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Drivers of background mortality in European mixed mountain forests of *Picea abies* (L.) Karst., *Abies alba* Mill., and *Fagus sylvatica* L.

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ABSTRACT

Mixed mountain forests of Norway spruce (*Picea abies* (L.) Karst.), silver fir (*Abies alba* Mill.), and European beech (*Fagus sylvatica* L.) are ecologically important across Europe, providing ecosystem services, supporting biodiversity, and contributing to the bioeconomy as crucial timber sources. Understanding background mortality in these forests is essential to distinguish the effects of this relatively continuous endogenous process from those induced by exogenous disturbances, and to inform sustainable management under changing conditions. To assess how stand density, tree-size dominance, species competition and diversity, site geomorphology, and climate influence background mortality, expressed as the annualised basal area loss rate, we applied generalised linear mixed models. We used tree measurements from 78 plots located in Bulgaria, Bosnia and Herzegovina, Slovenia, Slovakia, Poland, Germany, and Switzerland, inventoried from 1912 to 2016, with most of them first surveyed between 1953 and 1964. At the stand level, mortality increased with stand basal area, greater species diversity, and the interaction between fir dominance and drought. Spruce mortality increased with stand density, species diversity, and fir dominance, indicating a higher probability of spruce mortality under fir dominance pressure. Fir mortality increased with species diversity and mean annual temperature, revealing fir as sensitive to rising temperatures, and with the interaction between fir dominance and drought, with moisture effects varying along the fir dominance gradient. Beech mortality increased with stand density and fir dominance, suggesting that beech suffers more when fir occupies a dominant canopy position. These findings suggest that sustainable management of mixed mountain forests requires targeted silvicultural interventions to regulate stand density, manage species diversity, and limit fir size dominance.

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1. Introduction

Tree mortality, a natural process in all forest ecosystems which refers to the death of trees from causes other than harvesting (Ambrose et al., 2022), has key consequences in forest dynamics (Franklin et al., 1987), such as producing opportunities for regeneration by the creation of gaps, increasing the growth of surrounding trees through reduced competition, and adding large woody debris to the structure of stands (Adame et al., 2010). Deadwood is a critical component of forest ecosystems, supporting a large proportion of forest biodiversity, particularly saproxylic species, which are estimated to account for over 20–25% of forest species (Stokland et al., 2012), and play essential roles in nutrient cycling, soil fertility, and overall forest productivity. In addition, deadwood acts as a reservoir of water and nutrients, thereby buffering the effects of drought and contributing to their gradual release (Bütler et al., 2024). However, there is growing concern that increasing rates of tree mortality (Senf et al., 2018) could lead to rapid, substantial changes in forest properties as climate change progresses (McDowell et al., 2018; Bugmann et al., 2019; Hartmann et al., 2022; Holtmann et al., 2024). Indeed, in addition to the direct loss of trees, tree mortality may reduce forest regeneration capacity by decreasing the number of potential reproductive individuals and by altering microenvironmental conditions and biotic interactions (Royer et al., 2011). Moreover, tree mortality influences turnover rates, which critically impact carbon storage and, in turn, affect the climate system (Cailleret et al., 2019). Additionally, mortality affects water fluxes and biodiversity (Bugmann et al., 2019). While increasing mortality rates may indeed raise concerns from a timber production perspective, they also enhance microhabitat diversity and contribute to biological control through trophic interactions, providing habitat for predatory species associated with old trees and deadwood. Tree mortality should therefore not be viewed solely as a symptom of decline, but also as an integral component of forest self-regulation processes.

Understanding how tree mortality shapes forest properties therefore requires a clear framework for distinguishing its underlying drivers and mechanisms. In this context, tree mortality is generally categorised according to its underlying drivers: endogenous disturbances, which originate internally within a stand, and exogenous disturbances, which are externally imposed physical or biotic agents (White, 1979; Reilly and Spies, 2016). Background mortality arises from endogenous processes — including density-dependent competitive suppression, senescence, physical damage, and endemic pathogen and insect activity — and operates continuously at fine spatial scales, ultimately driving long-term patterns of structural development in forested ecosystems (Franklin et al., 2002; Weiskittel et al., 2011; Reilly and Spies, 2016). In contrast, exogenous disturbances such as storms, fires, flooding, or epidemic pest outbreaks are episodic and spatially variable in their effects, driving mortality across a wide spectrum of intensities — from partial stand replacement to complete stand-replacing events (Bréda et al., 2006; Camarero et al., 2015; Reilly and Spies, 2016; Gazol and Camarero, 2022). Importantly, endogenous and exogenous disturbances should not be treated as a strict dichotomy (Taccoen et al., 2019) but rather as endpoints of a continuum (White and Pickett, 1985; Reilly and Spies, 2016), as their effects on mortality rates frequently overlap and interact; for instance, drought may simultaneously elevate background mortality through physiological stress while also triggering epidemic insect outbreaks or increasing tree susceptibility to wind damage (Reilly and Spies, 2016; Csilléry et al., 2017). The present study focuses primarily on background mortality driven by endogenous processes, while acknowledging that severe episodic disturbances may also contribute to the observed mortality signal.

Interactions among abiotic and biotic agents frequently blur the distinction between these types of mortality drivers (Zhu et al., 2017; Griffin-Nolan et al., 2021). Among abiotic drivers, topographic factors, such as elevation, aspect, and slope, can influence tree mortality both directly (e.g., through increased tree downfall on steep slopes) and indirectly by contributing to spatial variability in the microclimate, which can either enhance or buffer broader climatic influences (Zhu et al., 2017; Redmond and Kelsey, 2018). Abiotic climatic factors, e.g. temperature and temperature-induced increases in either drought stress or the effectiveness of tree-killing insects and pathogens (Das et al., 2013), have been strongly related to tree mortality in many forest types (Bigler et al., 2006; Van Mantgem and Stephenson, 2007; Clifford et al., 2013). Furthermore, biotic agents, such as insects and fungal diseases, interact with these abiotic factors to accelerate mortality (Gea-Izquierdo et al., 2019). The timing of drought is also a relevant factor that, when combined with pathogens, may modify tree mortality (Caldeira, 2018). Stand factors, such as structure, species interactions, and ageing, also influence competition and resource availability. In European mountain forests, these factors are not only drivers of mortality but also the legacies of past and ongoing forest management practices. Silvicultural interventions, such as thinning regimes, harvesting intensity, and historical species selection, have shaped the trajectories of these stands, determining the levels of density, species dominance, and structural heterogeneity observed today (Pretzsch, 2009; Hilmers et al., 2019). Consequently, background mortality patterns often reflect the interaction between intrinsic ecological processes and these management-driven structures. These factors have been reported to be positively associated with tree mortality (Das et al., 2008, 2011; Luo and Chen, 2011; Trifković and Ficko, 2025) or not associated with it (Rozendaal et al., 2020). While density-dependent background mortality is often caused by competition-induced suppression, high stand density can also lead to slower growth rates, making trees more susceptible to epidemic insect outbreaks, thereby blurring the distinction between endogenous and exogenous mortality drivers (Weiskittel et al., 2011; Reilly and Spies, 2016). Ultimately, these factors are not mutually exclusive, exhibit non-additive effects, and vary in importance among species (Cailleret et al., 2019).

Despite the importance of background mortality, there is a limited understanding of the factors influencing tree death at the species and stand levels. This lack is due to the scarcity of research that considers a broad spectrum of drivers rather than single causal factors, and to a lack of data collected at census intervals of less than 10 years over long periods (Taccoen et al., 2019). Investigating the factors influencing background tree mortality requires data that capture the full range of variability across sites, species composition, and structure. The use of data from permanent sample plots across repeated censuses is the only way to meet these requirements and enable the direct quantification of annual mortality rates (Kim et al., 2017).

Mixed mountain forests of Norway spruce (*Picea abies* (L.) Karst), silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) cover more than 10 million hectares in Europe (Hilmers et al., 2019), comprising a large proportion of the Alps, the Balkans, and the Carpathian mountain ranges. These forests are biodiversity hotspots and provide essential ecosystem services far beyond the mountain regions themselves (Millennium Ecosystem Assessment MEA, 2005; Estreguil et al., 2012). Moreover, these forests have high socio-economic importance in Central and Eastern Europe due to the substantial mobilisation and processing of their wood resources (Hilmers et al., 2019). Because a long history of human intervention has shaped these systems, their current structural state—and the resulting mortality patterns—must be interpreted as an outcome of management legacies. Understanding how these human-mediated structures influence tree survival is therefore essential for developing adaptive silvicultural strategies. Given that their functional composition changes primarily result from tree mortality over relatively short time scales (Ruiz-Benito et al., 2017), the interest in investigating and modelling background tree mortality is well justified.

In this context, this study aimed to provide a comprehensive understanding of the drivers of tree mortality in mixed spruce-fir-beech mountain forests in Central and Southeast Europe. By identifying these drivers, we aimed to provide a scientific baseline that supports both timber production and ecosystem functioning, ensuring transparent interpretation of mortality patterns and strengthening the study's relevance to forest management. Specifically, we asked: (i) whether and how forest stand structure, heterogeneity, diversity and dominance features, together with geomorphological and climate conditions, are associated with background mortality at the stand level, and (ii) whether there are species-specific differences in the drivers of background mortality of spruce, fir and beech.

To accomplish our objectives and shed light on the factors contributing to background tree mortality, we considered data collected in 78 long-term experimental plots located in forests in Bulgaria, Bosnia and Herzegovina, Slovenia, Slovakia, Poland, Germany, and Switzerland, surveyed in 2 to more than 40 inventories from 1912 to 2016.

2. Materials and methods

2.1. Forest inventory data

We started the study considering forest inventory data from 92 permanent plots in mixed spruce-fir-beech mountain forests that are part of long-term forest monitoring programmes in Bulgaria, Bosnia and Herzegovina, Slovenia, Slovakia, Poland, Germany, and Switzerland (Fig. 1).

For each country, a detailed description of the plots' locations, the monitoring program, and the historical evolution of management activities is reported in the Supplementary material.

Forest inventories were conducted between 1912, i.e., the first year, and 2016, i.e., the last year of the study period, at intervals of 1–27 years.

The species and the diameter at breast height (DBH, 1.3 m stem height) of 10 cm and above were recorded during the repeated field surveys. Additionally, tree status was recorded during field surveys and classified into four levels: survivor, dead, ingrowth, and removed. Survivor status was recorded if a tree was present and alive at both the beginning and the end of the inventory period. Dead status was recorded in the following cases: a snag, i.e., a dead tree that was upright and decomposing naturally; a log, i.e., a dead tree (or part of one) that has fallen to the ground; and a tree that was uprooted or snapped while alive. Trees that died during the interval were included in mortality calculations. Ingrowth status was recorded if a tree reached a DBH of 10 cm during any observation period and survived until the last measurement of the period. The removed status was recorded when a tree disappeared between two consecutive surveys. Because it was not possible to determine, for managed plots, whether removed trees were harvested or died naturally and were later removed, we used the ratio of the basal area of removed spruce, beech, and fir to the plot's total basal area as the criterion for plot selection. Indeed, given that plots were located mainly in regularly managed forest stands by single tree selection or irregular shelterwood systems, to avoid potential distinct effects of thinning and harvesting on tree mortality, we excluded from our analysis individual inventories in which the percentage of basal area of removed trees exceeded 5% in a specific forest inventory period (Condés et al., 2025). While this threshold-based filtering isolates background mortality from intensive recent silvicultural interventions, we acknowledge that the underlying stand structure, species composition, and dominance patterns remain products of historical management legacies. Thus, the mortality rates analysed here reflect natural processes operating within human-mediated structural templates characteristic of European cultural landscapes. The application of our criterion, based on the basal area of removed trees, resulted in selecting plots with a maximum annual mortality rate of 4.9%.

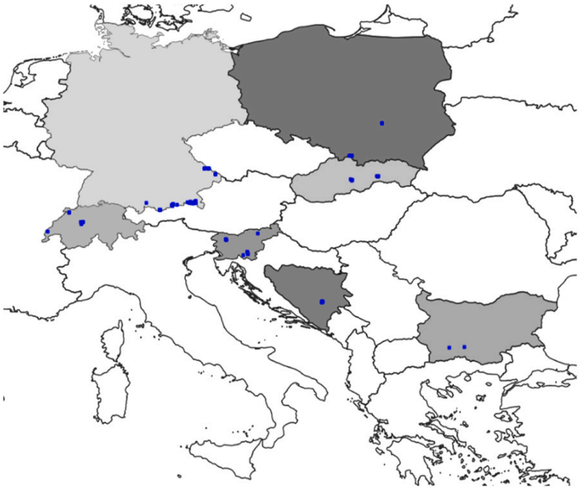

Fig. 1. Plot location in Bulgaria, Bosnia and Herzegovina, Slovenia, Slovakia, Poland, Germany, and Switzerland.

In addition, in our study, we used only plots with all three species present to avoid problems with species-level variables that could not be calculated when a species was absent.

After applying the selection criteria described above, we used data from 84,144 trees across 78 plots.

In Table 1, we provide information about forest inventory features of the 78 plots per country.

Table 2 summarises the mean values of the main dendrometric variables, as reported in the first forest inventory, for all species (fir, spruce, and beech) that composed the 78 plots.

The statistics describing the main geographical and geomorphological features of the 78 plots by country are reported in Table S1 of the Supplementary material.

2.2. Tree mortality rate at forest stand- and species-level

Annual mortality can be quantified either through the reduction in stem density (trees ha^{-1}) or through basal area loss (m^2 ha^{-1}). These two metrics offer different ecological inferences: while reduction in stem density is a key indicator of demographic transitions and the stem-exclusion stage of stand development (Westoby, 1984), basal area loss was selected as the primary response variable for this study. Our focus on the functional impacts of mortality on ecosystem services, timber availability, and carbon turnover justifies this choice. Basal area integrates both individual mortality events and the extent of the affected living area, providing a stronger correlation with total biomass or volume loss than stem density alone (Riofrío et al., 2025). Furthermore, given the high correlation between these two metrics in our dataset, the drivers identified for basal area loss are expected to be representative of general mortality patterns across the studied plots. To ensure comparability across the 78 plots, which featured remeasurement intervals ranging from 2 to 27 years (Table 1), we used the annualised compound interest formula suggested by Sheil et al. (1995). Regarding mortality rate formulations, Sheil et al. (1995) critically examined various measures of mortality rates. They highlighted flaws in the equations used to compute them, as well as the need for more complex formulations to facilitate comparison across different periods. For these reasons, we computed the background mortality rate at the stand level using the following equation (Sheil et al., 1995):

$$RG = 1 - \left[1 - \left(\frac{G - G_d}{G}\right)\right]^{\frac{1}{\Delta t}} * 100 \tag{1}$$

where RG is the annualised mortality rate of basal area loss (%), G is the basal area of the plot at the beginning of the forest inventory period (m^2 ha^{-1}), G_d is the basal area of trees that died during the period between surveys (m^2 ha^{-1}), and Δt is the length of the measurement interval in years. By incorporating the specific interval length (Δt) into the exponential calculation, the formula of Sheil et al. (1995) normalises the

Table 1
Per country, minimum and maximum number of surveyed plots, period of the surveys, number of surveys per plot, years between surveys, area and elevation of the plot.

Country	Number of plots	Time range of surveys	Number of surveys per plot		Years between surveys		Area of the plot (m^2)		Elevation (m a.s.l.)	
			min	max	min	max	min	max	min	max
Bulgaria	1	1995–2005	2	2	10	10	1500	1500	1569	1569
Bosnia and Herzegovina	5	2006–2016	2	2	10	10	10000	26300	1006	1291
Slovenia	7	1973–2017	3	5	5	20	400	8619	910	1443
Slovakia	7	1972–2010	2	3	2	16	3678	9872	621	845
Poland	10	1964–2016	3	6	8	12	2000	5000	425	1087
Germany	39	1953–2016	3	11	3	27	1560	10024	743	1463
Switzerland	9	1912–2014	3	17	5	14	5000	19960	558	1364

Table 2
Summary of the mean, minimum, maximum, and standard deviation values of the main dendrometric variables of the 78 plots referred to in the first forest inventory. N = number of trees per ha; G = basal area; dg = quadratic mean diameter; Sd = standard deviation; Mean, Min, Max = mean, minimum and maximum values, respectively.

	All species			*Picea abies*			*Abies alba*			*Fagus sylvatica*		
	N	G	dg	N	G	dg	N	G	dg	N	G	dg
	stems/ha	m^2/ha	cm	stems/ha	m^2/ha	cm	stems/ha	m^2/ha	cm	stems/ha	m^2/ha	cm
Min	81	12.81	17.03	1	0.12	15.80	2	0.06	11.00	1	0.05	10.93
Max	1331	79.69	63.17	460	68.09	84.88	499	57.06	90.66	729	44.46	64.52
Mean	443	38.09	34.80	156	15.42	38.51	139	14.01	38.13	128	7.79	28.06
Sd	189	11.80	8.64	121	11.94	12.61	106	11.03	14.06	144	9.08	11.11

mortality rate. It accounts for the non-linear nature of tree survival over time, preventing mathematical artefacts that might otherwise arise from varying census lengths.

In line with the equation [1], we calculated species-specific mortality rates for spruce, fir, and beech using each species' basal area at the beginning of the forest inventory period (*Gsp*) and the basal area of dead trees of that species (Gsp_d), as shown in [2], where *sp* denotes the species for which the rate is calculated, i.e. Pa for spruce, Aa for fir and Fs for beech.

$$RGsp = 1 - \left[1 - \left(\frac{Gsp - Gsp_d}{Gsp}\right)\right]^{\frac{1}{\Delta t}} * 100 \tag{2}$$

Thus, the response variables in the models represent annualised mortality rates expressed as percentages at the stand and species levels.

2.3. Explanatory variables used in the background mortality modelling

To model the background mortality, we computed several variables on the live trees at the stand and tree species level, grouped into the following categories (Torresan et al., 2020): (i) tree density, (ii) tree size, (iii) tree size heterogeneity, (iv) tree size dominance, (v) tree competition, (vi) species diversity and evenness. We also computed (vii) geomorphological and (viii) climatic site conditions.

2.3.1. Variables indicating tree density

Background mortality is primarily driven by density-dependent processes that occur as tree populations approach the site's carrying capacity (Trifković et al., 2023). Density-dependent mortality occurs when individuals become crowded as they accumulate biomass, leading to intensified competition for limited resources (Gendreau-Berthiaume et al., 2016; Pretzsch and Grote, 2023a, 2023b; Liu et al., 2025). This density-dependent competition is widely recognised as the primary mechanism governing mortality in self-thinning forest stands (Oliver and Larson, 1996; Brassard and Chen, 2006; Yang et al., 2024). We used stand basal area to quantify overall stand density and the basal areas of spruce, fir, and beech to quantify species-specific density, as basal area incorporates both tree number and size and is considered a reliable indicator of space occupancy (Brūmelis et al., 2020).

2.3.2. Variables indicating tree sizes at the stand and tree species level

Tree sizes determine the forest stand structural characteristics, which in turn influence temporal dynamics of vegetation, patterns of regeneration and gap dynamics, micro-climatic variation and forest productivity, and therefore ultimately affect mortality and differential vulnerability to climate change (Larson et al., 2015; Ford et al., 2017; Salas-Eljatib and Weiskittel, 2020). We computed the quadratic mean diameter at stand and species levels to characterise tree sizes. In addition, we calculated the 5th and 90th percentiles of the diameter at breast height (DBH) distribution on all live trees for the total stand and for spruce, fir and beech trees at the beginning of each forest inventory period for which tree mortality occurred.

2.3.3. Variables indicating tree-size heterogeneity at the stand and tree species level

Variation in tree sizes is a key driver of forest dynamics, affecting light interception, competitive pressure, and structural stability (Coomes and Allen, 2007). These size-related interactions strongly modulate background mortality patterns both within and among species (e.g., Ruiz-Benito et al., 2013). To quantify stand- and species-level tree-size heterogeneity, we computed the Gini coefficient (Gini, 1921), skewness, and coefficient of variation for DBH based on the DBH distributions at the stand and species levels, respectively. Percentile ratios in the diameter distribution were also used to quantify heterogeneity. We computed the ratio between DBHs at the top and the bottom (i.e., DBH at 90th divided by DBH at 10th percentile), the top half (i.e., DBH at 80th divided by DBH at 50th percentile) and the bottom half (i.e., DBH at 50th divided by the DBH at 20th) of the distribution as suggested by Martinez and Slivinski (2008). We computed all these variables at the stand and tree-species levels.

2.3.4. Variables indicating tree species size dominance

In forests, resource uptake depends not only on resource availability but also on an individual's uptake ability (Luo and Chen, 2011), which, in turn, influences background mortality. For this reason, we used relative size, as it more accurately reflects individuals' dominance when encountering others in the same forest stand. We quantified species size dominance as the mean size of a target species relative to the mean tree size in the plot, calculated by dividing the quadratic mean diameter of spruce, fir, and beech by the quadratic mean diameter of the stand. Moreover, we computed size dominance between species as the ratio of a species' quadratic mean diameter to the quadratic mean diameter of all other species (e.g., the quadratic mean diameter of spruce divided by that of fir). We specify that, although tree species size dominance is often correlated with competitive interactions, particularly asymmetric competition for light, it cannot be directly interpreted as competition per se, as size hierarchies may also arise from species-specific growth strategies, stand structural attributes, or past disturbance dynamics.

2.3.5. Variables indicating tree species competition

In forests, asymmetric competition refers to situations in which larger trees gain disproportionately more of a limiting resource—usually light—than smaller trees. A commonly used tree competition measure is the basal area in larger trees (BAL; Wykoff, 1990), which is, for a given subject tree, the sum of the basal area of all trees which are larger in DBH than the subject tree (Ledermann and Eckmüllner, 2004). High BAL values for the tree under consideration indicate that the others dominate it; i.e., it occupies the smallest size classes (Schütz and Pommerening, 2013). Since we are modelling species-level mortality rather than individual-tree mortality, we used the average BAL for each species (spruce, fir, and beech) to reflect the average competition pressure each species experiences within the stand.

2.3.6. Variables indicating tree species diversity and evenness

Despite significant recent research showing that tree species diversity improves forest productivity, few studies examine how tree diversity affects tree mortality (Searle et al., 2022). In our study, we expressed the tree species diversity, i.e., the relative abundance of species in the plot, as both the number of trees and the basal area of spruce, fir, beech, other angiosperm species, and other gymnosperm species, using the Shannon index (Shannon, 1948). In addition, we computed the equality in abundance, i.e., the evenness, by dividing the Shannon index by the natural logarithm of the number of trees or basal area of species present in the plot (Peet, 1974).

2.3.7. Variables indicating geomorphological site conditions

Geomorphological features, i.e., elevation, slope, roughness, and aspect, were extracted from the Copernicus Digital Elevation Model dataset at 90 m resolution using the CopernicusDEM package (Mouselimis, 2022) in R (R Core Team, 2025). To make aspect a suitable parameter for inclusion in the analysis, it was decomposed into two linear components: aspect easting (the sine of the aspect) and aspect northing (the cosine of the aspect), as calculated by MacLeod et al. (2008).

2.3.8. Variables indicating climatic site conditions

Climatic data were obtained from the Climate Downscaling Tool (ClimateDT, https://climatedt.org/), a geospatial web service that downscales a comprehensive set of climatic variables and indices across multiple climate scenarios (Marchi et al., 2024). The system operates on a 1 km × 1 km grid resolution, integrating CRU-TS v4.06 historical climate records (1901–present) with UKCP18 datasets for future projections. Spatial downscaling is achieved through dynamic lapse-rate adjustments combined with multiple interpolation methods (bilinear and inverse-distance weighting), enabling scale-free climate queries across the European domain (Marchi et al., 2024).

For each of the 78 permanent plots, geographic metadata — including plot identifier, coordinates, and elevation — were submitted to the ClimateDT server via a comma-separated values (.csv) file, with each record specifying a unique location identifier, latitude (decimal degrees), longitude (decimal degrees), and elevation (metres above sea level). Following server-side computation and downscaling, the output file containing climate variables at annual temporal resolution was retrieved for the entire study period (1912–2016).

Temperature-related indices included mean annual temperature and the Rivas-Martínez Thermicity Index (Rivas-Martínez et al., 2011), which characterises thermal conditions as $10(T + m + M)$, where T denotes mean annual temperature, m the mean minimum temperature of the coldest month, and M the mean maximum temperature of the coldest month. Precipitation and water balance indices comprised mean annual precipitation, precipitation seasonality — a measure of the intra-annual dispersion of rainfall — and a modified De Martonne Aridity Index (De Martonne, 1926), which quantifies site aridity by integrating both the annual water balance and the most water-limited period of the year, expressing the ratio of precipitation to temperature as a proxy for water availability. Heat-moisture balance was characterised by two indices: the annual heat-moisture index, which quantifies the equilibrium between thermal energy and water availability at the annual scale, and the summer heat-moisture index, computed analogously for the June–August period to capture seasonal water stress during the peak of the growing season. To characterise meteorological drought at short timescales, the monthly standardised precipitation index (SPI) and the monthly standardised potential evapotranspiration index (SPEI) were additionally considered. Both indices enable the identification and quantification of drought episodes by standardising precipitation and climatic water deficit, respectively, relative to a long-term reference distribution, thereby allowing for temporally consistent drought assessments across the study period. For each climate variable described above, we calculated the mean across all years between the two inventory periods to reflect the long-term environmental conditions influencing each plot. While this approach may mask the effects of short-term extreme events, it is better suited to identifying the drivers of background mortality, which is primarily regulated by long-term competitive interactions and by species' physiological adaptation to their average environment.

The statistics (minimum, maximum, mean, and standard deviation) for all variables described in Sections 2.3.1–2.3.8 above, along with their respective tables reporting variable name, acronym, meaning, and measurement units, are presented in Tables S2–S22 of the Supplementary Material. For stand structural variables (Sections 2.3.1–2.3.7), statistics refer to values recorded at each forest inventory date across the study period (1912–2016). For climatic variables (Section 2.3.8), statistics were computed on values averaged over the inter-census intervals between successive forest inventories, thereby representing the climatic conditions experienced by the stand between two consecutive measurement dates.

2.4. Modelling approach

We modelled background tree mortality using generalised linear mixed models (GLMM), with the annualised basal area mortality rate as the response variable at the forest stand level (i.e., equation [1]) and the species-specific mortality rates of spruce, fir, and beech as the response variables at the tree species level (i.e., equation [2]).

A common problem in forest inventories is that the surveys used to record mortality produce continuous data, resulting in a high proportion of true zeros. Statistical data analysis of zero-inflated continuous data is challenging, as ordinary distributions, such as the normal or gamma, often fail to fit the data well, and log-transformations or similar methods are not feasible due to the presence of zeros (Min and Agresti, 2002; Dons et al., 2016). When modelling tree mortality, the zeros are inherent to the data and must be included to obtain correct parameter estimates of background mortality. For these reasons, we applied the exponential dispersion model (EDM) family of distributions (Jørgensen, 1987). EDM distributions are response distributions for GLMMs and include the flexible Tweedie family, which has proven especially useful for modelling positive continuous data with a proportion of exact zeros (Smyth, 1996; Hasan and Dunn, 2011). The Tweedie family is suitable when the variability in the levels of the response variables is not constant, can exceed what the usual Poisson assumption implies (Li et al., 2022), and when there is over-dispersed continuous data with exact zeros (Dons et al., 2016). Tweedie GLMM imposes a multiplicative structure on the dependent variable by combining discrete and continuous probabilities, thereby providing valid estimates that include true zeros in the continuous response variable (Dons et al., 2016), improving fitting performance.

In our models, we included a random intercept for the country to account for group-level variation across Bulgaria, Bosnia and Herzegovina, Slovenia, Slovakia, Poland, Germany, and Switzerland, as we considered that the baseline response might differ between countries, assuming the effect of the covariates to be the same across them. We fitted one model at the stand level and three separate models, one for each species—spruce, fir, and beech—using maximum likelihood estimation via 'TMB' (Template Model Builder) with the 'glmmTMB' package in R (Brooks et al., 2017; McGillycuddy et al., 2025). To model the background mortality rate of spruce, fir and beech, we restricted each species-specific model to plots where that species contributed at least 10% of the stand basal area, because the death of a single tree could otherwise drive cases with species-specific mortality rates of 100% and would not be meaningful for modelling. After applying this selection criterion, we used 67 plots for modelling spruce and fir mortality and 53 for modelling beech mortality rate.

To identify the independent variables influencing background mortality, we first employed a screening pipeline in R for each group variable, enabling automatic model comparison across predictors within each group (see Tables S2-S22). For each group, we considered only variables with significant coefficients (p-value < 0.05). Once we identified candidate variables within each covariate group (density, size, heterogeneity, dominance, competition, diversity, site, climate), we performed final variable selection using a forward stepwise procedure based on residual deviance reduction. Starting from a null model containing only random effects, we sequentially added the single variable (from any group) that produced the largest significant decrease in residual deviance, as assessed via likelihood-ratio tests (LRTs, $\alpha = 0.05$). This process continued until no additional variable significantly improved the model fit. We tested interactions between climate variables and variables indicating tree species size dominance and competition only when climate variables were already significant.

At each step, we verified model assumptions using the check_model() function (performance package in R) and tested for overdispersion and zero-inflation patterns using simulated residuals (simulateResiduals(), DHARMa package in R; Hartig, 2024) with 150,000 simulations. Variables were retained only if they (i) significantly reduced deviance, (ii) did not violate model assumptions, and (iii) had variance inflation factors (VIF) below 5 to ensure minimal multicollinearity.

To assess the performance of the models, we computed the marginal and the conditional R-squared, the root mean squared error, the mean absolute error and the concordance correlation coefficient using the MuMIn (Bartoń, 2025), Metrics (Hamner et al., 2018) and DescTools (Signorell, 2025) packages in R. In addition, as goodness-of-fit measures, we used the ROC (Receiver operating characteristic) curve as well as the conditional (both fixed and random effects) and marginal (fixed effects) area under the curve (AUC) computed with the "roc" function in the "pROC" library (Robin et al., 2011). To this end, being aware that applying the ROC/AUC to our Tweedie models yielded misleading outputs because our models produce continuous values of mortality rate, we defined a binary threshold (attributing the value 1 to the upper mortality values at the median and 0 to all the others) to evaluate whether the models distinguished high mortality from low mortality.

3. Results

3.1. Annual basal area mortality rates at forest stand and species-levels

The average annual mortality rate, corresponding to the basal area loss rate, for all species over the period 1912–2016 was 0.62%, ranging from 0% to 13.67%. Spruce and fir had the highest mean annual mortality rates of 0.82% and 0.74%, respectively. Beech had a mean annual mortality rate of 0.49% (Table 3).

3.2. Tree mortality models at the forest stand and species levels and their performance

The results of the preliminary analysis, which identified, within each group, the variables with significant coefficients, are reported in Table S23 in the Supplementary material.

The equation [3] reports the selected model of background basal area mortality at the stand level, while equations [4], [5], and [6] report selected models of the background basal area mortality for spruce, fir and beech, respectively:

$$RG_{ij} = \beta_0 + \beta_1 G_{ij} + \beta_2 dgAa\_dg_{ij} + \beta_3 HSPEC_{ij} + \beta_4 SPI12_{ij} + \beta_5 dgAa\_dg_{ij} * SPI12_{ij} + b_{(c)j} \tag{3}$$

$$RGPa_{ij} = \beta_0 + \beta_1 G_{ij} + \beta_2 dgAa\_dgPa_{ij} + \beta_3 HSPEC_{ij} + b_{(c)j} \tag{4}$$

$$RGAa_{ij} = \beta_0 + \beta_1 dgAa\_dg_{ij} + \beta_2 HSPEC_{ij} + \beta_3 bio1_{ij} + \beta_4 SPI12_{ij} + \beta_5 dgAa\_dg_{ij} * SPI12_{ij} + b_{(c)j} \tag{5}$$

$$RGFs_{ij} = \beta_0 + \beta_1 G_{ij} + \beta_2 dgAa\_dgFs_{ij} + b_{(c)j} \tag{6}$$

In the equations, RG_{ij}, $RGPa_{ij}$, $RGAa_{ij}$, $RGFs_{ij}$ are the model expected background mortality rates for the forest stand, spruce, fir and beech, respectively, for plot $_i$ in country $_j$ (i.e., Bulgaria, Bosnia and Herzegovina, Slovenia, Slovakia, Poland, Germany, and Switzerland); β_0 is the fixed intercept; β_1, β_2, β_3, β_4, β_5 are the fixed-effect coefficients for predictors (the same covariate effects are assumed across countries); $b_{(c)j}$ is the random intercept for the country *c* that plot *i* belongs to; G is the basal area of the forest stand; dgAa_dg is the ratio between the quadratic mean diameter of fir and the overall quadratic mean diameter; HSPEC is the Shannon index calculated using the proportion of the number of trees of spruce, fir, beech, other coniferous and other deciduous in the plot; SPI12 is the 12-month SPI, dgAa_dgPa is the ratio between the quadratic mean diameter of fir and the quadratic mean diameter of spruce; dgAa_dgFs is the ratio between the quadratic mean diameter of fir and the quadratic mean diameter of beech; bio1 is the mean annual temperature.

Of the wide range of tree density, tree size, size heterogeneity, size dominance, competition and species diversity-related covariates, only a subset was retained in the final models. Tree size dominance-related variables were consistently maintained across the three species-specific and the stand-level models. In contrast, compositional factors (i.e., species diversity) were relevant in the spruce, fir, and stand models, whereas climatic factors were relevant only in the stand level and fir models. This outcome suggests that, in our dataset, background tree mortality is strongly associated with stand structure components related to species diversity and size dominance. In contrast, more detailed measures of size distribution, size heterogeneity and competition did not explain variability in basal area mortality rates.

The results of the DHARMa residual diagnostics for the stand-level and species-level background mortality models are reported in Figures S1-S4 of the Supplementary material. The stand-level model exhibited more pronounced deviations (KS test: $p < 0.001$; Figure S1), though dispersion tests remained adequate across all models ($p > 0.05$), indicating no systematic over- or under-dispersion. The spruce and beech models showed marginally significant deviations (KS tests: $p = 0.046$ and $p = 0.039$, respectively) but adequate dispersion and acceptable residual patterns (Figures S2 and S4). The fir model showed excellent diagnostics, with all tests non-significant (Figure S3).

The ROC curves for the stand-level and species-level mortality models are shown in Figure S5 of the Supplementary material. Across all models, the total model (including both fixed and random effects)

Table 3

Minimum (Min), maximum (Max), and mean (Mean) annualised mortality rates of basal area loss and annualised mortality rate of stem loss at forest stand level (i.e., RG and RN, respectively) and at species level (Pa = spruce; Aa = fir; Fs = beech) and standard deviation (Sd). N is the number of plots used in modelling. The sum of N per species is higher than the overall plot number (i.e., 78) since more than one species occurred in the same plot.

	RG	RN	RGPa	RNPa	RGAa	RNAa	RGFs	RNFs
Min	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Max	13.67	4.94	9.71	11.26	18.18	13.46	8.67	4.59
Mean	0.62	0.68	0.82	0.84	0.74	0.87	0.49	0.57
Sd	1.07	0.76	1.68	1.42	1.80	1.65	0.94	0.82
N	78	78	67	67	67	67	53	53

consistently outperformed the fixed-effects-only model at distinguishing high (i.e., mortality greater than the median mortality) from low mortality. The stand-level model achieved the highest discriminatory performance (AUC total = 0.79; Figure S5a), while among species-level models, fir showed the highest total AUC (0.72; Figure S5c), followed by beech (0.70; Figure S5d) and spruce (0.69; Figure S5b). Overall, the AUC values exceeded 0.69 across all models, indicating acceptable discriminatory ability, and country-level random effects contributed meaningfully to model performance.

Other model performance statistics, including the marginal and conditional coefficient of determination, root mean squared error, mean absolute error, the concordance correlation coefficient, and the marginal and conditional AUC, are reported in Table 4.

3.3. *Effects of covariates on background mortality at the forest stand and species levels*

At the stand level, background mortality was positively associated with basal area (G), relative fir size dominance (dgAa_dg), species diversity (HSPEC), and the interaction between the relative fir size dominance and the 12-month SPI (dgAa_dg*SPI12; Table 4). For spruce, mortality increased significantly with stand basal area (G) and with fir size dominance over spruce (dgAa_dgPa), indicating a higher probability of spruce mortality under fir dominance pressure. Spruce mortality also increased significantly with stand-level species diversity (HSPEC, Table 4). For fir, mortality was positively related to its relative dominance on all competitors (dgAa_dg), the diversity of species within the stand (HSPEC), the mean annual temperature (bio1), 12-month SPI (SPI12) and the interaction between its relative dominance on all competitors and meteorological drought based on precipitation anomalies over 12-month accumulation periods (dgAa_dg * SPI12, Table 4). Beech mortality increased with stand basal area (G) and with the size dominance of fir over beech (dgAa_dgFs; Table 4).

A critical aspect that emerged is that, in the mixture considered in our study, the fir size strongly influenced the mortality rates of the other two species. In practice, when the quadratic mean diameter of fir exceeds that of spruce or beech, it is also likely to exceed the overall stand quadratic mean diameter, thereby indirectly increasing spruce or beech mortality rates. At the same time, as fir's size dominance in the stand (dgAa_dg) increases, its own mortality also rises, suggesting strong intraspecific size dominance. This pattern indicates that, as fir becomes overwhelmingly dominant, its population density and size structure intensify competition for resources, increasing its susceptibility to background mortality.

Fig. 2a shows the predicted background mortality rate as a function of stand basal area for the different tree species and for the stand level. Overall, mortality rates tend to increase with basal area, but the magnitude and shape of this relationship differ among species. Beech exhibits a strong, positive, nonlinear relationship: mortality increases slowly at low basal areas and rises sharply beyond ~50–60 m^2 ha^{-1} , suggesting high sensitivity to density. Spruce follows a similar but less steep trend, with mortality progressively increasing across the entire range of basal area. In contrast, for fir mortality, stand basal area was not significant, possibly reflecting its shade tolerance and greater resistance to density-driven stress. The stand-level curve integrates these species-specific patterns, showing a moderate increase in mortality with basal area, suggesting that species mixture buffers extreme responses.

In Fig. 2b, the relationships reveal how increases in species diversity affected the predicted background mortality rates for individual species and the overall stand. According to our prediction, fir exhibits substantial exponential increases in mortality as species diversity increases. Indeed, as the stand becomes increasingly diverse, its predicted mortality rate rises to nearly 1.35 (see Table 3 to compare minimum, maximum and mean mortality values in the period 1912–2016), making

Table 4

Parameter estimates and p-values (Pr(>|z|)) for the basal area mortality models of spruce, fir and beech, and the forest stand. R^2m and R^2c are the marginal and conditional R^2 (marginal R^2 is the proportion of total variance explained through fixed effects, while conditional R^2 is the proportion of total variance explained through both fixed and random effects), respectively. RMSE and MAE are the root mean squared error and the mean absolute error, respectively. CCC is the concordance correlation coefficient. AUCm is the area under the curve of the fixed effects, while AUCc is the area under the curve of both fixed and random effects.

	RG		RGPa		RGAa		RGFs	
	Value	Pr(>|z|)	Value	Pr(>|z|)	Value	Pr(>|z|)	Value	Pr(>|z|)
Intercept	−5.6192	0.0000	−4.7705	0.0000	−5.4102	0.0000	−4.1631	0.0000
G	0.0319	0.0000	0.0256	0.0037			0.0506	0.0000
dgAa_dg	1.0442	0.0000			1.0642	0.0028		
dgAa_dgPa			0.7491	0.0030				
dgAa_dgFs							0.5897	0.0070
HSPEC	1.6446	0.0000	2.0379	0.0000	2.1742	0.0000		
bio1					0.2331	0.0083		
SPI12	1.0807	0.0836			2.6392	0.0036		
dgAa_dg * SPI12	−1.3459	0.0077			−2.4838	0.0006		
R^2m	0.0708		0.1098		0.1663		0.1423	
R^2c	0.8675		0.6708		0.5708		0.6430	
RMSE	0.9349		1.3212		1.4983		0.8868	
MAE	0.4890		0.7400		0.7025		0.4546	
CCC	0.3720		0.5807		0.4567		0.2694	
AUCm	0.6474		0.6428		0.6197		0.6132	
AUCc	0.7919		0.6918		0.7206		0.7043	

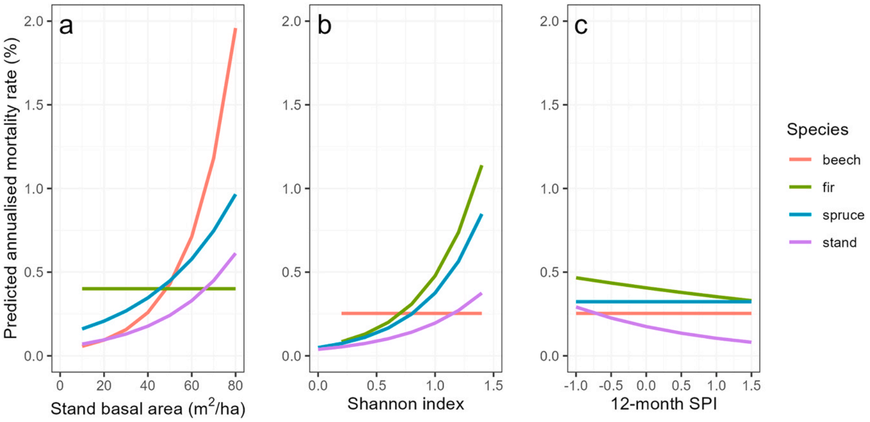

Fig. 2. Predicted background mortality rate at species and stand level as a function of stand basal area (a), species diversity (Shannon index) (b), and 12-month standardised precipitation index (c) (inventory period set at 10 years).

it the species with the highest mortality in such stands. Spruce is sensitive to diversity, though less than fir. The overall stand mortality rate also shows a gradual, positive increase as species diversity rises, rising from near 0.1 to around 0.4. This trend likely reflects the weighted average of the individual species trends, being pulled upward mainly by the highly sensitive fir. Stand-level mortality showed the strongest response to precipitation anomalies, declining markedly from dry to wet conditions, while fir maintained the highest predicted mortality across all SPI values with a slight decreasing trend under wetter conditions; both spruce and beech mortality remained virtually unresponsive to precipitation anomalies (Fig. 2c).

The response curves in Fig. 3 illustrate how interactions among stand density, species diversity, and the size dominance of fir over spruce influence the probability of background mortality in spruce. Spruce mortality begins to increase slightly in forest stands with basal area greater than 40 m^2/ha and with higher species diversity (Fig. 3a) or larger size dominance of fir over spruce (Fig. 3b).

Fir exhibits a higher background mortality rate in stands with higher species diversity, and this effect is amplified when fir is size-dominant in the stand (Fig. 4a). Higher temperatures increase background mortality in fir, particularly under higher species diversity (Fig. 4b). When fir is minor, wetter conditions increase fir mortality. When fir is dominant, the negative effect of the interaction means that wetter conditions no longer increase mortality, and may even reduce it (Fig. 4c).

At low values of basal area (i.e., sparse stands), mortality of beech is low and fairly similar across size dominance levels between fir and beech (Fig. 5). As the basal area increases, mortality rises sharply, especially in denser stands ($G > \sim 50$ m^2/ha). Higher size dominance of fir over beech generates higher background mortality of beech, suggesting that beech suffers more when fir occupies a dominant position in the canopy.

4. Discussion

4.1. Drivers of background mortality

This study presents a comprehensive analysis of background mortality in terms of basal area in European mixed spruce-fir-beech mountain forests, examining the relative importance of stand structure, species composition, tree-size dominance, tree-species competition, geomorphology and climate at both stand- and species-level, and testing a broad spectrum of variables.

None of the geomorphological site conditions examined — elevation, slope, or aspect — appeared to be important drivers of background mortality. In particular, we would expect species-specific mortality rates to vary with elevation, as species-specific growth rates do (Hilmers et al., 2019; Dulamsuren et al., 2017). Specifically, we expected beech to experience higher mortality at higher elevations than at lower ones, whereas the opposite might be true for spruce and fir. The absence of a significant elevation effect might reflect the influence of stand-structure variables (e.g., species composition and tree-size dominance), which may have absorbed the effects of geomorphological conditions in our models. However, this interpretation remains speculative and warrants further investigation.

Climatic factors played a role at the stand level and, more prominently, for silver fir. Fir mortality was influenced by both mean annual

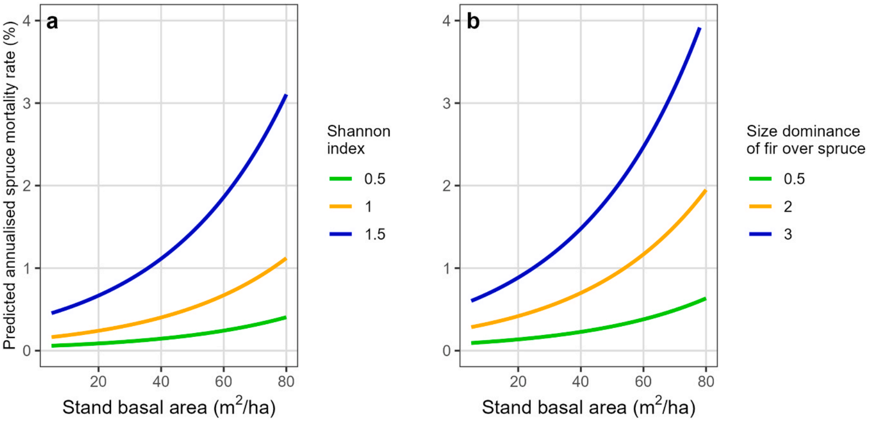

Fig. 3. Predicted background mortality of spruce in relation to stand basal area at different levels of species diversity (Shannon index) (a) and at different levels of size dominance of fir over spruce (b).

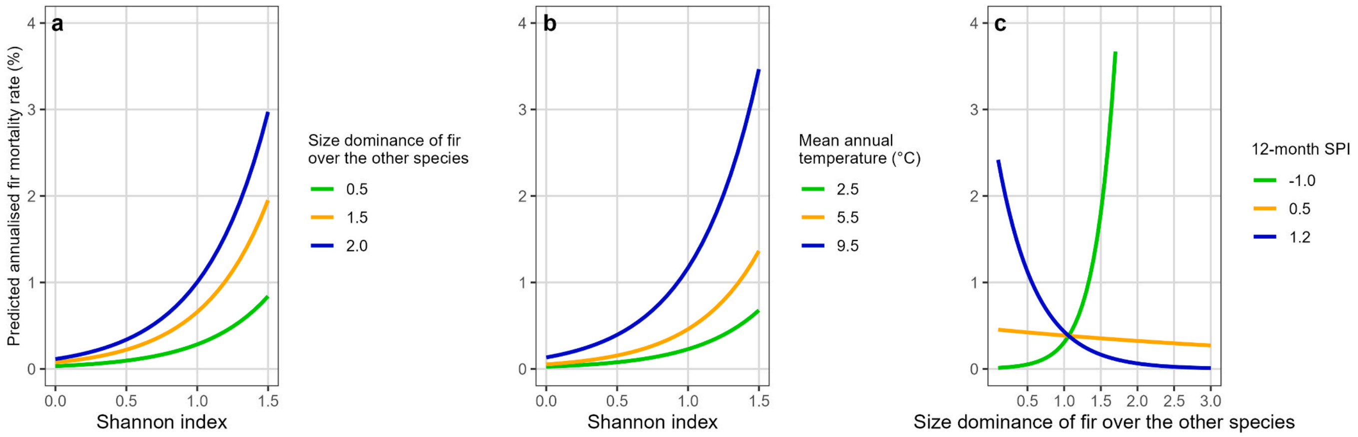

Fig. 4. Predicted background mortality of fir in relation to species diversity (Shannon index) at different levels of size dominance of fir over the other species (a) and at different levels of mean annual temperature (b). Predicted background mortality of fir in relation to the size dominance of fir over the other species at different levels of 12-month standardised precipitation index (c).

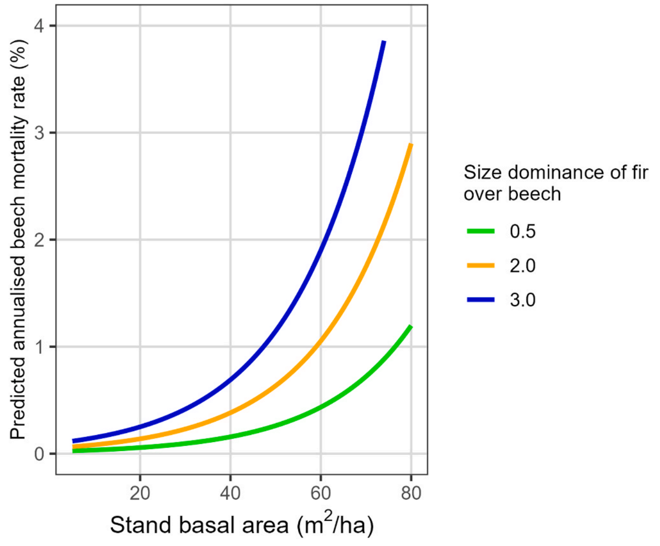

Fig. 5. Predicted background mortality of beech in relation to basal area at different levels of size dominance of fir over beech.

temperature and drought, as measured by precipitation anomalies over 12-month accumulation periods. Regarding mean annual temperature, our findings underscore the idea that long-term climatic warming appears to be a significant driver of growth decline in silver fir (Linares and Camarero, 2012) and consequently of its background mortality, due to its high vulnerability to environmental conditions and stand characteristics (Piedallu et al., 2023). The sensitivity of fir to temperature may indicate the beginning of a climatic constraint, consistent with observations of declining fir vitality at low-elevation and warm sites (Gazol and Camarero, 2022; Holtmann et al., 2024). The effect of annual moisture conditions on fir mortality depended strongly on its relative dominance within mixed stands. When other species dominated fir, wetter conditions were associated with higher mortality, possibly reflecting increased competitive pressure or heightened susceptibility to biotic agents such as root pathogens under favourable growth conditions (Camarero et al., 2015). However, as fir dominance increased, this relationship weakened and eventually reversed, with wetter conditions associated with lower mortality. A similar, though weaker, interaction between moisture conditions and fir dominance was detected at the stand level. In stands with low fir dominance, wetter conditions tended to increase total mortality, whereas this effect diminished or reversed in fir-dominated stands. In contrast, drought based on precipitation anomalies over 12-month accumulation periods was not a significant predictor of mortality for beech and spruce, suggesting that these species are less sensitive to moisture conditions and that fir's response largely drives the climate signal observed in total stand mortality. Our findings suggest that the long-term background mortality signal is significantly shaped by the baseline climate, which dictates overall resource availability and metabolic stress levels within the stand, even in the absence of extreme climatic events (Camarero et al., 2015).

Stand basal area was a significant driver of mortality at the stand level and for spruce and beech individually. The consistent positive effect of basal area on background mortality confirms the central role of density-dependent competition in limiting resources in mature European mixed mountain forests, aligning with recent research emphasising that competition is the main driver of background mortality (e.g., Das et al., 2011; Etzold et al., 2019; Taccoen et al., 2019; Kulha et al., 2023). Trees in denser stands experience greater competition for limited resources, which negatively impacts their fitness (Das et al., 2016; Ford et al., 2017) and accelerates self-thinning, a process characteristic of the stem-exclusion stage described by Westoby (1984), where a predictable reduction in stem density occurs as individual tree size increases. High stocking and tree ageing have been identified as predisposing factors increasing susceptibility to forest decline and mortality. Beech showed a particularly sharp increase in mortality at high stand basal areas, consistent with its shade tolerance and growth strategy, which prioritises competition for light in closed canopies (Pretzsch et al., 2015). Spruce mortality also increased with stand basal area, indicating that this species is sensitive to overall competitive conditions or to symmetric competition. It is important to interpret these findings within the context of European forest history: the specific levels of density observed in our plots are often the result of past thinning regimes and species selection, so the identified density-dependent mortality is not purely an intrinsic ecological phenomenon but also an indicator of how historical management legacies set the stage for current competitive interactions and tree survival.

Tree-size dominance was among the most influential drivers of background mortality across species. The size dominance of fir in the stand was the primary driver of fir background mortality itself. The positive relationship between fir dominance and fir mortality indicates strong intraspecific competition within this shade-tolerant species, possibly due to the accumulation of suppressed individuals under dense canopies. Fir mortality increased sharply with size dominance, rising from approximately 0% to 2% as the size dominance of fir over the other species increased from 0.5 to 2.0 (at a Shannon index of 1), suggesting that critical intraspecific competition thresholds are reached at intermediate to high dominance levels. Fir's ability to survive under shaded conditions may paradoxically lead to overstocking when it becomes dominant (Trifković et al., 2023), so that long-term coexistence dynamics ultimately structure mortality patterns through intraspecific dominance stress. Notably, the size dominance of fir resulted in higher mortality for fir itself rather than for the companion species — a pattern also observed by Condés et al. (2025) in mixed stands of Scots pine, birch, and spruce, where pine's size dominance resulted in higher mortality in pine than in the other two species. Fir dominance over spruce was also associated with higher spruce mortality, suggesting asymmetric interspecific competition between these two species (Pretzsch et al., 2020a). Similarly, fir's size dominance over beech was a significant driver of beech mortality, highlighting that interspecific interactions strongly mediate beech background mortality. This pattern aligns with studies emphasising fir's competitive resilience and late-successional niche occupation (Rohner et al., 2012; Cailleret et al., 2019), and with the findings of Boeck et al. (2014), who found that competition indices were significantly associated with beech mortality in Southern Germany, while tree size alone did not add predictive value.

Species diversity, as measured by the Shannon index, was a significant driver of fir background mortality at the stand level. Some studies have not found evidence that mortality rates change with diversity in mature forests (Liang et al., 2007; Lasky et al., 2014). In contrast, our findings align with those of Searle et al. (2022), who found higher mortality rates in more diverse stands, particularly in temperate forests, with species richness being an important predictor of mortality. Consistent with our outcomes, their results suggest that under background (non-disturbance) conditions, increased species diversity may intensify competitive interactions rather than buffer stress. This apparent paradox may be scale-dependent: at large spatial scales, higher diversity enhances resilience to disturbances, whereas at the stand level, it may intensify density-driven mortality through structural heterogeneity and vertical stratification (Jucker et al., 2014; Ruiz-Benito et al., 2017). This interpretation is further supported by Pretzsch and Grote (2023a), (2023b), who reported approximately 33% higher mortality rates in mixed compared to monospecific stands of Scots pine and European beech across Europe, driven primarily by alien thinning —the interspecific competitive elimination of trees. The steeper thinning slope observed in mixed stands indicates that interspecific competition accelerates tree dropout beyond levels expected from intraspecific competition alone. This dynamic was further amplified under higher water availability, where above-ground competition for light intensifies. These findings corroborate the notion that, at the stand level, species mixing can exacerbate rather than alleviate density-driven mortality, particularly for less competitive species.

4.2. Relevance of the results for forest management

Our results gain practical relevance only when background mortality, the continuous, low-intensity losses driven by endogenous processes such as density-dependent competition, size-asymmetric suppression, and senescence, is distinguished from excess mortality, in which endogenous or exogenous drivers push mortality above the self-thinning baseline and threaten stand stability, yield and successional trajectories. The drivers identified here (stand basal area, fir size dominance, species diversity, mean annual temperature, and 12-month standardised precipitation index) operate across this continuum and must be interpreted accordingly.

The findings complement earlier productivity analyses on the same network of long-term plots. Hilmers et al. (2019) reported that, despite pronounced warming over the past three decades, stand-level productivity remained stable (approximately 9.3 m^3 ha^{-1} yr^{-1}), while species-specific trajectories diverged: spruce productivity declined, beech productivity was stable, and fir productivity increased, consistent with recovery from historical sulphur-dioxide pollution and a positive response to warming. Torresan et al. (2020) further showed that stand productivity peaks under a right-skewed (reverse-J) diameter distribution, that is, one numerically dominated by small trees, and when spruce retains a high proportion of basal area, and declines as the three species become evenly distributed across size classes. The two studies describe productivity at different hierarchical levels, namely a species-level temporal trend and a stand-level structural response, and are therefore complementary.

Our mortality results reconcile the apparent tension between fir’s rising share of basal area and its increasing mortality. Fir’s recovery primarily occurs through enhanced recruitment, ingrowth, and the release of advanced regeneration. In contrast, mortality among mature fir individuals rises with fir size dominance and mean annual temperature, consistent with the trade-off between vigour and longevity reported for this species (Linares and Camarero, 2012; Gazol and Camarero, 2022). Fir’s net gain in dominance is therefore sustained only because spruce, and to a lesser extent beech, mortality rises at a higher rate, in line with the steeper decline in spruce productivity reported by Hilmers et al. (2019) and with the known vulnerability of spruce to warming, drought and bark beetles (Senf et al., 2018). Two mechanistically distinct pathways operate simultaneously: a structural and competitive pathway, in which fir size dominance ($dgAa\_dg > 1$) imposes asymmetric competition on spruce and beech, and an abiotic stress pathway, in which warming erodes the vigour of mature fir.

Three management implications follow from this combined evidence. First, maintaining spruce in the upper canopy remains essential for stand productivity (Torresan et al., 2020) but is increasingly constrained by warming and by fir’s asymmetric competition. Thinning from above and spatial partitioning at the sub-stand scale can mitigate both components of spruce mortality. Second, the positive association between species diversity and background mortality reported here is not inconsistent with the stable stand-level productivity of Hilmers et al. (2019): the two outcomes coexist through a compositional insurance effect, whereby asynchronous species responses and functional redundancy allow losses among suppressed individuals of one species to be offset by the growth of surviving individuals of complementary species (Jucker et al., 2014; Morin et al., 2014). Rising mortality related to diversity should therefore not be equated with declining stand performance. Third, the regulation of fir size dominance follows from the integrated productivity and mortality synthesis rather than from the mortality analysis alone: mortality of all three species rises sharply when dgAa_dg exceeds approximately 1, while the same structural condition depresses stand-level productivity (Torresan et al., 2020). Silvicultural regimes that favour a reverse-J diameter distribution, retain spruce in the largest size classes and confine fir to intermediate and understorey strata are therefore most likely to optimise the trade-off between productivity and mortality under a changing climate.

Finally, background mortality should be managed rather than minimised. A baseline of endogenous mortality sustains a continuous supply of deadwood, which provides obligate habitat for saproxylic insects, fungi and cavity-nesting birds (Merganičová et al., 2012; Seibold and Thorn, 2018; Löfroth et al., 2023). Its additional effects on nutrient cycling and soil water retention are, however, context-dependent in managed mountain forests subject to partial or salvage harvesting and depend on the amount, species identity and decay stage of retained deadwood (Lassauce et al., 2011; Seibold et al., 2015); realising these functions therefore requires species-specific retention targets rather than general deadwood retention alone. Conversely, the temperature-driven rise in fir mortality at warmer sites and the competitive exclusion of spruce and beech under excessive fir dominance represent excess-mortality signals warranting active silvicultural mitigation. This distinction between functional background mortality and excess mortality provides a coherent basis for reconciling timber provisioning, biodiversity conservation and climate adaptation in mixed mountain forests.

4.3. Study limitations and methodological considerations

Our study leverages a unique dataset spanning over a century (1912–2016) across seven European countries, yet some inherent limitations warrant consideration.

Plot sizes varied considerably (400–26300 m^2), potentially influencing estimates of mortality rates. Small plots pose challenges for quantifying background mortality, as low event frequencies and limited sample sizes yield wide confidence intervals (Holzwarth et al., 2013; Siipilehto et al., 2020). This issue is further compounded when estimating species-specific rates, as few individuals per species are available. While previous studies suggest that a minimum sample size of 100 stems is needed for valid confidence interval estimates (Woods et al., 2021), our inclusion criterion—requiring each modelled species to contribute at least 10% of stand basal area—ensures that we focus on species that are functionally important in the mixture. However, this compositional threshold does not guarantee adequate sample sizes in all plots. We employed generalised linear mixed models with a random country intercept to partially address these scale-related uncertainties, though plot-size effects on precision remain important caveats.

Some inventory intervals yielded mortality values exceeding the typical 0.5–2% annual background range (Das et al., 2016). We retained these based on our basal area removal criterion ($\leq$5% per interval), designed to exclude disturbance-driven events. While this threshold-based filtering aims to distinguish regular mortality from catastrophic disturbances (Hart and Kleinman, 2018), the boundary is not always discrete. The maximum observed mortality rate of 4.9% (see Table 3) remained well below the $>$ 10% threshold used elsewhere to identify high-intensity disturbances (e.g., Etzold et al., 2019; Idoate-Lacasia et al., 2025), suggesting effective filtering. However, residual disturbance effects may persist given the gradient nature of mortality drivers.

Potentially important site attributes were not included in modelling. Soil types were available only at a scale of detail that was not comparable to that of our study. Soil properties—depth, texture, nutrient availability—were unavailable across all plots. Given that soil conditions strongly influence water and nutrient availability, some variation we attribute to stand structure or species composition may be mediated by site-specific edaphic properties. Similarly, we did not account for differences in tree height and crown dimensions among species. Mature beech trees exhibit considerably shorter stature than fir or spruce of equivalent diameter, which affects vertical canopy positioning and light interception, even when diameter-based size dominance metrics suggest parity. The strong influence of fir size dominance on mortality across all species may partly reflect fir's ability to maintain dominant canopy positions due to greater height at given diameter—an effect our diameter-based metrics cannot fully capture.

We did not explicitly model long-term temporal trends or interactions between climate change and stand structure, despite our study period spanning more than a century. Climatic conditions and management practices have changed substantially over this period (Pretzsch et al., 2014). By averaging climatic variables within inventory intervals, we capture local conditions during mortality periods but do not assess whether climate–mortality relationships have shifted over time (Etzold et al., 2019). Future research should explore these dynamics using census-year covariates, time-varying coefficients, or period-specific submodels to determine whether the identified drivers remain stable or have shifted directionally over time.

Our dataset encompasses plots with varying structural characteristics—stand age structure, developmental stage, and management history. While this heterogeneity enhances generality across diverse forests, it introduces unmeasured variation that our models do not fully capture. The moderate explanatory power (marginal $R^2 \approx$ 7–15%) indicates that structural variables, species dominance, and climate explain only a portion of the variation in mortality, with substantial residual variance attributable to unmeasured factors, stochastic processes, and fine-scale biotic interactions (Hülsmann et al., 2016, 2017). Mixed-effects models with country-level random intercepts account for some unobserved heterogeneity. Still, finer-scale sources—such as plot-level management history, micro-topography, and disturbance legacies—remain unaccounted for.

Despite these limitations, our study provides robust evidence that stand density, tree-size dominance (particularly fir), and species diversity are key structural drivers of background mortality in mixed spruce–fir–beech mountain forests, with climate playing a secondary but significant role for fir. The consistency of these patterns across seven countries and diverse conditions lends credence to our conclusions (Ruiz-Benito et al., 2017; Pretzsch et al., 2020b), even as we recognise that unmeasured attributes, species-specific allometry, temporal trends, and stochastic processes contribute to unexplained variation. Future work integrating soil data, crown architecture metrics, temporal covariates, and detailed disturbance histories will refine the mechanistic understanding of background mortality and its response to environmental change.

5. Conclusions

This research presents a comprehensive analysis of the drivers of background tree mortality in European mixed mountain forests of spruce, fir, and beech using forest inventory data collected in 78 permanent plots located in seven countries (Bulgaria, Bosnia and Herzegovina, Slovenia, Slovakia, Poland, Germany, and Switzerland), and spanning 1912–2016. Based on statistical modelling of these data, including more than 84,000 trees, we can provide insights into the drivers of background mortality for three of the most common tree species in European mixed mountain forests in the absence of disturbances.

The consistent importance of tree-size dominance factors underscores that density-dependent processes remain a major force shaping mortality patterns in mature European mixed mountain forests in the absence of specific disturbances. Specifically, fir dominance significantly influences the mortality rates of spruce and beech, as well as its own mortality rate, through size-structure-mediated effects.

The findings of our study are particularly relevant in the context of climate change, as background mortality represents a key but often overlooked component of forest carbon turnover, resilience, and the provision of essential ecosystem services across mountain regions and beyond. Further research is needed to gain a mechanistic understanding of fir's critical dominance threshold. Additionally, investigations of temporal dynamics are required to understand, for example, whether the species diversity effect remains stable or changes under climate change. Moreover, future research should quantify the impacts of silvicultural interventions on mortality.

CRediT authorship contribution statement

Torben Hilmers: Writing – review & editing, Data curation. **Jonas Glatthorn:** Data curation. **Aida Ibrahimspahić:** Data curation. **Matija Klopčič:** Writing – review & editing, Data curation. **Martina L. Hobi:** Data curation. **Chiara Torresan:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Andrej Bončina:** Writing – review & editing, Data curation. **Sonia Condés:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kamil Bielak:** Writing – review & editing, Data curation. **Michal Bosela:** Data curation. **Maciej Pach:** Writing – review & editing, Data curation. **Miren del Río:** Writing – review & editing, Supervision. **Thomas A. Nagel:** Writing – review & editing, Data curation. **Hans Pretzsch:** Writing – review & editing, Data curation. **Tzvetan Zlatanov:** Data curation. **Leszek Bartkowicz:** Data curation. **Zuzana Sitkova:** Data curation. **Admir Avdagić:** Data curation.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author(s) used Claude, Gemini, NotebookLM, and ChatGPT to assist with producing R code for data processing and synthesising text content. After using these tools, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the published article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.124017.

Data availability

Data will be made available on request.

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