 2008; Benito Garzón *et al.*, 2013; Ruiz-Benito *et al.*, 2013; Allen *et al.*, 2015) and particularly affects populations at the driest edge of species distributions (Benito Garzón *et al.*, 2018). Among the biotic factors, competition for limited resources may be an important cause of tree mortality and may also interact with climate, notably through a higher increase in mortality rates in areas that are both dry and dense (Ruiz-Benito *et al.*, 2013; Vilà-Cabrera *et al.*, 2013; Young *et al.*, 2017). Moreover, tree mortality responses can differ widely depending on whether we consider intra- or inter-specific competition (Condés & del Río, 2015). However, how intra- and interspecific competition interact with climatic drought to shape range-wide mortality patterns remains unknown.

Tree mortality sensitivity to biotic and abiotic factors vary along species' ecological strategies, from stress-tolerators to competitors and from angiosperms to gymnosperms (Choat *et al.*, 2012; Ruiz-Benito *et al.*, 2017a). European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.) are two widely distributed European tree species with different life history strategies. Beech is a highly competitive, shade-tolerant and late-successional species while Scots pine is a weakly competitive and light demanding pioneer tree (San-Miguel-Ayanz *et al.*, 2016). Scots pine is considered as a drought-avoiding species, which has narrow xylem vessels (tracheids) and withstands droughts by closing its stomata early and maintaining a reduced metabolism (isohydric response; McDowell *et al.*, 2008). By contrast, beech is known to be sensitive to drought (van der Maaten, 2012; Chen *et al.*, 2015), has wide vessels more prone to cavitation and maintains a more constant metabolism but a narrower margin of hydraulic safety under droughts (anisohydric response; McDowell *et al.*, 2008). Regional scale studies suggested that both species are being progressively replaced by other species in the southern part of their distribution (Vilà-Cabrera *et al.*, 2013; Galiano *et al.*, 2010) and in some inner Alpine valleys in the case of *P. sylvestris* (Rigling *et al.*, 2013).

Our main objective was to understand and predict range-wide patterns of background mortalities in Scots pine and European beech. To that end, we parameterised individual-level logistic regression models, as a function of climatic drought and basal area of heterospecific and conspecific trees (used as a proxy of inter and intra-competition or facilitation, at the plot level), using records from five National Forest Inventories covering the entire European latitudinal gradient, from Spain to Finland. We hypothesised that (i) mortality in both species is influenced by climatic drought, basal area and their interaction but with a higher influence of basal area in the case of Scots pine; and (ii) that despite these differences in their sensitivity to drought and basal area, both species display similar spatial patterns of mortality across their ranges: high mortality in the south resulting from increasingly dry climates, especially in the Mediterranean biome.

2 MATERIAL AND METHODS

2.1 Forest inventory data

We used mortality data from five national forest inventories (NFIs) covering the entire European latitudinal gradient, from the Mediterranean to boreal biome. Data from four of the NFIs had been previously harmonised as part of FunDivEUROPE project (Spain, Germany, Sweden and Finland) and the French NFI was added to this study. In each NFI, trees were recorded in temporary or permanent plots depending on the country. Plots in the German, Finnish and Swedish inventories are gathered within clusters (see Appendix S1 for details of the survey design and sampling methods for each NFI). We selected plots in which at least one of our two target species (i.e. *F. sylvatica* or *P. sylvestris*) was recorded. These plots were classified into Mediterranean, cool temperate and boreal biomes (see the map of biome boundaries in Fig. S1.1) and were unevenly distributed along the latitudinal gradient (Fig. S1.2). The final datasets contained 57,191 beech trees and 161,720 Scots pine trees in 10,150 plots and 16,669 plots, respectively. From those trees, 1,490 (2.6%) and 7,649 (4.7 %) were recorded as dead for beech and Scots pine, respectively.

As explanatory variables of tree mortality, we selected tree *DBH* (diameter at breast height) as *DBH* is known to influence individual tree mortality (Ruiz-Benito *et al.*, 2013). We additionally calculated three proxies of indirect competition between trees (or facilitation) (Fig. S2.1): basal area of neighbouring trees considering all tree species (i.e. *BAall*, $m^2\ ha^{-1}$), basal area of neighbouring conspecifics (i.e. *BAintra*, $m^2\ ha^{-1}$) and basal area of neighbouring heterospecifics (i.e. *BAinter*, $m^2\ ha^{-1}$).

2.2 Drought-related variables

Climatic drought intensity over the study period (Fig. S2.2) was characterised by a water availability index: $WAI = (MAP-PET) / PET$, where *MAP* is the mean annual precipitation (mm) and *PET* the mean potential evapotranspiration (mm). For each plot, *PET* was extracted from the CRU v3.24.01 monthly gridded dataset at 0.5-degree resolution (Harris *et al.*, 2013) and *MAP* was calculated from a downscaled version of E-OBS at 1 km resolution (Moreno & Hasenauer, 2016). For each plot, *WAI* was averaged over the period between two years before the first survey date and the second survey date to include delayed effects of drought on mortality (Greenwood *et al.*, 2017).

Changes in climatic drought intensity over the study period (i.e. temporal variability of drought intensity) were described by the Standardized Precipitation Evapotranspiration Index (*SPEI,* Fig. S2.2; Vicente-Serrano *et al.*, 2009), obtained from a gridded dataset at 0.5-degree resolution (Beguería & Vicente Serrano, 2017). *SPEI* is a multi-scalar drought index whose variations have been shown to be highly correlated with tree response to climate (Greenwood *et al.*, 2017). Its calculation considers both *PET* and *MAP*, with *PET* derived from the Penman-Monteith equation. *SPEI* compares drought intensity during a long-term reference period (i.e. from 1901 to 2015) to that of a given period from 3 to 48 months. In our study, we selected a 12-month period to consider both current and previous year water shortage. *SPEI* is expressed as a standardised index relative to each site, with a standard deviation of 1, where negative values indicate more intense drought over the timescale considered compared to reference conditions. For each plot, we calculated mean *SPEI* (hereafter *SPEI*) over the period from two years before the first survey date to the second survey date.

2.3 Model description

We parameterised two species-specific models, where P_i is the annual probability of mortality for each individual tree *i*. We used a logistic regression model with a link *cloglog* to allow the sigmoidal curve of the mortality probability to be asymmetrical and deal with zero inflated distributions (Zuur *et al.*, 2009):

$$P_i = 1 - \exp(-\exp(\alpha_0 + \alpha_{country} + k_{i,sp} + \log(t_i))) \quad (1)$$

where α_0 is an intercept term (set to zero); $\log(t_i)$ is an offset variable that takes into account the survey interval length t_i (years) for each tree *i*; $\alpha_{country}$ is the random country intercept to include the sampling differences between each NFI and $k_{i,sp}$ is a species-specific linear function that includes the relationship between the mortality of tree *i* of the species *sp* (i.e. *F. sylvatica* or *P. sylvestris*) and the explanatory fixed-effect variables. Although clusters and plots could be considered as a source of variation for each tree, we did not consider cluster and plot as random terms because most of the clusters contained only one plot and in many plots no trees died between the two survey dates. We used the function "glmer" of the "lme4" package to run the model described in equation 1 in R 3.3.3 (R Core Team 2017).

For both species, we explained mortality patterns using four fixed-effect predictors with low collinearity (i.e. Spearman correlation coefficient: $r < 0.59$, and Variance Inflection Factor: VIF < 2; Dormann *et al.*, 2013), namely: *BAintra*, *BAinter*, *WAI* and *SPEI.* Conspecific and heterospecific basal area (i.e. *BAintra* and *BAinter*) were both included in the model as they can have different effects on tree mortality (Condés & del Río, 2015). To ensure a linear relationship between each explanatory variable and tree mortality, *BAinter*, *WAI* and *SPEI* were log transformed (see Appendix S3 for details).

Tree size (*DBH*) was included as a covariate in our model, as we were not directly interested in the importance of tree size on mortality. As we required a single parameter per predictor to estimate the relative importance of each predictor (see section 2.5), we calculated a non-linear variable from *DBH*: $DBHnl_{sp} = DBH + r_{sp} \times \log(DBH)$ (see Appendix S3 for details).

To understand how tree mortality was affected by basal area and climatic drought, we included the main effect of each variable and first-order interaction terms between abiotic and biotic variables. Herewith, the function *k* from equation 1 took the form:

$$\begin{aligned} k_{i,sp} = {} & \beta_{1,sp} \times \log(WAI_i) + \beta_{2,sp} \times \log(SPEI_i) \\ & + DBHnl_{i,sp} \times (\beta_{3,sp} + \gamma_{1,sp} \times \log(WAI_i) + \gamma_{2,sp} \times \log(SPEI_i)) \\ & + BAintra_i \times (\beta_{4,sp} + \gamma_{3,sp} \times \log(WAI_i) + \gamma_{4,sp} \times \log(SPEI_i)) \\ & + \log(BAinter_i) \times (\beta_{5,sp} + \gamma_{5,sp} \times \log(WAI_i) + \gamma_{6,sp} \times \log(SPEI_i)) \end{aligned} \quad (2)$$

where β_x and γ_x are the estimated coefficients of the main and interaction effects, respectively (Table S3.1).

2.4 Model performance and evaluation

Binned residuals plots were used to ensure our final species-specific models were well-calibrated (Fig. S3.3-4). To evaluate the discrimination accuracy of our models, we computed the mean area under the curve (AUC) on 100 bootstrap samples among the predicted and observed values. AUC values of 0.6-0.7 show a fair discrimination accuracy, between 0.7 and 0.8 good and above 0.8 excellent (Hurst *et al.*, 2011). We used independent cross-validation to measure the generalisation power of the model, for which we used 75% of the data to fit the model and the remaining 25% to independently validate our predictions.

2.5 Relative importance of climatic drought and basal area on mortality

Following Ratcliffe *et al.*, (2016), we explored the relative importance of each predictor on individual tree mortality in relation to the other predictors by considering the predictors' main effects and their interactions. For doing so, we first computed the absolute importance of each predictor using our model coefficients. For instance, to compute $A_{BAintra,i}$ the absolute importance of *BAintra* on the probability of mortality of the tree i, we applied the following equation separately for each species:

$$A_{BAintra,i,sp} = \beta_{4,sp} + \gamma_{3,sp} \times \log(WAI_i) + \gamma_{4,sp} \times \log(SPEI_i) \qquad (3)$$

where β_x and γ_x are the estimated coefficients of the single predictors and their interaction effects respectively; WAI_i and $SPEI_i$, are the plot values corresponding to these variables.

Secondly, the relative importance of each predictor was computed for each tree by dividing the absolute importance of the focal predictor by the maximum absolute importance between all predictors of the target tree. For instance, to estimate the relative importance of *BAintra* for the tree i, we calculated for each species: $|A_{BAintra,i,sp}| / \max(|A_{BAintra,i,sp}|, |A_{SPEI,i,sp}|, |A_{WAI,i,sp}|, |A_{BAinter,i,sp}|)$; where $A_{SPEI,i}$, $A_{WAI,i}$ and $A_{BAinter,i}$ are the absolute importance of *SPEI*, *WAI* and *BAinter* for tree i, respectively. For each tree i, the predictor that had the greatest influence on individual tree mortality probability had a relative importance of one.

3 RESULTS

3.1 Model performance and validation

Scots pine and beech models showed good agreement between observed and predicted values (AUC = 0.73 and 0.71, respectively). The Scots pine model performed well in predicting annual tree mortality probability across the European latitudinal gradient as predicted and observed values exhibited similar patterns (Fig. 1a). Nevertheless, caution is needed to interpret the results at the southern part of the latitudinal gradient where Scots pine mortality probability was slightly underestimated. In the beech model, mortality probability was accurately predicted in the southern half of the latitudinal gradient but was overestimated between 48° and 54° latitude, which corresponds mainly to northern Germany (Fig. 1b). Model and partial residual plots for each predictor showed no strong spatial patterns, thus supporting the validity of the models (Fig. S3.3-4).

3.2 Relative importance of climatic drought and basal area across latitude

In the case of Scots pine, basal area variables (i.e. *BAintra* and *BAinter*) were more important than drought-related variables (i.e. *WAI* and *SPEI*) in explaining the probability of mortality across the latitudinal gradient (Fig. 2a and Table 1). The conspecific basal area was the most important driver from south to north with a mean relative importance of 0.96 (Table 1). The order of importance of the four predictors was stable across latitude, except from 43° to 45° latitude (corresponding to the French part of the Mediterranean biome) where drought-related variables (mainly *SPEI*) were nearly as important as basal area variables (Fig. 2a). From south to north, high levels of both conspecific and heterospecific basal area and increases in drought intensity (i.e. low *SPEI*) were correlated with higher probability of mortality (Fig. 2a). In contrast, low *WAI* was associated with high mortality probabilities in the Mediterranean biome and with low mortality probabilities in the boreal biome (see changes from negative to positive influence in Fig. 2a).

For beech trees, drought-related variables were more important than basal area variables in explaining mortality probability across the major part of the latitudinal gradient (except in the south) with a mean relative importance of 0.74 and 0.70 for *WAI* and *SPEI*, respectively (Fig. 3a and Table 1). Low *WAI* and *SPEI* were associated with higher mortality rates (see negative influence in Fig. 3a). The relative importance of conspecific basal area remained stable across latitude whereas that of heterospecifics varied from being the most important variable explaining beech mortality in the Mediterranean biome to being the least important one in the cool temperate biome (Fig. 3a and Table 1). Beech mortality probability increased with conspecific basal area and decreased with heterospecific basal area (Fig. 3A and Table 1).

3.3 Interactions between climatic drought and basal area

In the Scots pine model, all interactions between drought-related variables (i.e. *WAI* and *SPEI*) and basal area variables (i.e. *BAintra* and *BAinter*) were significant (Table S3.1). The strongest interaction was between climatic drought intensity and conspecific basal area (i.e. *WAI* and *BAintra*; Fig 3b & Table S3.1): regardless of drought intensity, the probability of mortality remained weak when the conspecific basal area was low or intermediate, whereas it strongly increased in dry areas where the conspecific basal area was high (Fig. 2b; see Fig. S4 for the other interactions that affected mortality weakly, albeit significantly).

In the beech model, the only significant interaction was that between climatic drought and heterospecific basal area (*WAI* and *BAinter*; Table S3.1): the probability of mortality increased in dry areas where heterospecific basal area was low or intermediate, while the probability of mortality remained stable (and always low) in dry areas where heterospecific basal area was high (Fig. 3b).

3.4 Spatial patterns of predicted tree mortality across Europe

Across their range, the predicted annual probability of Scots pine mortality was on average higher than that of beech (0.0061 and 0.0038, respectively; Table 1) but followed the same trend across the latitudinal gradient (Fig. 4). The highest predicted mortality rates for both species were in south-eastern France, at the ecotone between the Mediterranean and cool temperate biomes (Fig. 4).

The predicted rates of Scots pine mortality were highest in the Mediterranean biome (mean value of 0.0077 for 62,165 trees), intermediate in the cool temperate biome (mean value of 0.0063 for 62,914 trees) and lowest in the boreal biome (mean value of 0.0033 for 36,641 trees) (Table 1). Similarly, the predicted individual probability of beech mortality was higher in the Mediterranean biome (mean value of 0.0052 for 9,315 trees) than in the cool temperate biome (mean 0.0035 for 47,876 trees) (Table 1). However, the gap between mortality rates in the Mediterranean biome and the more northern biomes is likely to be higher than predicted as the Scots pine model slightly underestimated mortality probability in the Mediterranean biome (Fig. 1a) and the beech model overestimated mortality probability in the cool temperate biome (Fig. 1b).

4 DISCUSSION

Exploring the drivers of background tree mortality at a continental scale opens a new perspective for understanding tree mortality patterns across species' ranges, including some demographic events observed at a smaller scale (Carnicer *et al.*, 2011). Although considerable attention has been paid to the effects of drought and basal area on tree mortality (Mantgem *et al.*, 2009; Greenwood *et al.*, 2017; Hember *et al.*, 2017; Ruiz-Benito *et al.*, 2013), our results demonstrate that the combination of the two, through direct and indirect effects that vary along geographical gradients and between the two species (Fig. 2 and 3), is shaping background mortality across species' ranges (see also Ruiz-Benito *et al.*, 2013; Jump *et al.*, 2017; Young *et al.*, 2017). Interestingly, both species had similar patterns of predicted mortality, with the highest mortality rates in the southern French part of the Mediterranean biome (Fig. 4).

4.1 Increase in climatic drought intensity associated with higher mortality rates

Drought-related variables were more important for beech mortality than Scots pine (Fig. 2 and 3), probably reflecting functional differences in species responses to drought (Choat *et al.*, 2018). Scots pine is a drought-avoiding species (e.g. a species which rapidly closes its stomata to maintain high water status; McDowell *et al.*, 2008), that can survive from wet to dry environments (San-Miguel-Ayanz *et al.*, 2016), whereas beech is a drought-sensitive species (van der Maaten, 2012; Chen *et al.*, 2015) with an anisohydric response to drought (e.g. a species that keeps its stomata open until late during droughts to maintain carbon uptake; McDowell *et al.*, 2008). Nevertheless, both beech (i.e. an angiosperm and broad-leaved species) and Scots pine (i.e. a gymnosperm and evergreen species) exhibited higher mortality rates in areas that were subject to increasing droughts during the study period (negative *SPEI*; Fig. 2 and 3). This result suggests that major phylogenetic and functional groups could display a similar mortality response to increasing drought (Greenwood *et al.*, 2017) and is consistent with the results of a multi-species study suggesting that climatic extremes (like extreme droughts) are affecting tree mortality in Europe (Neumann *et al.*, 2017).

The increase in drought intensity that occurred at about 45° latitude during the study period (see the lowest *SPEI* values in Fig. S2.1 and S2.3b) could be responsible for the higher tree mortality rates in the Mediterranean biome (Fig. 4), which is also supported by the high relative importance of the increase in drought intensity at this latitude (see the highest values of *SPEI* in Fig. 2 and 3). Moreover, we observed higher mortality rates in the driest areas (i.e. low *WAI*), as already reported for Scots pine in some inner Alpine valleys (Rigling *et al.*, 2013) and in the Iberian Peninsula (Vilà-Cabrera *et al.*, 2011; Galiano *et al.*, 2011). Nevertheless, the stronger effect of increasing droughts over the study period (i.e. *SPEI*) than that of drought intensity (i.e. *WAI*) on Scots pine mortality could mean that mortality events tend to occur when drought conditions exceed the average in a given area, suggesting a certain degree of Scots pine adaptation to local conditions (Savolainen *et al.*, 2007).

Drought-related variables were key drivers of beech mortality and were comparatively more important than heterospecific and conspecific basal area. A regional study of tree mortality suggested that competition between trees is more important than climate (Ruiz-Benito *et al.*, 2013), but that study did not cover a climatic gradient as large as our study. Drought-induced mortality could also be studied under the assumption that mortality events follow a period of reduced growth (Caillleret *et al.*, 2016). This assumption needs to be used with caution for beech, which can survive long periods of reduced growth before death (Hülsmann *et al.*, 2018). In addition, beech growth-based studies produced contradictory results, showing both drought-induced reduction in growth (Jump *et al.*, 2006) and drought-associated increase in growth (Tegel *et al.*, 2014). Contrarily, Scots pine growth variations (i.e. and those of gymnosperms in general; Cailleret *et al.*, 2016) can be used to predict upcoming drought-induced mortality events because, although more drought-resistant, Scots pine does not support long periods of reduced growth (Hülsmann *et al.*, 2018).

4.2 Conspecific and heterospecific neighbours can affect individual tree mortality differently

Competition is a critical driver of forest structure (Kunstler *et al.*, 2016), which strongly influences tree mortality and is comparatively more important for shade-intolerant than shade-tolerant species (Ruiz-Benito *et al.*, 2013). High mortality rates were associated with high conspecific basal area in both species and high heterospecific basal area in Scots pine. However, high heterospecific basal area was correlated with low mortality rates in beech (Fig. 2 and 3). Scots pine is a shade-intolerant tree which is highly sensitive to competition for light (Ruiz-Benito *et al.*, 2013), which might explain why both intra and inter-specific competition strongly and positively influenced its mortality rate (Condés & del Río, 2015). In contrast, beech is a late successional and shade-tolerant species (Hülsmann *et al.*, 2018) that outcompetes other species in fertile sites (Condés & del Río, 2015). This is consistent with our observation of high mortality rates with high conspecific basal area but also with low heterospecific basal area: beech mainly suffers from the presence of conspecific neighbours, but not from heterospecific neighbours, which are necessarily less competitive species. This result is supported by growth studies showing that beech benefits from admixture with other species but is highly sensitive to intra-specific competition (Pretzsch *et al.*, 2013a; Ratcliffe *et al.*, 2015).

The heterospecific basal area affected the mortality rates of both species less than the conspecific basal area (Table S3.1, Fig. 2 and 3). The dominant nature of both Scots pine and beech in European forests may partly explain this difference as the basal area of heterospecifics was much lower than that of conspecifics all along the latitudinal gradient (Fig. S2.1). Nevertheless, the overdominance of intra-specific competition, a key process for stabilising ecosystems, is a globally-observed pattern (Kunstler *et al.*, 2016), which could be linked to how interspecific differences determine complementarity mechanisms and, consequently, individual resource-use and coexistence mechanisms (Ruiz-Benito *et al.*, 2017b).

4.3 The effects of climatic drought and basal area should be considered jointly in mortality studies

Competition with neighbours can be expressed as asymmetric competition for light on small suppressed trees (Ruiz-Benito *et al.*, 2013) but also as symmetric competition for limited resources, like water or nutrients (Franklin *et al.*, 1987; Gessler *et al.*, 2017). Drought-induced mortality may be strong in areas with high levels of competition, because plants are more stressed and small changes in water availability could result in massive mortality events (Bradford and Bell, 2017; Ruiz-Benito *et al.*, 2013; Young *et al.*, 2017). In the case of Scots pine, the strong interaction between drought intensity and conspecific basal area reinforces this assumption (Table S3.1). Indeed, mortality rates were high in dry areas with high conspecific basal area whereas in areas with lower conspecific basal area, trees had still sufficient resources to survive despite reduced water availability (Fig. 2b). This result suggests that Scots pine suffers from the presence of neighbouring trees only when resources are scarce (Young *et al.*, 2017).

In the case of beech, the influence of conspecific basal area on mortality was not modulated by drought (Table S3.1), suggesting that resource depletion does not exacerbate competitive pressure among beech trees. However, the probability of beech mortality in the driest areas was considerably higher when heterospecific basal area, the most important predictor in the Mediterranean biome (Fig. 3a & Table 2), was low (Fig. 3b). These findings suggest that beech survival in the driest part of its range is positively influenced by its neighbours (facilitation), which are mainly *Q. pyrenaica*, *P. sylvestris* and *C. sativa* (Table S5.1). Our results can only be compared to those of growth studies because the effect of mixing species has been more investigated in growth than mortality studies. Beech trees were shown to be more resilient and resistant to drought in mixed stands with oaks (Pretzsch *et al.*, 2013b). By contrast, Bosela *et al.* (2018) found that the growth of beeches mixed with fir trees or in pure stands was equally negatively affected by long-term droughts but they didn't explore the south-western part of beech distribution. Overall, these results suggest that beech growth and mortality are influenced by interspecific interactions that vary along the European drought gradient: from neutral interactions in wet areas where beech co-occurs mainly with *Abies alba* and *Picea abies*, to facilitation in dry areas where beech co-occurs with more Mediterranean species (Fig 3b & Table S5.1). However, the mechanisms behind these interspecific interactions, particularly in dry areas, are still largely unknown. Identifying associations of species that can survive droughts could help to better understand drought-related mortality patterns in the coming years.

In the case of Scots pine, previous regional studies reported contradictory interaction effects between competition and drought: higher rate of decline in dry areas but only at low competition levels (Vilà-Cabrera *et al.*, 2013), low mortality rates related to high heterospecific basal area in wet areas (Condés & del Río, 2015) and only additive effects of competition and drought on mortality with no interaction effects (Galiano *et al.*, 2010). Our study is the first to describe interaction patterns between drought and basal area at the scale of the distribution of each species (Fig. 2, 3 and S4). As we found four significant interactions (albeit three of which only slightly affect mortality) influencing Scots pine mortality and only one in the case of beech (Table S3.1), we can assume that Scots pine mortality is affected directly and indirectly by drought through interactions with basal area while beech mortality was more directly affected by drought.

4.2 Tree mortality patterns along latitude and potential associated range shifts

Predicted probability of mortality in both beech and Scots pine was higher in the southern part of their distribution, mainly corresponding to the French part of the Mediterranean biome and the Pyrenees in the case of beech (Fig. 4). In these areas, beech and Scots pine mortality rates were accurately predicted (Fig. 1), except at the southern end of Scots pine range where mortality rates are likely to be slightly higher than predicted (Fig. 1a). These accurate predictions in the southern part of species ranges were expected as we chose climatic variables related to droughts, generally more important in the Mediterranean biome (Fig. S2.3). Surprisingly, the association of drought and competition-related variables alone explained Scots pine mortality patterns in the northern part of its distribution (Fig. 1a) but overestimated the probability of beech mortality in northern Germany (Fig. 1b) suggesting that other factors come into play in these areas to explain beech mortality patterns (see 4.3 Limitations).

An unexpected result was that French Mediterranean Scots pines and beech trees suffered even more from climatic drought than those in Spain, where several studies reported high mortality or defoliation rates in the Iberian Peninsula in both species (Carnicer *et al.*, 2011; Vilà-Cabrera *et al.*, 2011, 2013; Benito Garzón *et al.*, 2013). Nevertheless, this pattern may be explained by the high altitudes at which both species occur in Spain, and the calcareous soils of southeastern France, which do not retain water and are consequently very dry. In the case of Scots pine, we also hypothesise that local adaptation to temperature explains our underestimated mortality predictions in the southernmost part of the gradient (Savolainen *et al.*, 2007): populations in these areas may be highly locally-adapted to drought conditions and therefore less resistant to changing climate (Benito Garzón *et al.*, 2011).

The high mortality rates predicted in the French part of the Mediterranean biome could be explained by the increase in drought intensity during the study period in that region (Fig. S2.3b), suggesting that mortality plays a critical role in delimiting the driest part of the species ranges (Gaston, 2009; Benito Garzón *et al.*, 2013; Ruiz-Benito *et al.*, 2017a), in particular in the Mediterranean biome, which is expected to face drier conditions in the coming decades. In addition to direct effects of climate change, Scots pine and beech are exposed to more intense fires in the driest parts of their range (Fréjaville *et al.*, 2018) and these should increase the likelihood of range contraction at the ecotone between Mediterranean and cool temperate biomes.

4.3 Limitations

Until recently, European forests have been extensively exploited and forest management is still widespread, particularly in the Scandinavian countries (Schelhaas *et al.*, 2018). Although we removed the direct effects of management in our study (i.e. by removing plots in which trees were noted as harvested), management may still result in both an overestimation (e.g. by reducing competition pressure in thinned plots) and an underestimation of natural mortality rates through salvage loggings (i.e. the harvest of dead trees after a natural disaster) or sanitation fellings (i.e. the harvest of diseased trees).

Other factors also affect tree mortality, either directly, indirectly or through interactions, such as: changes in disturbance regimes (Seidl *et al.*, 2017), insect outbreaks (Anderegg *et al.*, 2015), mistletoe (Dobbertin & Rigling, 2006), atmospheric pollutants (Dietze & Moorcroft, 2011), populations genetic differentiation and plasticity (Benito Garzón *et al.*, 2011), soil characteristics (Dietze & Moorcroft, 2011). However, given our concern to limit the model complexity and the lack of large-scale data, we decided not to include them in our study and to focus on comparing the effects of drought and competition on mortality.

CONCLUSIONS

Mortality of Scots pine and beech was affected by climatic drought intensity and indirect competition from neighbouring trees, but in different ways. Drought directly affected beech mortality rates and beech trees benefited from mixing with other species, particularly in the Mediterranean biome. Scots pine mortality suffered mostly from competition and was indirectly affected by drought through interactions with competitors, especially in southeastern France. In this area, which experienced a marked increase in drought intensity during the study period, high mortality rates were predicted for both species, as expected for temperate trees for which the Mediterranean biome corresponds to the southernmost part of the distribution. In a warming climate, our study is a step further in understanding geographical patterns of tree mortality in Europe and shed light on the high mortality risks faced by European tree species, regardless of their different life-history strategies, especially at the ecotone between the Mediterranean and cool temperate biomes. In this priority area, beech could benefit from mixing with other species and pine from reduced competition.

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443 BIBLIOGRAPHY

Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6, 1–55. https://doi.org/10.1890/ES15-00203.1

Anderegg, W.R.L., Hicke, J.A., Fisher, R.A., Allen, C.D., Aukema, J., Bentz, B., Hood, S., Lichstein, J.W., Macalady, A.K., McDowell, N., Pan, Y., Raffa, K., Sala, A., Shaw, J.D., Stephenson, N.L., Tague, C., Zeppel, M., 2015. Tree mortality from drought, insects, and their interactions in a changing climate. New Phytol 208, 674–683. https://doi.org/10.1111/nph.13477

Beguería, S., Vicente Serrano, S.M., 2017. SPEIbase v.2.5. http://dx.doi.org/10.20350/digitalCSIC/8508

Benito Garzón, M., Alía, R., Robson, T.M., Zavala, M.A., 2011. Intra-specific variability and plasticity influence potential tree species distributions under climate change. Global Ecology and Biogeography 20, 766–778. https://doi.org/10.1111/j.1466-8238.2010.00646.x

Benito Garzón, M., Muñoz, N.G., Wigneron, J.-P., Moisy, C., Fernández-Manjarrés, J., Delzon, S., Jordan, G., 2018. The legacy of water deficit on populations having experienced negative hydraulic safety margin. Global Ecology and Biogeography 27, 346–356. https://doi.org/10.1111/geb.12701

Benito Garzón, M., Ruiz-Benito, P., Zavala, M.A., 2013. Interspecific differences in tree growth and mortality responses to environmental drivers determine potential species distributional limits in Iberian forests. Global Ecology and Biogeography 22, 1141–1151. https://doi.org/10.1111/geb.12075

Bradford, J.B., Bell, D.M., 2017. A window of opportunity for climate-change adaptation: easing tree mortality by reducing forest basal area. Frontiers in Ecology and the Environment 15, 11–17. https://doi.org/10.1002/fee.1445

Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Čada, V., Camarero, J.J., Cherubini, P., Cochard, H., Coyea, M.R., Čufar, K., Das, A.J., Davi, H., Delzon, S., Dorman, M., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hartmann, H., Hereş, A.-M., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Kramer, K., Lens, F., Levanic, T., Linares Calderon, J.C., Lloret, F., Lobo-Do-Vale, R., Lombardi, F., López Rodríguez, R., Mäkinen, H., Mayr, S., Mészáros, I., Metsaranta, J.M., Minunno, F., Oberhuber, W., Papadopoulos, A., Peltoniemi, M., Petritan, A.M., Rohner, B., Sangüesa-Barreda, G., Sarris, D., Smith, J.M., Stan, A.B., Sterck, F., Stojanović, D.B., Suarez, M.L., Svoboda, M., Tognetti, R., Torres-Ruiz, J.M., Trotsiuk, V., Villalba, R., Vodde, F., Westwood, A.R., Wyckoff, P.H., Zafirov, N., Martínez-Vilalta, J., 2017. A synthesis of radial growth patterns preceding tree mortality. Glob Change Biol 23, 1675–1690. https://doi.org/10.1111/gcb.13535

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., Peñuelas, J., 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. PNAS 108, 1474–1478. https://doi.org/10.1073/pnas.1010070108

Chen, K., Dorado-Liñán, I., Akhmetzyanov, L., Gea-Izquierdo, G., Zlatanov, T., Menzel, A., 2015. Influence of climate drivers and the North Atlantic Oscillation on beech growth at marginal sites across the Mediterranean. Climate Research 66, 229–242. https://doi.org/10.3354/cr01345

Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., López, R., Medlyn, B.E., 2018. Triggers of tree mortality under drought. Nature 558, 531–539. https://doi.org/10.1038/s41586-018-0240-x

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012. Global convergence in the vulnerability of forests to drought. Nature 491, 752–755. https://doi.org/10.1038/nature11688

Condés, S., Río, M. del, 2015. Climate modifies tree interactions in terms of basal area growth and mortality in monospecific and mixed Fagus sylvatica and Pinus sylvestris forests. Eur J Forest Res 134, 1095–1108. https://doi.org/10.1007/s10342-015-0912-0

Das, A.J., Stephenson, N.L., Davis, K.P., 2016. Why do trees die? Characterizing the drivers of background tree mortality. Ecology 97, 2616–2627. https://doi.org/10.1002/ecy.1497

Dietze, M.C., Moorcroft, P.R., 2011. Tree mortality in the eastern and central United States: patterns and drivers. Glob Change Biol 17, 3312–3326. https://doi.org/10.1111/j.1365-2486.2011.02477.x

Dobbertin, M., Rigling, A., 2006. Pine mistletoe (Viscum album ssp. austriacum) contributes to Scots pine (Pinus sylvestris) mortality in the Rhone valley of Switzerland. Forest Pathology 36, 309–322. https://doi.org/10.1111/j.1439-0329.2006.00457.x

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree Death as an Ecological Process. BioScience 37, 550–556. https://doi.org/10.2307/1310665

Fréjaville, T., Curt, T., Carcaillet, C., 2018. Higher potential fire intensity at the dry range margins of European mountain trees. Journal of Biogeography 45, 2003–2015. https://doi.org/10.1111/jbi.13386

Galiano, L., Martínez-Vilalta, J., Lloret, F., 2010. Drought-Induced Multifactor Decline of Scots Pine in the Pyrenees and Potential Vegetation Change by the Expansion of Co-occurring Oak Species. Ecosystems 13, 978–991. https://doi.org/10.1007/s10021-010-9368-8

Gaston, K.J., 2009. Geographic range limits: achieving synthesis. Proceedings of the Royal Society of London B: Biological Sciences rspb.2008.1480. https://doi.org/10.1098/rspb.2008.1480

Gessler, A., Schaub, M., McDowell, N.G., 2017. The role of nutrients in drought-induced tree mortality and recovery. New Phytologist 214, 513–520. https://doi.org/10.1111/nph.14340

Gómez-Aparicio, L., García-Valdés, R., Ruiz-Benito, P., Zavala, M.A., 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. Global Change Biology 17, 2400–2414. https://doi.org/10.1111/j.1365-2486.2011.02421.x

Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C.D., Fensham, R., Laughlin, D.C., Kattge, J., Bönisch, G., Kraft, N.J.B., Jump, A.S., 2017. Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. Ecol Lett 20, 539–553. https://doi.org/10.1111/ele.12748

Harris, I., Jones, P.D., Osborn, T.J., Lister, D.H., 2013. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. International Journal of Climatology 34, 623–642. https://doi.org/10.1002/joc.3711

Hartmann, H., Schuldt, B., Sanders, T.G.M., Macinnis-Ng, C., Boehmer, H.J., Allen, C.D., Bolte, A., Crowther, T.W., Hansen, M.C., Medlyn, B.E., Ruehr, N.K., Anderegg, W.R.L., 2018. Monitoring global tree mortality patterns and trends. Report from the VW symposium ‘Crossing scales and disciplines to identify global trends of tree mortality as indicators of forest health.’ New Phytol 217, 984–987. https://doi.org/10.1111/nph.14988

Hember, R.A., Kurz, W.A., Coops, N.C., 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. https://doi.org/10.1111/gcb.13428

Hülsmann, L., Bugmann, H., Cailleret, M., Brang, P., 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. https://doi.org/10.1002/eap.1668

Hurst, J.M., Allen, R.B., Coomes, D.A., Duncan, R.P., 2011. Size-Specific Tree Mortality Varies with Neighbourhood Crowding and Disturbance in a Montane Nothofagus Forest. PLOS ONE 6, e26670. https://doi.org/10.1371/journal.pone.0026670

Jump, A.S., Hunt, J.M., Peñuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of Fagus sylvatica. Global Change Biology 12, 2163–2174. https://doi.org/10.1111/j.1365-2486.2006.01250.x

Jump, A.S., Ruiz-Benito, P., Greenwood, S., Allen, C.D., Kitzberger, T., Fensham, R., Martínez-Vilalta, J., Lloret, F., 2017. Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. Glob Change Biol 23, 3742–3757. https://doi.org/10.1111/gcb.13636

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J.H.C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., Onoda, Y., Peñuelas, J., Poorter, H., Uriarte, M., Richardson, S., Ruiz-Benito, P., Sun, I.-F., Ståhl, G., Swenson, N.G., Thompson, J., Westerlund, B., Wirth, C., Zavala, M.A., Zeng, H., Zimmerman, J.K., Zimmermann, N.E., Westoby, M., 2016. Plant functional traits have globally consistent effects on competition. Nature 529, 204–207. https://doi.org/10.1038/nature16476

van der Maaten, E., 2012. Climate sensitivity of radial growth in European beech (Fagus sylvatica L.) at different aspects in southwestern Germany. Trees 26, 777–788. https://doi.org/10.1007/s00468-011-0645-8

Manion, P.D., 1981. Tree disease concepts. Tree disease concepts.

Mantgem, P.J. van, Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread Increase of Tree Mortality Rates in the Western United States. Science 323, 521–524. https://doi.org/10.1126/science.1165000

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytologist 178, 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

Millar, C.I., Stephenson, N.L., 2015. Temperate forest health in an era of emerging megadisturbance. Science 349, 823–826. https://doi.org/10.1126/science.aaa9933

Moreno, A., Hasenauer, H., 2016. Spatial downscaling of European climate data. International Journal of Climatology 36, 1444–1458. https://doi.org/10.1002/joc.4436

Neumann, M., Mues, V., Moreno, A., Hasenauer, H., Seidl, R., 2017. Climate variability drives recent tree mortality in Europe. Glob Change Biol 23, 4788–4797. https://doi.org/10.1111/gcb.13724

Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H., Kohnle, U., Nagel, J., Spellmann, H., Zasada, M., Zingg, A., 2013a. Productivity of mixed versus pure stands of oak (Quercus petraea (Matt.) Liebl. and Quercus robur L.) and European beech (Fagus sylvatica L.) along an ecological gradient. Eur J Forest Res 132, 263–280. https://doi.org/10.1007/s10342-012-0673-y

Pretzsch, H., Schütze, G., Uhl, E., 2013b. 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. https://doi.org/10.1111/j.1438-8677.2012.00670.x

Ratcliffe, S., Holzwarth, F., Nadrowski, K., Levick, S., Wirth, C., 2015. Tree neighbourhood matters – Tree species composition drives diversity–productivity patterns in a near-natural beech forest. Forest Ecology and Management 335, 225–234. https://doi.org/10.1016/j.foreco.2014.09.032

Ratcliffe, S., Liebergesell, M., Ruiz-Benito, P., González, J.M., Castañeda, J.M.M., Kändler, G., Lehtonen, A., Dahlgren, J., Kattge, J., Peñuelas, J., Zavala, M.A., Wirth, C., 2016. Modes of functional biodiversity control on tree productivity across the European continent. Global Ecology and Biogeography 25, 251–262. https://doi.org/10.1111/geb.12406

R Core Team (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.R-project.org/.

Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., Graf, U., Mayer, P., Vacchiano, G., Weber, P., Wohlgemuth, T., Zweifel, R., Dobbertin, M., 2013. Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. Global Change Biology 19, 229–240. https://doi.org/10.1111/gcb.12038

Ruiz-Benito, P., Lines, E.R., Gómez-Aparicio, L., Zavala, M.A., Coomes, D.A., 2013. Patterns and Drivers of Tree Mortality in Iberian Forests: Climatic Effects Are Modified by Competition. PLOS ONE 8, e56843. https://doi.org/10.1371/journal.pone.0056843

Ruiz-Benito, P., Ratcliffe, S., Jump, A.S., Gómez-Aparicio, L., Madrigal-González, J., Wirth, C., Kändler, G., Lehtonen, A., Dahlgren, J., Kattge, J., Zavala, M.A., 2017a. Functional diversity underlies demographic responses to environmental variation in European forests. Global Ecology and Biogeography 26, 128–141. https://doi.org/10.1111/geb.12515

Ruiz-Benito, P., Ratcliffe, S., Zavala, M.A., Martínez-Vilalta, J., Vilà-Cabrera, A., Lloret, F., Madrigal-González, J., Wirth, C., Greenwood, S., Kändler, G., Lehtonen, A., Kattge, J., Dahlgren, J., Jump, A.S., 2017b. Climate- and successional-related changes in functional composition of European forests are strongly driven by tree mortality. Glob Change Biol 23, 4162–4176. https://doi.org/10.1111/gcb.13728

San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A., Tinner, W., Ballian, D., Beck, P., Birks, H., Eaton, E., Enescu, C., Pasta, S., Popescu, I., Ravazzi, C., Welk, E., Abad Viñas, R., Azevedo, J., Barbati, A., Barredo, J., Benham, S., Boca, R., Bosco, C., Caldeira, M., Cerasoli, S., Chirici, G., Cierjacks, A., Conedera, M., Da Ronch, F., Di Leo, M., García-Viñas, J., Gastón González, A., Giannetti, F., Guerrero Hue, N., Guerrero Maldonado, N., López, M., Jonsson, R., Krebs, P., Magni, D., Mubareka, S., Nieto Quintano, P., Oliveira, S., Pereira, J., Pividori, M., Räty, M., Rinaldi, F., Saura, S., Sikkema, R., Sitzia, T., Strona, G., Vidal, C., Vilar, L., Zecchin, B., 2016. European atlas of forest tree species. Publications Office of the European Union. https://doi.org/10.2788/4251

Savolainen, O., Pyhäjärvi, T., Knürr, T., 2007. Gene Flow and Local Adaptation in Trees. Annual Review of Ecology, Evolution, and Systematics 38, 595–619. https://doi.org/10.1146/annurev.ecolsys.38.091206.095646

Schelhaas, M.-J., Fridman, J., Hengeveld, G.M., Henttonen, H.M., Lehtonen, A., Kies, U., Krajnc, N., Lerink, B., Dhubháin, Á.N., Polley, H., Pugh, T.A.M., Redmond, J.J., Rohner, B., Temperli, C., Vayreda, J., Nabuurs, G.-J., 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. https://doi.org/10.1371/journal.pone.0207151

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyer, C.P.O., 2017. Forest disturbances under climate change. Nature Climate Change 7, 395–402. https://doi.org/10.1038/nclimate3303

Sitch, S., Huntingford, C., Gedney, N., Levy, P.E., Lomas, M., Piao, S.L., Betts, R., Ciais, P., Cox, P., Friedlingstein, P., Jones, C.D., Prentice, I.C., Woodward, F.I., 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). Global Change Biology 14, 2015–2039. https://doi.org/10.1111/j.1365-2486.2008.01626.x

Stephenson, N.L., Mantgem, P.J. van, 2005. Forest turnover rates follow global and regional patterns of productivity. Ecology Letters 8, 524–531. https://doi.org/10.1111/j.1461-0248.2005.00746.x

Tegel, W., Seim, A., Hakelberg, D., Hoffmann, S., Panev, M., Westphal, T., Büntgen, U., 2014. A recent growth increase of European beech (Fagus sylvatica L.) at its Mediterranean distribution limit contradicts drought stress. Eur J Forest Res 133, 61–71. https://doi.org/10.1007/s10342-013-0737-7

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2009. A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. J. Climate 23, 1696–1718. https://doi.org/10.1175/2009JCLI2909.1

Vilà-Cabrera, A., Martínez-Vilalta, J., Galiano, L., Retana, J., 2013. Patterns of Forest Decline and Regeneration Across Scots Pine Populations. Ecosystems 16, 323–335. https://doi.org/10.1007/s10021-012-9615-2

Vilà-Cabrera, A., Martínez-Vilalta, J., Vayreda, J., Retana, J., 2011. Structural and climatic determinants of demographic rates of Scots pine forests across the Iberian Peninsula. Ecological Applications 21, 1162–1172. https://doi.org/10.1890/10-0647.1

Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., Latimer, A.M., 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. Ecol Lett 20, 78–86. https://doi.org/10.1111/ele.12711

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. GLM and GAM for Absence–Presence and Proportional Data, in: Mixed Effects Models and Extensions in Ecology with R, Statistics for Biology and Health. Springer, New York, NY, pp. 245–259. https://doi.org/10.1007/978-0-387-87458-6_10 Statistics for Biology and Health., pp. 245–259. Springer, New York, NY.

DATA ACCESSIBILITY

The data are available upon request to the co-authors.

Figure 1. Predicted and observed annual probability of mortality along the latitudinal gradient covered by the NFIs plots a) for *P. sylvestris* and b) for *F. sylvatica*. Predicted and observed values were estimated at the individual-level and were clustered at 1° latitude resolution. A locally weighted regression was used to obtain the smooth solid lines ("loess" method of the geom_smooth function in "ggplot2" R package). Dotted lines indicate 95% confidence intervals. The acronyms MED., TEMP. and BOR. in grey bars refer to the Mediterranean, cool temperate and boreal biome, respectively. The white section for *P. sylvestris* in the Mediterranean biome represents missing data (due to its distribution in Spain).

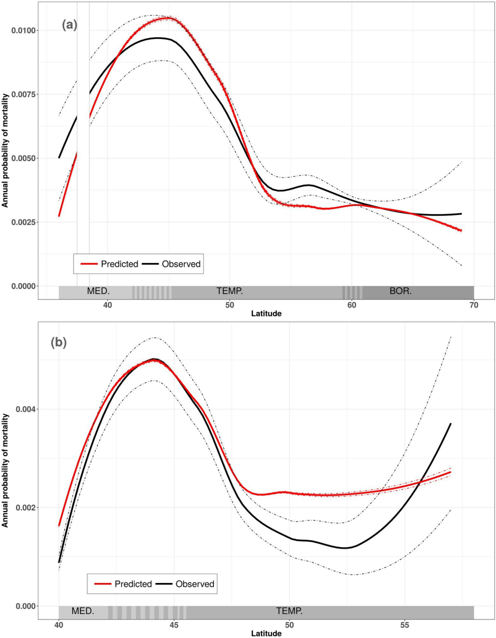

(a)
Annual probability of mortality
0.0100
0.0075
0.0050
0.0025
0.0000
Predicted
Observed
MED.
TEMP.
BOR.
40
50
60
70
Latitude
(b)
Annual probability of mortality
0.004
0.002
0.000
Predicted
Observed
MED.
TEMP.
40
45
50
55
Latitude

Figure 2. Effects of drought-related variables and basal area on Scots pine mortality. a) Relative importance of the changes in climatic drought intensity over the study period (i.e. *SPEI*), climatic drought intensity (i.e. *WAI*), conspecific basal area (i.e. *BAintra*) and heterospecific basal area (i.e. *BAinter*) on Scots pine predicted probability of mortality. The relative importance of each variable was computed for each tree from the logistic regression model (see section 2.5), by giving a value of one to the most influencing variable and scaling the remaining variables accordingly. For each variable, the relative importance values were aggregated by 1° latitude resolution and the points of the graph correspond to the average values. The grey areas around the curves correspond to the 95% confidence intervals. The acronyms MED., TEMP. and BOR. in grey bars refer to the Mediterranean, cool temperate and boreal biome, respectively. The white section corresponds to missing data at that latitude (due to Scots pine distribution in Spain). **b) Interactions between conspecific basal area (i.e. *BAintra*) and climatic drought intensity (i.e. *WAI*) on Scots pine probability of mortality.** This interaction was considered significant if its z value was lower than -2 or higher than 2 and was the most important interaction influencing Scots pine mortality (Table S3.1). Scots pine mortality was predicted at three different levels of conspecific basal area (mean value, 99.5th percentile and 0.005th percentile; proxies of average, high and low competition, respectively) along a drought gradient while the other predictors were fixed at their mean value.

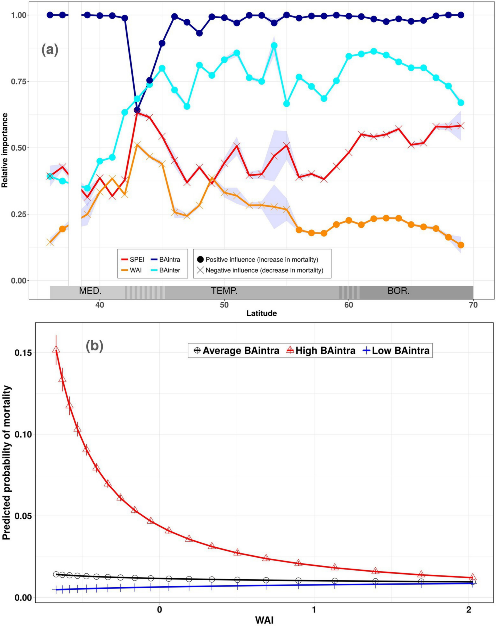

(a)
Relative importance
1.00
0.75
0.50
0.25
0.00
SPEI
WAI
BAintra
BAinter
● Positive influence (increase in mortality)
× Negative influence (decrease in mortality)
MED.
TEMP.
BOR.
40
50
60
70
Latitude
(b)
Predicted probability of mortality
0.15
0.10
0.05
0.00
Average BAintra
High BAintra
Low BAintra
0
1
2
WAI

Figure 3. Effects of drought-related variables and basal area on beech mortality. a) Relative importance of the changes in climatic drought intensity over the study period (i.e. *SPEI*), climatic drought intensity (i.e. *WAI*), conspecific basal area (i.e. *BAintra*) and heterospecific basal area (i.e. *BAinter*) on beech predicted probability of mortality. The relative importance of each variable was computed for each tree from the logistic regression model (see section 2.5), by giving a value of one to the most influencing variable and scaling the remaining variables accordingly. For each variable, the relative importance values were aggregated by 1° latitude resolution and the points of the graph correspond to the average values. The grey areas around the curve correspond to the 95% confidence intervals. The acronyms MED. and TEMP. in grey bars refer to the Mediterranean and cool temperate biome, respectively. **b) Interaction between heterospecific basal area (i.e. *BAinter*) and climatic drought intensity (i.e. *WAI*) on beech probability of mortality.** This interaction was considered significant as its z value was higher than 2 (see Table S3.1). Beech mortality was predicted at three different levels of heterospecific basal area (mean value, 99.5th percentile and 0.005th percentile; proxies of average, high and low competition, respectively) along a drought gradient while the other predictors were fixed at their mean value.

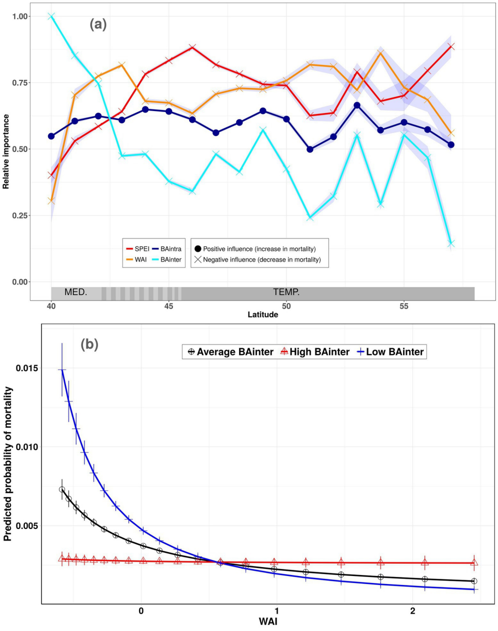
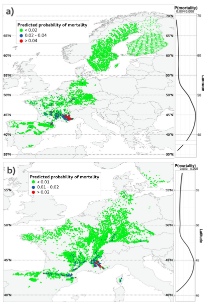
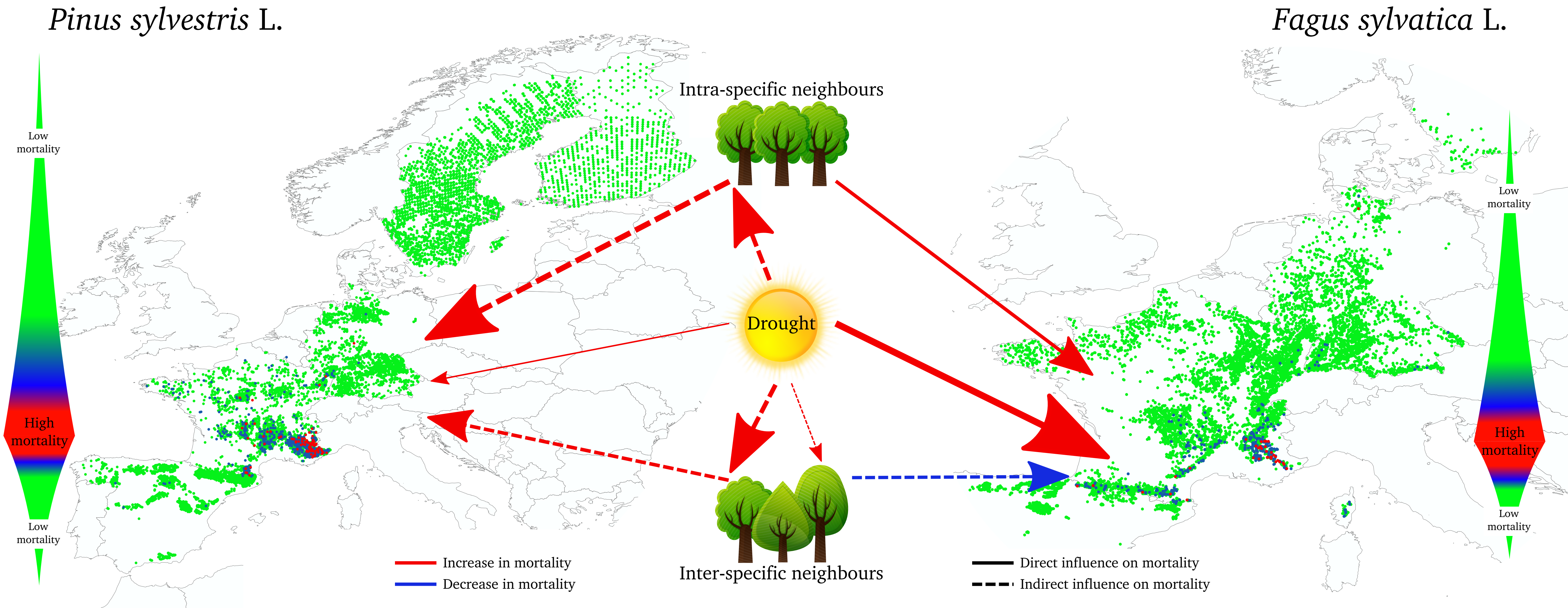

(a)
Relative importance
1.00
0.75
0.50
0.25
0.00
SPEI
WAI
BAintra
BAinter
Positive influence (increase in mortality)
Negative influence (decrease in mortality)
MED.
TEMP.
40
45
50
55
Latitude
(b)
Average BAinter
High BAinter
Low BAinter
Predicted probability of mortality
0.015
0.010
0.005
0
1
2
WAI

Figure 4. Spatial projection of the annual predicted probability of mortality at the individual-level across Europe for a) *P. sylvestris* and b) *F. sylvatica*. Graphs in the right panels display predictions (noted as *P(mortality)*) across latitude. For both species, predictions were calculated for all trees from the logistic regression model and were clustered at 1° latitude resolution. A locally weighted regression was used to obtain the smooth solid lines ("loess" method of the geom_smooth function in "ggplot2" R package). Grey areas indicate 95% confidence intervals (almost confused with the curves). The white section for *P. sylvestris* in the Mediterranean biome represents missing data at that latitude (due to its distribution in Spain).


a)
Predicted probability of mortality
● < 0.02
● 0.02 - 0.04
● > 0.04
P(mortality)
0.004 0.008
Latitude
70°N
65°N
60°N
55°N
50°N
45°N
40°N
35°N
70
60
50
40
b)
Predicted probability of mortality
● < 0.01
● 0.01 - 0.02
● > 0.02
P(mortality)
0.003 0.005
55°N
50°N
45°N
40°N
55
50
45
40

		P. sylvestris				***F. sylvatica***		
		All biomes	**Mediterranean biome**	**Cool temperate biome**	**Boreal biome**	**All biomes**	**Mediterranean biome**	**Cool temperate biome**
Relative importance	***BAintra***	0.96 (0.9616; 0.9630)	0.95 (0.9455; 0.9482)	0.96 (0.9625; 0.9644)	0.99 (0.9860; 0.9870)	0.61 (0.6134; 0.6162)	0.64 (0.6411; 0.6465)	0.61 (0.6076; 0.6107)
	BAinter	0.67 (0.6755; 0.6737)	0.52 (0.5235; 0.5258)	0.73 (0.7308; 0.7331)	0.83 (0.8293; 0.8314)	0.54 (0.5377; 0.5426)	0.80 (0.7915; 0.8010)	0.49 (0.4878; 0.4928)
	WAI	0.31 (0.3089; 0.3114)	0.35 (0.3509; 0.3552)	0.32 (0.3191; 0.3233)	0.22 (0.2169; 0.2201)	0.74 (0.7390; 0.7442)	0.71 (0.6997; 0.7130)	0.75 (0.7456; 0.7513)
	SPEI	0.44 (0.4370; 0.4397)	0.40 (0.3976; 0.4017)	0.42 (0.4218; 0.4258)	0.53 (0.5265; 0.5311)	0.70 (0.7018; 0.7066)	0.61 (0.6055; 0.6168)	0.72 (0.7196; 0.7249)
Annual predicted mortality		0.0061 (0.00611; 0.00618)	0.0077 (0.00763; 0.00775)	0.0063 (0.00619; 0.00631)	0.0033 (0.00332; 0.00337)	0.0038 (0.00374; 0.00382)	0.0052 (0.00506; 0.00530)	0.0035 (0.00347; 0.00354)

Table 1. Mean relative importance of each predictor and mean annual predicted probability of both species mortality per biome. See Fig. S1.1 for biome boundaries. The relative importance of each variable was first computed for each tree from the logistic regression model (see section 2.5), by giving a value of one to the most influencing variable and scaling the remaining variables accordingly. Secondly, the relative importance and the annual predicted probabilities of mortality (P_i in the equation 1) were average for each biome. Numbers in brackets refer to 95% confidence intervals. *BAintra*: conspecific basal area (m^2 ha^{-1}), *BAinter*: heterospecific basal area (m^2 ha^{-1}), *WAI*: water availability index (adimensional), *SPEI*: Standardised Precipitation-Evapotranspiration Index (adimensional).



Pinus sylvestris L.
Fagus sylvatica L.
Low mortality
High mortality
Low mortality
Intra-specific neighbours
Drought
Inter-specific neighbours
Low mortality
High mortality
Low mortality
Increase in mortality
Decrease in mortality
Direct influence on mortality
Indirect influence on mortality