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RESEARCH ARTICLE

Trends in background mortality in unmanaged forests across Europe over the last century

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Abstract

1. Anthropogenic climate change has led to increasing background tree mortality rates worldwide. Tree species have different ways of dealing with changing environmental conditions due to their life-history strategies and location within their ecological niche. Trees growing further from the centre of their niche are likely to experience higher levels of climatic stress and potentially higher mortality, whereas trees growing closer to the niche centre may experience higher intraspecific competition.
2. To study the complex interplay of abiotic and biotic factors leading to tree mortality, we used a comprehensive network of permanent plots with repeated censuses spanning from 1936 to 2020 in 299 unmanaged forest reserves across Europe. The database includes 1.5 million stem records covering a total sampled area of 853.7 ha. We (1) calculated background mortality rates, (2) analysed trends in mortality rates and (3) investigated how the trends relate to the location of each tree within its ecological niche. We used Species Distribution Models (SDMs) to locate trees within their niche and generalized linear mixed models (GLMMs) to model mortality.
3. We observed an overall median annual background mortality rate of 1.1%. Spruce-dominated forests had the largest increase in annual mortality from 1.5% to 3%. Similarly, the models showed a significant increase in oak-dominated forests, whereas beech-dominated forests showed a significant decrease in annual mortality rates over time.

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4. We identified three distinct mortality responses with respect to the location of trees in their ecological niche. For oak, spruce and mountain pine, higher mortality probabilities occurred when they were located further from their niche centre. Hornbeam, ash and Scots pine showed the opposite pattern and beech and fir featured an almost negligible effect of distance from the niche centre.

5. *Synthesis*. In contrast to previous studies, our results suggest that dominant tree species in European natural forests have not consistently experienced increasing background mortality under anthropogenic climate change. Conversely, forest reserves dominated by competitive species such as beech may have benefitted from warmer growing conditions. Most studied tree species show no clear effect of distance from the niche centre, indicating high resilience and adaptability to environmental stress.

KEYWORDS
dynamics of unmanaged temperate forests, ecological niche, long-term annual background mortality rate, pan-European tree mortality, tree demography

1 | INTRODUCTION

Tree mortality is a fundamental demographic process that exerts strong control on forest dynamics and ecosystem functions (Franklin et al., 1987). In recent decades, anthropogenic climate change has severely impacted forest ecosystems, particularly through more frequent and intense insect outbreaks (Teshome et al., 2020), and extreme events such as forest fires (Bowman et al., 2020) and windstorms (Dale et al., 2001). In addition, a higher frequency and severity of droughts accompanied by higher temperatures (i.e. hotter droughts) have been globally observed, which is linked to an increase in background mortality globally (Allen et al., 2010, 2015). Disentangling disturbance-induced and background tree mortality is challenging, but it is pivotal to understand the causes and consequences of the increase in tree mortality rates observed worldwide over recent decades (Allen et al., 2015; Hartmann et al., 2022; McDowell et al., 2016; Senf et al., 2020).

In this study, we focus on background tree mortality, defined as tree mortality events that occur continuously at low rates and in the absence of high-intensity disturbances (Das et al., 2016; Taccoen et al., 2022; van Mantgem et al., 2009). Increases in background mortality over time have been observed at the global scale, even in forests growing in non-water-limited areas (Allen et al., 2010, 2015). In moist tropical forests of South America, Africa, Southeast Asia, northern Australia, Amazonia and the western United States, the observed increase in mortality has been attributed to water stress (Bauman et al., 2022; McDowell et al., 2018; Phillips et al., 2004; van Mantgem et al., 2009). In Europe, studies using the ICP network of managed forests (ICP Forests, International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests) have detected an overall temporal increase in tree mortality related to decreasing soil moisture for various species (George et al., 2022). In addition, mortality hotspots have been found in northern and southern Europe (Neumann et al., 2017). Based on remote sensing of temperate forests across Europe, canopy mortality has increased over the past three decades, which has primarily been attributed to a combination of increased harvesting, natural disturbances and climate stress (Senf et al., 2020, 2021). However, remotely sensed data over large areas are too coarse to detect background mortality of single trees and cannot easily separate natural mortality from harvesting, making it difficult to detect long-term trends in background mortality (International Tree Mortality Network, 2025).

In order to quantify background mortality, long-term monitoring of forest demography in unmanaged forests, without the confounding influence of forest management, is particularly important. For example, recent studies of European temperate old-growth forests did not find a general increase in mortality rates over time, but more stochastic mortality dynamics associated with past disturbances (Nagel et al., 2021; Šamonil et al., 2023; Woods et al., 2021). However, these studies have been largely site specific and lack sufficient data to capture temporal trends in mortality across European forests. Leveraging long-term permanent plot data from unmanaged forest reserves across Europe offers the possibility to characterize mortality over a range of forest types and environmental conditions (Forest Europe, 2020; Sabatini et al., 2018).

Tree mortality patterns are known to be species specific and affected by the location of trees within their ecological niche (Gazol et al., 2023). The ecological niche of a species is defined by combinations of biotic and abiotic environmental influences (e.g. competition, temperature, soil moisture, soil nutrients) that allow the population to survive (Hutchinson, 1957; Polechová & Storch, 2019) and reproduce. The abundant-centre hypothesis (Brown, 1984) posits that species are most abundant and perform best near the centre of their geographic range, which reflects their ecological niche, where environmental conditions are assumed to be optimal (Pironon et al., 2017). Recent studies have supported this hypothesis, including a broad analysis of 73 tree species across the Northern Hemisphere (Astigarraga et al., 2024), as well as regional studies in the Pacific Northwest (Ettinger et al., 2011), Eastern US (Purves, 2009) and in Europe (Kunstler et al., 2021). In Switzerland, for example, annual mortality rates have not consistently increased over the last decades, but mortality patterns differ by species and site conditions (Etzold et al., 2019).

On the one hand, differences in mortality patterns may support the abundant-centre hypothesis suggesting that growing further from the niche centre increases the probability of tree mortality, since growing conditions are suboptimal and trees are subject to high levels of stress (Taccoen et al., 2022). On the other hand, the species-specific mortality probability may be reduced with increasing distance from the centre of the niche because of lower intraspecific competition and pressure from specialist insects and pathogens (Das et al., 2016). Furthermore, populations growing near the niche edges may exhibit genetic or phenotypic adaptation to the harsher local conditions and thus may be better equipped to withstand extreme climatic events (Gazol et al., 2023; George et al., 2017). However, the effect of the distance from the niche centre remains unclear for many species and understanding tree mortality remains a challenge due to the complex interplay of abiotic and biotic factors (Teshome et al., 2020; Trugman et al., 2021).

To understand this interplay of factors over time and because forest ecosystems develop relatively slowly, long-term monitoring in unmanaged forest is needed to detect changes in mortality (Meyer, 2020). In this study, we use a long-term and large-scale European network of permanent plots in strict forest reserves, compiled within the European Forest Reserves Initiative (EuFoRIa, www.euforia-project.org). The network features a broad range of forest types across widely ranging environmental gradients, providing an ideal setting to analyse species-specific patterns of background mortality. We aim to answer the following research questions:

RQ1: What is the range of background tree mortality rates across unmanaged European forests, and how does this variability differ among forest types? We expect to find differences between forest types due to species-specific life histories.

RQ2: Are there trends in tree mortality rates in European forests? Based on the literature, we expect to observe an increase in background mortality rates in recent decades.

RQ3: Are there differences in the mortality probabilities of trees related to their distance from the centre of their ecological niche? We hypothesize that mortality probability increases with distance from the niche centre, and we expect to find species-specific responses due to their different life histories.

2 | MATERIALS AND METHODS

2.1 | European forest reserves—Tree census data

The forest census data of the EuFoRIa network used for this study comprises 6540 permanent plots in 299 forest reserves and is maintained by 18 research institutes and universities across Europe, covering a total sampled area of 853.7 ha (Käber et al., 2023). The reserves span a large geographical area (Figure S1) and include the main forest types and tree species of temperate Europe. We used inventory data from permanent plots that have been measured at least two times, covering the period from 1936 to 2020, with an average census interval of 13 years. Tree census data were repeatedly collected in each inventory, consisting of standard inventory measurements, including species identity, diameter at breast height (dbh) and tree status (alive/dead). In total, 579,201 unique stems were recorded, resulting in close to 1.5 million measurements across multiple censuses. Many reserves have been left unmanaged for several decades to centuries prior to their designation, and some are primary forests in an old-growth stage of development. The network covers a large climatic and environmental gradient, with annual temperature ranging from −0.9 to 12.8°C and the annual precipitation sum from 550 to 2270 mm (period from 1990 to 2020; CRU TS Version 4.05; Harris et al., 2020).

2.1.1 | Data processing and plot selection

As a first step we harmonized the individual data sets from the EuFoRIa network to deal with the large variability in plot sizes and minimum tree size measurement thresholds (see Appendix S1, Figure S2 for a more detailed description of the data screening process). This harmonized dataset contained 865 plots with 2308 measurements (i.e. number of censuses across all plots), and plot sizes ranging from 0.2 to 5.52 ha with a median of 0.9 ha. We used a dbh threshold ≥8 cm and excluded all trees below this threshold.

Since we focus on background mortality, we need to exclude plots affected by high-intensity disturbance-induced mortality events (Das et al., 2016; van Mantgem et al., 2009), that is, catastrophic events sensu Hart and Kleinman (2018). Using the per-capita annual mortality rate calculation described below, we excluded plots with mortality rates higher than 10% year^{-1} to filter out stand-replacing events. This criterion led to the exclusion of 10 plots out of 865 (2nd step of Figure S2). We also excluded plots with low stand basal area (BA) of less than 10 m^2 ha^{-1}, as we consider these either to be very 'young' forest stands or stands recovering from a stand-replacing disturbance that occurred before the initial inventory. The chosen thresholds represent a compromise between having a homogeneous data set and a large enough sample size. Plots affected by either criterion (high mortality events or low basal area) were removed from the study entirely, rather than simply removing the census period in question.

To address RQ1 and RQ2, where we analysed mortality over time at the plot level, we excluded plots with fewer than three inventories, as modelling a trend requires at least two census intervals per plot (last step of Figure S2). Thus, for this first part of this study we used a subset of 804 censuses at the plot level. To address RQ3, where we evaluated the species-specific size-dependent mortality probability in relation to distance from the centre of the niche, we analysed individual trees located on plots with at least two censuses (3rd step of Figure S2). We set a minimum of 20,000 unique stem measurements to retain a species in the analysis. This final tree-level dataset had 461,732 observations from a total of 321,431 unique stems and included eight species: the deciduous European beech (*Fagus sylvatica* L.), European hornbeam (*Carpinus betulus* L.), European ash (*Fraxinus excelsior* L.) and oak as a group of species (*Quercus robur* L., *Q. pubescens* Willd., *Q. petraea* Liebl., *Q.* × *rosacea*, *Q. cerris* L., *Q. frainetto* Ten.); the coniferous silver fir (*Abies alba* Mill.), Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.) and mountain pine (*Pinus mugo* Turra) (Figure S3). As a pragmatic approach, we clustered the oak species as their ecological requirements (e.g. drought tolerance) are not substantially different when compared to the other studied tree species.

2.1.2 | Mortality rates

We estimated per-capita annual mortality rates (m_a) between each inventory period for each plot using an equation from Sheil et al. (1995):

$$m_a = 1 - \left(N_{S_T}/N_0\right)^{1/T}, \tag{1}$$

where N_{S_T} is the count of individual stems that survive from the initial count N_0, and T is the interval in years between the inventories (eq. 5 in Kohyama et al., 2018). This metric assumes a constant probability of mortality throughout the census period and for the entire tree population on a plot. However, the probability of mortality depends on tree species and tree size, which strongly correlates with tree age. Hence, when comparing mortality rates from different census periods, it is advisable to do so between homogeneous subpopulations (i.e. calculating the mortality rate for individual tree species and different size classes), in order to account for the bias towards lower mortality rates in heterogenous populations (Sheil & May, 1996). We opted to estimate the annual mortality rate at the plot level and not by homogeneous subpopulations, because our first two research questions deal with forest types rather than individual tree species within different size classes with the same census intervals. Moreover, in a subsequent step, we classified the plots into forest types and analysed them within their respective category, which helped to reduce the variability in mortality probabilities among plots.

2.2 | Data analysis

2.2.1 | Forest structure metrics and forest types

We calculated the stand density as the total number of stems (N) per hectare ($\mathrm{N\,ha^{-1}}$), the total BA ($\mathrm{m^2\,ha^{-1}}$) of each plot at each census and the share of BA per species in each plot. We then categorized each plot as a forest type that corresponds to the most abundant species measured by its share of total BA. The eight most common forest types in our dataset corresponded to the eight most common tree species listed above. These categories were used to answer the first and second research questions, in which we studied the plot-level mortality rates over time and by forest type.

2.2.2 | Climatic variables

We obtained climatic variables from CRU TS v4.05 (Climatic Research Unit gridded Time Series), a spatially interpolated monthly meteorological database at 0.5° resolution (Harris et al., 2020). We first extracted monthly potential evapotranspiration (PET; mm), average temperature (°C) and total precipitation (mm). We then calculated the annual degree-day sum (DDS) using Bugmann's (1994) modified sine wave approach (Allen, 1976) and a threshold temperature of 5.5°C. We calculated monthly climatic water balance (CWB) as precipitation minus PET (Thornthwaite, 1948), since it is an index widely used in Europe (Senf et al., 2020; Vicente-Serrano et al., 2012). Finally, we generated the average annual values of DDS and CWB for each inventory period of each plot (Figure S4).

2.2.3 | Location of trees within their ecological niche space

We used Species Distribution Models (SDMs) to define the location of the individual trees within their ecological niche space as a probability of occurrence (Righetti et al., 2019). We followed the methodology by Mauri et al. (2022) for variable selection, model formulation, calibration and validation. The process is explained in detail in Appendix S3. In the last step, we obtained a probability of occurrence map for each tree species (Figure S5) and extracted the value for all trees in the EuFoRIa dataset based on their locations.

2.2.4 | Statistical modelling

To investigate the variability in annual mortality rates between forest types (RQ1), we calculated the weighted arithmetic mean for each forest type and for each year, based on the total number of stems (N) of each plot. We used the R package TAM (Robitzsch et al., 2024) to calculate the weighted arithmetic mean annual mortality rate and the associated 2.5% and 97.5% weighted percentiles, and visualized them together. To study the trends in annual mortality rates (RQ2) and the relationship between tree location within their ecological niche and mortality probabilities (RQ3), we developed two series of generalized linear mixed models (GLMM) using the R package *glmmTMB* (Brooks et al., 2017). In total, we developed 16 individual models, one series of eight models for each forest type (RQ2) and a second series of eight for each studied tree species (RQ3). We used random effects to account for the hierarchical nature of the data and the repeated measurements (i.e. multiple plots within reserves were measured multiple times). This approach ensured that the random effects accurately captured the design of the study that features nested and repeated measurements.

In the first series of models focusing on the plot level (RQ2), we analysed the mortality rates (Equation 1) over time of the eight most common forest types in our dataset, to test for a trend (see Table S2). We used a GLMM with binomial distribution and the *logit* link function (i.e. logistic regression with random effects), because the response variable consists of proportions (i.e. fraction of the number of dead stems out of the total number of stems; see Equation 1) (McCullagh & Nelder, 1989). We included the total number of stems in the plot as a weighting term using the 'glmmTMB' function with the argument 'weights' from the R package *glmmTMB* (Brooks et al., 2017). All explanatory variables were z-transformed. We modelled the annual mortality rate per plot for the midpoint year of the respective census interval, creating individual models for each forest type. We also included covariates that potentially affect mortality rates, that is, the average CWB and DDS between the inventories and BA at the beginning of the inventory period. We included an interaction term between CWB and DDS, and we expected that humid conditions (high CWB) would offset or reduce the potential negative effect of warmer temperatures (high DDS) during such periods. The random effect was defined for the intercept using plots as a grouping variable to account for the repeated measurements. We did not include a random effect for plots nested within forest reserves, since some forest reserves only contained one plot. The residuals (Figure S10) were assessed using the R package 'DHARMa' (Hartig, 2022).

In the second series of models focusing on the tree level (RQ3), we studied the relationship between the location of the trees within their ecological niche and their mortality probability (see Table S4). We fitted eight species-specific, tree size-dependent models in which we analysed the mortality probability of the individual trees based on their probability of occurrence, used as a proxy for their ecological niche position. We excluded trees with a dbh above the 99th percentile for each species, as these outliers could act as leverage points and disproportionately influence the effect sizes of the models. We included plot-level BA at the census before the mortality event and CWB within the census interval as covariates since they may play a pivotal role in tree mortality (Young et al., 2017). We also added dbh from the census before the mortality event and probability of occurrence, as well as an interaction between these two variables since we expected different sensitivities based on tree size. The random effects for the intercept included trees nested within plot and nested within forest reserve as grouping variables. We could account for the hierarchical structure of the dataset and the repeated measurements since in all cases the response variable was large enough, having >20,000 observations for each tree species (see N_r in Table S5). The log-transformed length of the census interval of each plot was included as an offset term to account for the different interval lengths (Leite et al., 2024). We used the binomial distribution and the complementary *cloglog* link function since the number of observations differed between the two outcomes of a mortality event (0 alive; 1 dead) (Zuur et al., 2009), as used earlier in this type of analysis (cf. Archambeau et al., 2020; Portier et al., 2020). We used the 'glmmTMB' function from the R package *glmmTMB* (Brooks et al., 2017). All data analyses were performed using R v4.3.1 (R Core Team, 2023).

3 | RESULTS

3.1 | Long-term background mortality rates in European forest reserves

We found no general distinct pattern in the temporal variation of the observed annual mortality rates across European unmanaged forests, but rather forest type-specific trends (Figure 1). In hornbeam-dominated forests, the weighted mean annual mortality increased from 1.0% to 2.0% year^{-1} between 1972 and 2013. Similarly, spruce-dominated forests experienced higher annual mortality rates during recent census periods, increasing from 1.5% to 3.1% year^{-1}. This was especially noticeable at certain sites, such as in Latemar (South Tyrol), in most sites in Germany, and in the Derborence and Scatlè reserves of Switzerland, where annual mortality rates increased to >3% after 2000. Conversely, beech- and oak-dominated forests, the dominant broadleaved-dominated forests in Europe, showed no noticeable trend, with annual mortality rates close to 1% year^{-1}. Ash-, fir- and Scots pine-dominated forests showed a slight increase in their mean annual mortality rate over time, whereas the mortality rate in mountain pine-dominated forests decreased from ≈1.5% year^{-1} in 1979 to ≈0.5% year^{-1} in the last inventoried years. We found the highest annual mortality rates of ≈3% year^{-1} in spruce-dominated forests in the last census period, closely followed by ash-dominated forests, with values >2% year^{-1} in the last decades (Figure 1). In the case of beech-, oak- and spruce-dominated forests, we observed greater variability in the weighted mean annual mortality rates after the 1960s, as most plots were established after that decade.

3.2 | Predicted trends in mortality rates

In the first series of models, we used annual mortality rates calculated at the plot level for each census interval, and we included 804 mortality rates from 1103 censuses carried out in 299 unique plots in 122 forest reserves. Annual mortality rates at the plot level varied widely from 0% to 7.6% year^{-1}, with a median of 1.1% year^{-1}. Ash-dominated forests had the highest median (2.0% year^{-1}), and mountain pine-dominated forests showed the lowest median (0.6% year^{-1}) (Figure 2).

The results of the models (Figure 2; Table S3) showed contrasting results for the different forest types. We found predicted

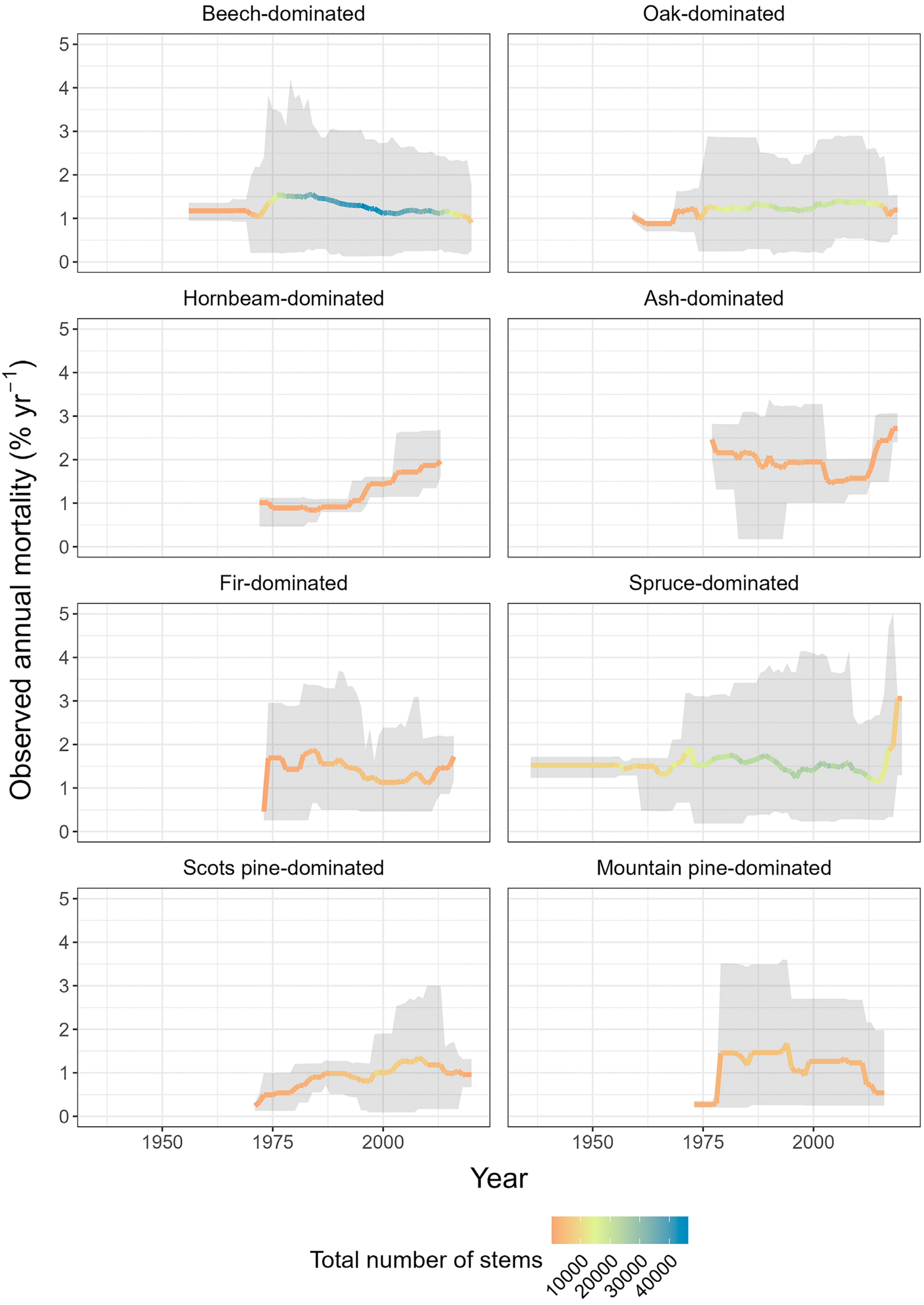

FIGURE 1 Weighted arithmetic means of observed annual mortality rates by forest type. The grey area shows the 2.5% and 97.5% weighted percentiles of the data. Line colours show the number of stems measured in each period. In total, 299 unique permanent plots, and 1103 censuses were used (last step of Figure S2).

annual mortality to increase over time for oak-, hornbeam-, spruce- and mountain pine-dominated forests. This effect was statistically significant (i.e. $p \leq 0.05$) for oak-dominated ($p = 0.02$) and spruce-dominated forests ($p = 0.05$). For spruce and mountain pine forests, predicted annual mortality over time showed small increases (ca. 0.2% during their respective monitored periods). Conversely, in the case of beech-, ash-, fir-, and Scots pine-dominated forests, we found predicted annual mortality to decrease over time, but being significant only for beech-dominated forests ($p = 0.02$).

When looking at the covariates included in the model (Table S3), we found BA in the preceding inventory to be positively related to the mortality rate in all forest types except for ash-dominated forests (Figure S7). The effect was significant for fir- ($p = 0.04$), spruce- ($p = 0.02$) and Scots pine-dominated forests ($p = 0.03$) and marginally significant for mountain pine-dominated forests ($p = 0.05$). Low CWB values were linked to higher mortality in hornbeam- and spruce-dominated forests, which was also significant ($p < 0.01$). However, for the remaining forest types, the effect was positive and significant for beech- ($p < 0.001$) and ash-dominated forests ($p = 0.03$), indicating higher mortality with moister conditions (Figure S8). High DDS values were related to higher mortality rates of beech-, ash- and fir-dominated forests and significantly for Scots pine-dominated forests ($p = 0.01$) (Figure S9). The effect of the interaction term between CWB and DDA was negative for hornbeam-, ash- and spruce-dominated forests, and significantly for beech- ($p = 0.01$) and mountain pine-dominated forests ($p = 0.01$), and positive for oak-, fir- and significantly for Scots pine-dominated forests ($p = 0.03$).

3.3 | Tree mortality and niche position

Most of the trees in our dataset were located close to the centre of their ecological niche, indicating high probabilities of occurrence. More than 60% of the beech, ash, hornbeam, fir and mountain pine trees were found to have a probability of occurrence >0.9 (Figure S6). The distribution was less skewed for the other species; oak, in particular, had a median value of 0.62 (cf. Table S4).

We identified three distinct patterns regarding the relationship between probability of occurrence and mortality probability (Figure 3; Table S5): (1) No relationship; this was the case for beech and fir, which also featured low overall mortality probability. (2) Positive relationship; hornbeam, ash and Scots pine featured this pattern, but only for small tree sizes (dbh <20 cm). (3) Negative relationship for oak at small tree sizes and for spruce and mountain pine at larger tree sizes (dbh >50 cm for spruce and >25 cm for mountain pine).

The confidence intervals for most species were wide, particularly for the smallest and largest tree sizes, as well as for medium and low probabilities of occurrence, since the majority of the trees in our dataset were medium-sized and growing close to the centre of their niche (Figure S6). High stand basal area increased the probability of mortality in all cases, while larger annual CWB decreased it, albeit not in the case of fir, spruce and mountain pine (Table S5).

4 | DISCUSSION

There is a growing concern that background mortality rates are increasing in forests worldwide. By using repeated single tree measurements from a long-term pan-European dataset of permanent plots in unmanaged forest reserves, covering a wide environmental range, we document trends in background mortality across European forests and discuss potential predictors. Specifically, we provide robust estimates of background mortality rates across different forest types, and we found that they increased significantly during the inventory period in spruce- and oak-dominated forests and decreased significantly in beech-dominated forests. The overall positive effects of basal area on mortality rates show that besides disturbances, also density-dependent effects, and thus competition effects, are of high relevance for tree mortality under climate change. Moreover, we identified three groups of tree species based on their mortality patterns in their ecological niche space. The mortality rates of the majority of the studied tree species were not influenced by their distance from the centre of their niche, indicating high resilience and adaptability to environmental stress. Nevertheless, increased mortality with greater distance from the niche centre was found for spruce, mountain pine and oak, suggesting that mortality will increase with current and future climate change, especially when growing in suboptimal conditions, potentially leading to a biogeographical shift.

4.1 | Long-term background mortality rates in European forest reserves

We found that the observed weighted mean mortality rates of the European forest reserves calculated in our study were within the range of values found for other European forests, which are in the absence of severe disturbance events, reported to be between 0.5% and 2% year^{-1} (Etzold et al., 2019; Nagel et al., 2021; Woods et al., 2021). In our study, however, spruce-dominated forests showed substantially higher annual mortality rates towards the end of the monitored period (up to 3% year^{-1}), although with wider confidence intervals (Figure 1), indicating a higher environmental variation of the plots only added to the network in the last decades.

4.2 | Predicted trends in mortality rates

We uncovered a substantial increase in mortality rates over time in oak-dominated forests and a slight increase in spruce-dominated forests (Figure 2), similar to the increase found in other forest ecosystems worldwide (Bauman et al., 2022; McDowell et al., 2018;

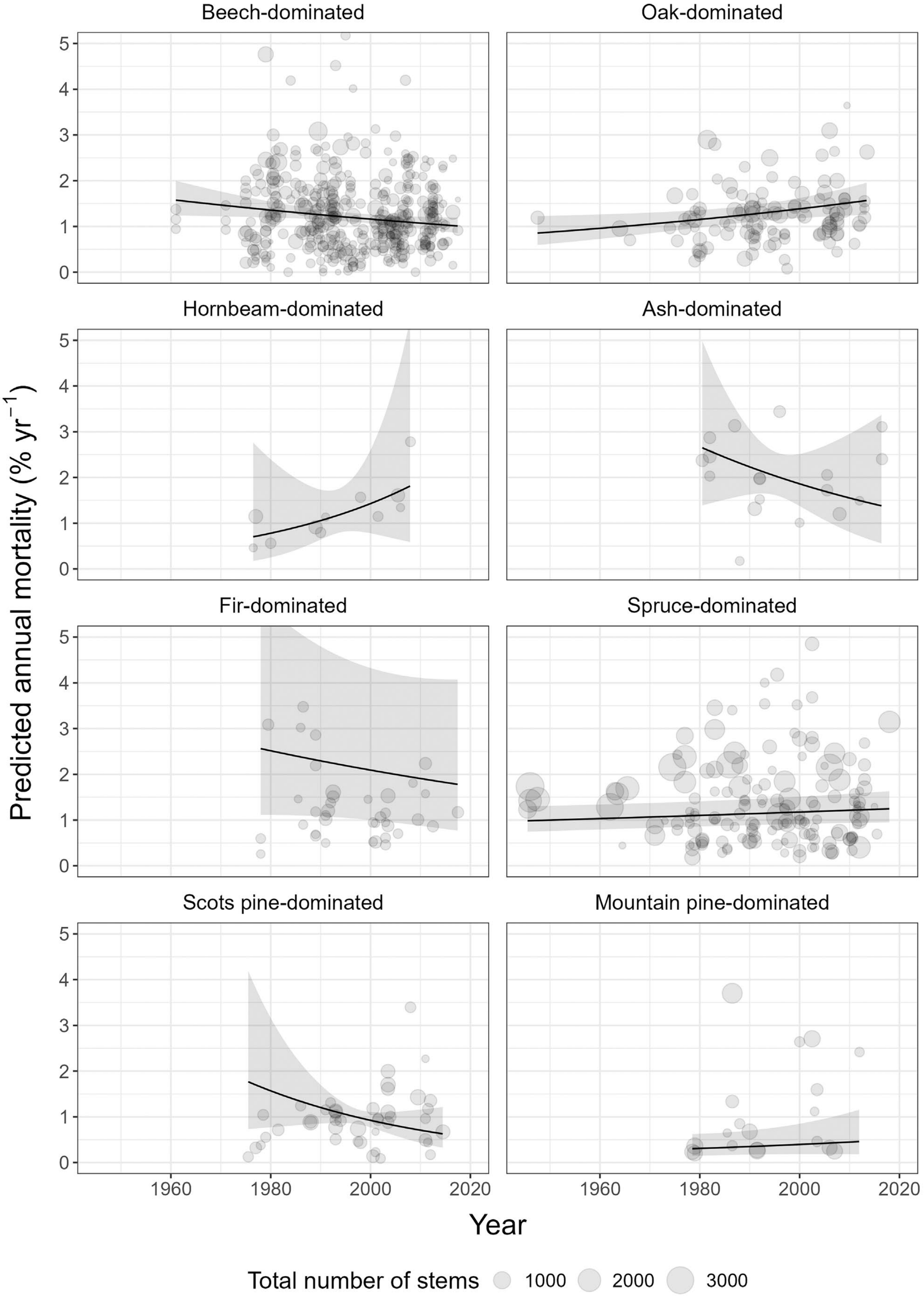
Beech-dominated
Oak-dominated
Hornbeam-dominated
Ash-dominated
Fir-dominated
Spruce-dominated
Scots pine-dominated
Mountain pine-dominated
Predicted annual mortality (% yr^{-1})
0
1
2
3
4
5
1960
1980
2000
2020
Year
Total number of stems
1000
2000
3000

FIGURE 2 Predicted annual mortality rates as a function of time. The curves were predicted based on the mean value of all other variables in the model. Predictions are restricted to the time intervals covered by each forest type to avoid extrapolation. The shaded area shows the 95% confidence intervals. Observed mortality rates are shown as grey dots and their size varies based on the number of stems used to calculate the mortality rates (i.e. amount of data used as weighting term in the models). To facilitate interpretation, the *y* axis is restricted to 5% year^{-1} annual mortality, even though there are higher observed values: 7.6% year^{-1} in 2013 in spruce-dominated forests, 5.7% year^{-1} in 1999 in fir-dominated forests, and 5.2% year^{-1} in 1995 in beech-dominated forests. All model coefficients are shown in Table S3.

Phillips et al., 2004; van Mantgem et al., 2009) and in Europe (Neumann et al., 2017; Senf et al., 2020). Also, a recent study in Europe found a linear increasing trend in annual mortality for spruce and oak, among other tree species (George et al., 2022). Oak-dominated forests showed increased mortality with higher CWB, and this has also been reported for oaks in Swiss forest reserves, which was linked to increasing competition affecting mostly small trees (Rohner et al., 2012). Spruce-dominated forests showed a negative effect of DDS, even though not significant, which suggests that they are not negatively affected by an increase in temperature (Marchand et al., 2023). They also featured a negative effect of CWB, indicating higher mortality in drier periods, which indicates a climatic signal (i.e. increase in frequency and intensity of dry periods). Therefore, at least for spruce-dominated forests, it is expected that this upward trend in mortality will continue with the projected increase in the duration and intensity of droughts (Breshears et al., 2013; Hammond et al., 2022). This can also be explained by the fact that spruce-dominated forests are additionally impacted by the interplay between drought-induced weakening and increased susceptibility to bark beetle infestation (Wermelinger, 2004). Individual trees already weakened by drought events are more likely to be infested by the bark beetle and under climate change the probability for such drought-mediated bark beetle infestation will increase (Seidl et al., 2016).

Beech-, ash-, fir- and Scots pine-dominated forests showed decreasing predicted annual mortality rates over time. These results are in contrast to findings indicating that beech and Scots pine show an upward trend, while fir does not (George et al., 2022). Nevertheless, other studies of old-growth fir-beech-Norway spruce forests of Slovenia also showed an increase in fir mortality (Diaci et al., 2011). These four forest types showed a positive effect of CWB, being only significant for beech- and ash-dominated forests, which has already been reported for oak and beech (Rohner et al., 2012). The reduction in the predicted mortality rates is likely not evenly distributed across the study area as they depend on local conditions (Ruiz-Pérez & Vico, 2020). These findings indicate that the above-mentioned forest types have not been negatively affected by recent changes in climatic conditions and suggest some resilience of unmanaged forests to novel conditions. However, this may reflect a delayed response, with the full impact on mortality potentially becoming evident only in the future, since trees are long-lived organisms that often exhibit slow responses to environmental changes and are to some degree resilient to such changes. This lack of an upward trend in annual mortality in the case of beech-dominated forests, which are one of the most common forest types in Europe (Leuschner et al., 2006), is striking. Beech is a species that is relatively vulnerable to drought (Landolt, 1977; Leuschner & Ellenberg, 2017) and is expected to be outcompeted by more drought-tolerant species in drier areas due to climate change (Huber et al., 2021; Leuschner, 2020). Even though our plots covered a wide diversity of soil types and other abiotic factors, as well as the impact of the 2003 severe drought that affected European forests (Bréda et al., 2006), this result may indicate a bias of our studied beech-dominated forest reserves towards higher elevations and humid sites, where trees may have even benefited from recent warming. In beech forest reserves in Germany, the increased mortality observed during recent drought years was confined to suppressed trees (Meyer et al., 2022). This suggests that the detected decrease in mortality may be attributed to a reduction in density-dependent mortality, as the self-thinning process decelerates following canopy closure.

4.3 | Influence of ecological niche position on tree mortality

By studying mortality probabilities in relation to distance from the niche centre, we identified three groups of tree species based on their responses. The first group consisted of beech and fir, which showed a negligible effect of the location within the climatic niche, as well as overall low mortality probabilities. These two tree species share similar traits. They are among the most competitive European tree species in part due to their very high shade tolerance (Brzeziecki & Kienast, 1994; Körner, 2005). In addition, both are long-lived, late successional species (Heiri et al., 2009) and have moderate to high sensitivity to drought (Landolt, 1977; Leuschner & Ellenberg, 2017). The absence of an effect of the distance from the niche centre suggests that these species have a high capacity to adapt to changing growing conditions and highlights their potential resilience in the face of future climate change. However, these results need to be interpreted with a bit of caution, since for both species, very few trees were located far from their niche centre. In light of reports that these two species were suffering during the 2018 drought in Europe (Rohner et al., 2021), it may also indicate that most of the studied individual trees are not located in water-limited sites and have not reached a threshold beyond which they cannot sustain the new, drier conditions.

In the second group, we found hornbeam, ash and Scots pine, which exhibited generally low mortality probabilities that

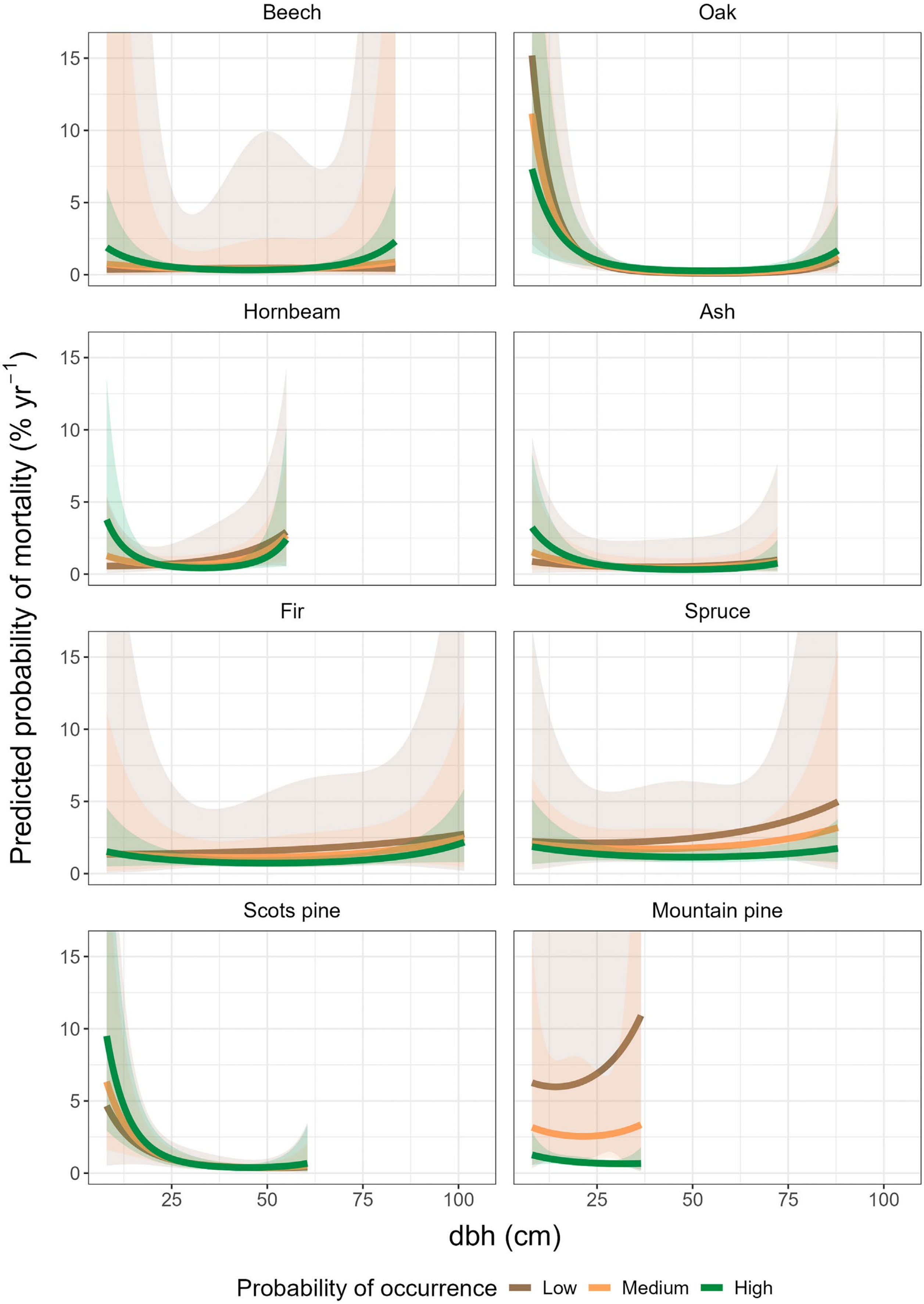
Beech
Oak
Hornbeam
Ash
Fir
Spruce
Scots pine
Mountain pine
0
5
10
15
25
50
75
100
Predicted probability of mortality (% yr^{-1})
dbh (cm)
Probability of occurrence
Low
Medium
High

FIGURE 3 Predicted annual mortality probability reported as % year^{-1} for the eight studied tree species as a function of dbh and three different levels of probability of occurrence. Based on the individual outputs of the SDMs for each species, low, medium and high probability of occurrence correspond to values of 0.2, 0.5 and 0.9 respectively. These curves were predicted based on the mean value of all other variables in the model. The shaded area shows the 95% confidence intervals. Predictions are restricted to the dbh range covered by each tree species to avoid extrapolation. The *y*-axis is restricted to the maximum predicted mortality probability value, even though confidence intervals reach higher values, to facilitate interpretation of results. Model coefficients are shown in Table S5.

nonetheless increased for smaller trees, especially when they are growing closer to the centre of the niche. Hornbeam and ash are moderately shade-tolerant and have a moderate sensitivity to drought (Leuschner & Ellenberg, 2017) and other types of stress (Rudow, 2024). Therefore, if growing conditions are favourable, other species will outcompete them, especially when they are young and thus weaker competitors (Fernández-de-Uña et al., 2023). Scots pine has a very low tolerance to shade but a high tolerance to drought (Leuschner & Ellenberg, 2017). It is undemanding in terms of nutrients, water balance and climate, and it becomes dominant in locations where it avoids competition (Rudow, 2024). A recent literature review of drought-induced mortality of Scots pine revealed an increased mortality in already dry and warm locations, as well as in the centre of the niche in more recent decades (Bose, Doležal, et al., 2024; Bose, Gessler, et al., 2024). Since this species is characteristic of abiotically harsh conditions, populations growing at the range margins may exhibit genetic or phenotypic adaptations to drought (George et al., 2017). These populations may thus be better equipped to withstand extreme climatic events (e.g. droughts of 2015 and 2018 in Europe) than populations growing at the centre of their distribution range.

The third and last group consisted of spruce, mountain pine and oak. These three species showed a higher mortality probability further from the centre of their niche. For spruce and mountain pine, this pattern was more pronounced for large trees. These two species have contrasting ecological traits: spruce is moderately shade-tolerant but highly sensitive to drought, whereas mountain pine is highly drought-resistant but has low tolerance to shade (Leuschner & Ellenberg, 2017; Rudow, 2024). Mountain pine typically grows in extreme climatic conditions or in sites with poor soil conditions, usually at higher elevations and in peat bogs. Both species can grow together in the transition between the subalpine and upper subalpine zone (Frehner et al., 2020). Spruce has a wider distribution and has been historically planted or promoted outside of its natural range, which was the case in some of the formerly managed reserves and therefore still slightly reflected in the studied dataset. The increased mortality observed further from the niche centre in these species suggests that, due to the predicted increase in temperature and seasonal droughts, mortality will increase, especially for large individuals growing in less than optimal conditions.

Of the eight species in these three groups, oak featured the highest mortality probability at small size especially when growing further from the centre. Mature oak trees are known to be well-adapted to drought and very competitive, but as a light-demanding species it needs canopy gaps to recruit (Leuschner & Ellenberg, 2017; Rudow, 2024). Our results are in line with recent studies that showed higher drought-related mortality of oaks that were growing in already dry sites in the Northern hemisphere (Bose, Doležal, et al., 2024; Bose, Gessler, et al., 2024) and particularly in France (Taccoen et al., 2022). We also showed that annual mortality rates in oak-dominated forests have increased over time. Since migration or adaptation is limited, future climate change is likely to push more individuals further from the centre of their niche, thus increasing their mortality and potentially leading to a biogeographical shift (Batllori et al., 2020). Nevertheless, oaks are often considered resilient species capable of withstanding future climatic conditions, potentially outperforming beech under the scenario of intense climate change (Meyer et al., 2020). This is why oak species are increasingly seen as vital for the future of European forests due to their resilience and adaptability to warmer, drier conditions (Schroeder et al., 2021). For example, in the Montseny mountains (Catalonia, NE Spain) it has already been reported that Holm oak (*Quercus ilex* L.) is progressively replacing beech at medium elevations (Peñuelas & Boada, 2003). Our results highlight the need for caution in assuming the supremacy of oak under different scenarios of climate stress, since species-specific responses to climate change are context dependent. Nonetheless, it should be noted that as our dataset disproportionately represents the optimum conditions, our results should be interpreted with caution in less-represented areas of the ecological niche of oaks.

5 | CONCLUSIONS

The observed mean background mortality rates in this study cover a range of approximately 0.5% to 3% year^{-1} and vary by forest type. In the majority of them, there was an increase in the mortality rates over time or they fluctuated around a mean value. Using the model-based results by forest type, we found this upward trend in the mortality rates in forests dominated by oak, hornbeam, spruce and mountain pine, which may indicate a climatic signal. We observed no trend or even a decrease in the modelled mortality rates over time in beech-, ash-, fir and Scots pine-dominated forests, which may indicate a higher capacity to deal with the novel current and future growing conditions. However, this pattern could also reflect a lag effect, with potential increases in mortality only becoming apparent after a longer time period. Furthermore, the species level modelling showed an increase in tree mortality probability when the individuals were growing further from the centre of their ecological niche in the case of oak, spruce and mountain pine. This last result suggests that these three tree species are at high risk since climate change will shift the growing conditions, and more individuals will be growing in harsher environments.

The European Forest Reserve Initiative (EuFoRIa) is, due to its very comprehensive data set covering the most important forest types of Europe, a very valuable resource to study long-term mortality trends in the absence of management for the most common European forest types and tree species. Forest ecosystems develop slowly, and thus detecting changes in mortality due to climate is not possible without large plot networks spanning many decades. This underlines the need to continue such forest monitoring in the future as Europe is likely to experience more extreme droughts and other climatic anomalies.

AUTHOR CONTRIBUTIONS

Jokin Idoate-Lacasia, Martina Hobi, Peter Brang, Jonas Stillhard, Jeanne Portier, Harald Bugmann, Christof Bigler, Thomas A. Nagel and Yannek Käber participated in the conceptualisation and framing of the study. Jokin Idoate-Lacasia led the data analysis and interpretation and created the draft of the article. Jonas Stillhard, Jeanne Portier, Joan Casanelles-Abella and Christof Bigler supported data analysis. Yannek Käber, Jokin Idoate-Lacasia, Jonas Stillhard, Thomas A. Nagel, Tuomas Aakala, Markus Blaschke, Bogdan Brzeziecki, Marco Carrer, Eugenie Cateau, Georg Frank, Shawn Fraver, Jan Holik, Stanislav Kucbel, Anja Leyman, Peter Meyer, Renzo Motta, Pavel Samonil, Lucia Seebach, Miroslav Svoboda, Jerzy Szwagrzyk, Kris Vandekerkhove, Ondrej Vostarek and Tzvetan Zlatanov contributed data and supported the process of data harmonization. All co-authors critically reviewed the draft and contributed to paper writing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data and script to reproduce the analysis is available at the Environmental Data Portal EnviDat https://www.doi.org/10.16904/envidat.669 (Idoate-Lacasia, 2025).

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SUPPORTING INFORMATION

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

Appendix S1. Dataset and data screening.

Appendix S2. Annual mortality rates and the climate during census interval.

Appendix S3. Location of trees within their ecological niche space.

Appendix S4. Models of mortality rates over time: Covariates and coefficients.

Appendix S5. Models of mortality probability and probability of occurrence: Covariates and coefficients.

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