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1 TITLE

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

4

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21

22 1 INTRODUCTION

23 Tree mortality plays a major role in shaping forest dynamics, structure and composition
24 (Franklin *et al.*, 1987; Ruiz-Benito *et al.*, 2017a), species range shifts (Benito Garzón *et al.*, 2013),
25 ecosystem functioning and services (Millar & Stephenson, 2015), carbon fluxes and feedback to the

26 global climate system (Sitch *et al.*, 2008). Therefore, understanding and predicting tree mortality is
27 a key challenge in ecology, particularly in a changing climate.

28 Global change is exacerbating drought-induced tree mortality (Allen *et al.*, 2015). Recent
29 forest die-off events have occurred in all major biomes and on every wooded continent (Allen *et al.*,
30 2015) and background tree mortality also appears to have increased in North America (Mantgem *et*
31 *al.*, 2009; Hember *et al.*, 2017) and in Spain (Carnicer *et al.*, 2011). Less conspicuous than die-offs
32 events, minor large-scale changes in tree background mortality can have a huge impact on forest
33 ecosystems and dynamic, including changes in productivity rates, functional composition and
34 species turnover (Stephenson & Mantgen, 2005; Ruiz-Benito *et al.*, 2017b). Yet, an empirical
35 quantification of background tree mortality at continental scale is missing and whether or not forest
36 mortality follows an increasing global trend that will keep rising under global change remains
37 unclear (Hartmann *et al.*, 2018). Moreover, mortality is a major process which delimits species
38 range (Gaston, 2009), notably at the driest edge of their distribution (Benito Garzón *et al.*, 2013).
39 Therefore, large scale studies that capture the entire species distribution are essential to determine
40 how climate change induced mortality might affect species distribution.

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

50 In European forests, background tree mortality is strongly driven by climate variability
51 (Neumann *et al.*, 2017). Among the climatic factors affecting tree mortality, drought plays a major
52 role (McDowell *et al.*, 2008; Benito Garzón *et al.*, 2013; Ruiz-Benito *et al.*, 2013; Allen *et al.*,
53 2015) and particularly affects populations at the driest edge of species distributions (Benito Garzón
54 *et al.*, 2018). Among the biotic factors, competition for limited resources may be an important cause
55 of tree mortality and may also interact with climate, notably through a higher increase in mortality
56 rates in areas that are both dry and dense (Ruiz-Benito *et al.*, 2013; Vilà-Cabrera *et al.*, 2013; Young
57 *et al.*, 2017). Moreover, tree mortality responses can differ widely depending on whether we
58 consider intra- or inter-specific competition (Condés & del Río, 2015). However, how intra- and
59 interspecific competition interact with climatic drought to shape range-wide mortality patterns
60 remains unknown.

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

74 2013; Galiano *et al.*, 2010) and in some inner Alpine valleys in the case of *P. sylvestris* (Rigling *et*
75 *al.*, 2013).

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

86

87 **2 MATERIAL AND METHODS**

88 **2.1 Forest inventory data**

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

99 and 161,720 Scots pine trees in 10,150 plots and 16,669 plots, respectively. From those trees, 1,490
100 (2.6%) and 7,649 (4.7 %) were recorded as dead for beech and Scots pine, respectively.

101 As explanatory variables of tree mortality, we selected tree *DBH* (diameter at breast
102 height) as *DBH* is known to influence individual tree mortality (Ruiz-Benito *et al.*, 2013). We
103 additionally calculated three proxies of indirect competition between trees (or facilitation) (Fig.
104 S2.1): basal area of neighbouring trees considering all tree species (i.e. *BAall*, m² ha⁻¹), basal area of
105 neighbouring conspecifics (i.e. *BAintra*, m² ha⁻¹) and basal area of neighbouring heterospecifics (i.e.
106 *BAinter*, m² ha⁻¹).

107 **2.2 Drought-related variables**

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

115 Changes in climatic drought intensity over the study period (i.e. temporal variability of
116 drought intensity) were described by the Standardized Precipitation Evapotranspiration Index
117 (*SPEI*, Fig. S2.2; Vicente-Serrano *et al.*, 2009), obtained from a gridded dataset at 0.5-degree
118 resolution (Beguería & Vicente Serrano, 2017). *SPEI* is a multi-scalar drought index whose
119 variations have been shown to be highly correlated with tree response to climate (Greenwood *et al.*,
120 2017). Its calculation considers both *PET* and *MAP*, with *PET* derived from the Penman-Monteith
121 equation. *SPEI* compares drought intensity during a long-term reference period (i.e. from 1901 to
122 2015) to that of a given period from 3 to 48 months. In our study, we selected a 12-month period to
123 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 Inflation 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

148 between each explanatory variable and tree mortality, *BAinter*, *WAI* and *SPEI* were log transformed
149 (see Appendix S3 for details).

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

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

$$\begin{aligned} 157 \quad k_{i,sp} = & \beta_{1,sp} \times \log(WAI_i) + \beta_{2,sp} \times \log(SPEI_i) \\ 158 \quad & + DBHnl_{i,sp} \times (\beta_{3,sp} + \gamma_{1,sp} \times \log(WAI_i) + \gamma_{2,sp} \times \log(SPEI_i)) \\ 159 \quad & + BAintra_i \times (\beta_{4,sp} + \gamma_{3,sp} \times \log(WAI_i) + \gamma_{4,sp} \times \log(SPEI_i)) \\ 160 \quad & + \log(BAinter_i) \times (\beta_{5,sp} + \gamma_{5,sp} \times \log(WAI_i) + \gamma_{6,sp} \times \log(SPEI_i)) \end{aligned} \quad (2)$$

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

163 2.4 Model performance and evaluation

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

171

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:

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

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. *BA_{intra}* and *BA_{inter}*) 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).

222 3.3 Interactions between climatic drought and basal area

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

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

234 3.4 Spatial patterns of predicted tree mortality across Europe

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

239 The predicted rates of Scots pine mortality were highest in the Mediterranean biome (mean
240 value of 0.0077 for 62,165 trees), intermediate in the cool temperate biome (mean value of 0.0063
241 for 62,914 trees) and lowest in the boreal biome (mean value of 0.0033 for 36,641 trees) (Table 1).
242 Similarly, the predicted individual probability of beech mortality was higher in the Mediterranean
243 biome (mean value of 0.0052 for 9,315 trees) than in the cool temperate biome (mean 0.0035 for
244 47,876 trees) (Table 1). However, the gap between mortality rates in the Mediterranean biome and
245 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; Caillleret *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

346 growth of beeches mixed with fir trees or in pure stands was equally negatively affected by long-
347 term droughts but they didn't explore the south-western part of beech distribution. Overall, these
348 results suggest that beech growth and mortality are influenced by interspecific interactions that vary
349 along the European drought gradient: from neutral interactions in wet areas where beech co-occurs
350 mainly with *Abies alba* and *Picea abies*, to facilitation in dry areas where beech co-occurs with
351 more Mediterranean species (Fig 3b & Table S5.1). However, the mechanisms behind these
352 interspecific interactions, particularly in dry areas, are still largely unknown. Identifying
353 associations of species that can survive droughts could help to better understand drought-related
354 mortality patterns in the coming years.

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

365 **4.2 Tree mortality patterns along latitude and potential associated range shifts**

366 Predicted probability of mortality in both beech and Scots pine was higher in the southern
367 part of their distribution, mainly corresponding to the French part of the Mediterranean biome and
368 the Pyrenees in the case of beech (Fig. 4). In these areas, beech and Scots pine mortality rates were
369 accurately predicted (Fig. 1), except at the southern end of Scots pine range where mortality rates
370 are likely to be slightly higher than predicted (Fig. 1a). These accurate predictions in the southern

371 part of species ranges were expected as we chose climatic variables related to droughts, generally
372 more important in the Mediterranean biome (Fig. S2.3). Surprisingly, the association of drought and
373 competition-related variables alone explained Scots pine mortality patterns in the northern part of
374 its distribution (Fig. 1a) but overestimated the probability of beech mortality in northern Germany
375 (Fig. 1b) suggesting that other factors come into play in these areas to explain beech mortality
376 patterns (see 4.3 Limitations).

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

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

395 **4.3 Limitations**

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

403 Other factors also affect tree mortality, either directly, indirectly or through interactions,
404 such as: changes in disturbance regimes (Seidl *et al.*, 2017), insect outbreaks (Anderegg *et al.*,
405 2015), mistletoe (Dobbertin & Rigling, 2006), atmospheric pollutants (Dietze & Moorcroft, 2011),
406 populations genetic differentiation and plasticity (Benito Garzón *et al.*, 2011), soil characteristics
407 (Dietze & Moorcroft, 2011). However, given our concern to limit the model complexity and the
408 lack of large-scale data, we decided not to include them in our study and to focus on comparing the
409 effects of drought and competition on mortality.

410

411 **CONCLUSIONS**

412 Mortality of Scots pine and beech was affected by climatic drought intensity and indirect
413 competition from neighbouring trees, but in different ways. Drought directly affected beech
414 mortality rates and beech trees benefited from mixing with other species, particularly in the
415 Mediterranean biome. Scots pine mortality suffered mostly from competition and was indirectly
416 affected by drought through interactions with competitors, especially in southeastern France. In this
417 area, which experienced a marked increase in drought intensity during the study period, high
418 mortality rates were predicted for both species, as expected for temperate trees for which the
419 Mediterranean biome corresponds to the southernmost part of the distribution. In a warming

420 climate, our study is a step further in understanding geographical patterns of tree mortality in
421 Europe and shed light on the high mortality risks faced by European tree species, regardless of their
422 different life-history strategies, especially at the ecotone between the Mediterranean and cool
423 temperate biomes. In this priority area, beech could benefit from mixing with other species and pine
424 from reduced competition.

425

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435

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444 DATA ACCESSIBILITY

445 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).

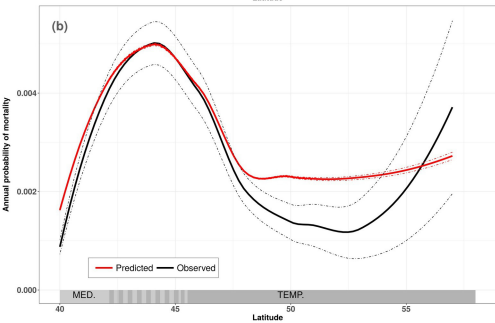
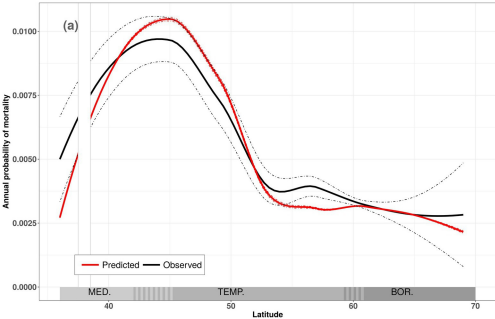


Figure 2. Effects of drought-related variables and basal area on Scots pine mortality. a) **Relative importance of the changes in climatic drought intensity over the study period (i.e. *SPEI*), climatic drought intensity (i.e. *WAI*), conspecific basal area (i.e. *BA_{intra}*) and heterospecific basal area (i.e. *BA_{inter}*) 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. *BA_{intra}*) 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.

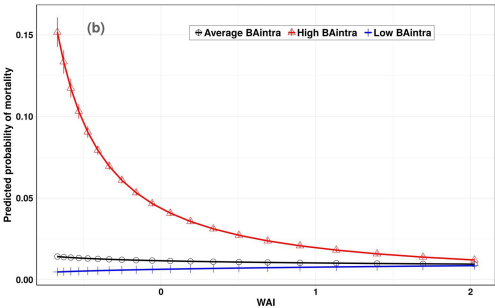
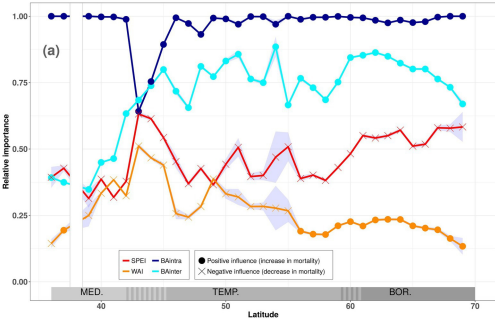


Figure 3. Effects of drought-related variables and basal area on beech mortality. a) Relative importance of the changes in climatic drought intensity over the study period (i.e. *SPEI*), climatic drought intensity (i.e. *WAI*), conspecific basal area (i.e. *BA_{intra}*) and heterospecific basal area (i.e. *BA_{inter}*) 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. *BA_{inter}*) 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.

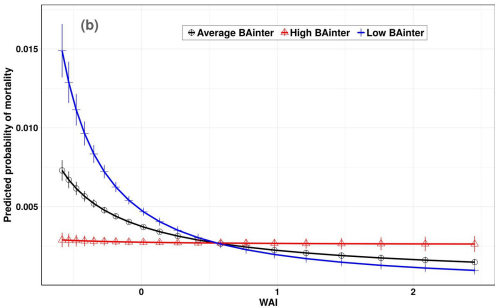
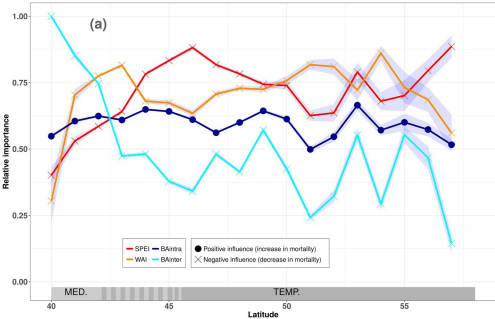
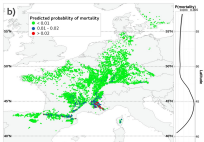
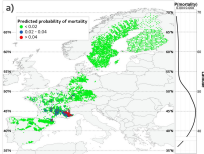


Figure 4. Spatial projection of the annual predicted probability of mortality at the individual-level across Europe for a) *P. sylvestris* and b) *F. sylvatica*. Graphs in the right panels display predictions (noted as $P(\text{mortality})$) across latitude. For both species, predictions were calculated 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).



		<i>P. sylvestris</i>				<i>F. sylvatica</i>		
		All biomes	Mediterranean biome	Cool temperate biome	Boreal biome	All biomes	Mediterranean biome	Cool temperate biome
Relative importance	<i>BAintra</i>	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)
	<i>BAinter</i>	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)
	<i>WAI</i>	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)
	<i>SPEI</i>	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 ($\text{m}^2 \text{ha}^{-1}$), *BAinter*: heterospecific basal area ($\text{m}^2 \text{ha}^{-1}$), *WAI*: water availability index (adimensional), *SPEI*: Standardised Precipitation-Evapotranspiration Index (adimensional).

Pinus sylvestris L.

Fagus sylvatica L.

