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RESEARCH

Influence of species interactions and climate on tree mortality in mixed stands of *Pinus sylvestris, Betula spp.*, and *Picea abies*

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Abstract

Tree mortality is a complex process associated with endogenous factors such as tree size, species composition or stand density, which may interact with each other and/or with exogenous factors such as climate. We studied the influence of these factors on background tree mortality in Scots pine, Norway spruce, and downy and silver birch mixed forests located in Central and Northern European continental (Poland) and boreal (NE Poland, Lithuania, Sweden and Norway) regions. Our main objective was to disentangle how species interactions influence background mortality along a gradient of climate conditions. To achieve this, we developed mortality models using a set of 188405 sample trees in 6840 permanent sample plots, taken from the National Forest Inventories of the four countries. Our results indicate that tree mortality and the effects of competition were species-specific. The competition from pine resulted in higher tree mortality for the pine itself rather than for birch or spruce, and the competition from spruce was usually the greatest, causing higher tree mortality in the three studied species. Temperature modified the effects of competition, always magnifying the effects of intra- or inter-specific competition depending on the species. However, the effect of temperature was complex, as the density-dependent and the density-independent mortality varied in different ways with temperature. In general, mixing pine with spruce and birch increases pine mortality, whereas it favors spruce and birch survival, especially at warmer sites. These findings may be useful for the management of these mixtures in the context of climate change.

Introduction

Climate change and the increase in catastrophic events that it is likely to bring will influence tree mortality, either directly due to storms or floods, or indirectly through forest fires or pest outbreaks. Climate change has also been associated with changes in the mortality rates observed in stands where the aforementioned extreme phenomena have not occurred (Dale et al. 2001). The mortality rates observed in these stands without severe and abrupt disturbances are often referred to as background (non-catastrophic) mortality (Taccoen et al. 2019). The direct effects of climate change due to extreme climate events and disturbances can lead to important forest dieback over a short period, while average climatic conditions change only gradually and influence the background mortality (Neumann et al. 2017) although at long-term their effects carbon mitigation capacity of forests could exceed those produced by the catastrophic events (van Mantgem et al. 2009). The more direct effects of climate change have been extensively studied (Dale et al. 2001; Hammond et al. 2022; Hartmann et al. 2022), but the extent to which climate change increases background mortality remains unclear

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(Lindner et al. 2010; Taccoen et al. 2019), particularly where these climate effects interact with other causes of mortality, such as competition or stand characteristics (Pretzsch et al. 2014; Taccoen et al. 2021; Socha et al. 2023).

Tree mortality is a key factor in species dynamics that shape the forest structure in terms of diameter distribution, stand density and species diversity (Lebourgeois et al. 2013; Hulsmann et al. 2017). Particularly, climate change-induced mortality can influence the species composition due to differences in species vulnerability (Greenwood et al. 2017; Wessely et al. 2024). The dynamic vegetation models, which are considered highly useful for assessing long-term consequences of climate change, reveal high sensitivity to the mortality sub-models (Bugmann et al. 2019), the drawback being that they tend to be coarse and lack empirical bases (Hulsmann et al. 2018). Consequently, there is a need to develop mortality models with wider applicability to provide adequate tools for large scale dynamic models (Hulsmann et al. 2017). In this regard, it is crucial to decipher how species-specific effects together with site condition effects (e.g. climate, site productivity) determine tree mortality (Etzold et al. 2019; Socha et al. 2023).

Tree mortality is a complex process associated with several endogenous and exogenous interacting factors that are difficult to disentangle (Waring 1987; van Mantgem et al. 2009; Wang et al. 2012; Taccoen et al. 2021; Trugman et al. 2021). Among the endogenous processes, which lead to differences in competition intensity between trees, probably the best-known are those related to the individual tree size and competition for space. The latter can be depicted by stand structural characteristics such as basal area, stand density, or tree size variation (e.g. Lu et al. 2019; Zhang et al. 2020), while the effects of species diversity have not yet been widely explored (Searle et al. 2022). Among the exogenous factors, climate is considered one of the most important drivers of background mortality (van Mantgem et al. 2009; Zhang et al. 2020; Taccoen et al. 2021). The effects of temperature and precipitation on tree mortality, especially through heat and drought stress, have been the subject of recent studies, e.g. (Neumann et al. 2017; Taccoen et al. 2019, 2021).

Identifying the patterns of endogenous factors driving tree mortality is of particular interest in the context of climate change, since these patterns can be modified by forest management practices (Wessely et al. 2024). Those affecting stand density and species composition have been highlighted as two effective practices for forest adaptation to climate change (Ammer 2016; Sohn et al. 2016) by reducing competition for resources among trees (Keskitalo 2011; Kerhoulas et al. 2013; Brang et al. 2014). Stand density is probably the most important endogenous factor affecting tree mortality given its strong relationship to inter-tree competition. Hence, mortality can also be classified as density-dependent or density-independent. Density-dependent mortality occurs in stands at close to maximum density (self-thinning line), particularly affecting dominated or unhealthy trees while also helping to maintain the balance between resource supplies and demands (Tilman 1980). By contrast, density-independent mortality refers to the death of individuals regardless of stand density and/or competition pressure and it also affects larger trees. The two types of mortality rarely act independently, both can be related to disturbance dynamics caused by climate conditions, and should therefore be considered in analysis, modelling, and discussion (Crouchet et al. 2019).

A more diverse species composition is linked to higher adaptive capacity because species differences in functional traits, which result in different demands for resources and capacity for resource capture. This in turn can lead to different niche occupancies and facilitative effects (Knoke et al. 2008; Pretzsch and Biber 2016; Jactel et al. 2017; Grossiord 2020). Species interactions modify tree behavior and stand structure, resulting in changes in forest dynamics (Pretzsch 2018). Although the effects of species interaction on productivity and resilience have been extensively studied in recent years (e.g. Steckel et al. 2019; Pretzsch et al. 2020b; Ruiz-Peinado et al. 2021; Aldea et al. 2022), scarce information is available on the effects of species interactions on the mortality processes (Condés and del Río, 2015; Pretzsch et al. 2020a). Furthermore, it should be taken into account that the effects of species interaction can vary along gradients of climatic conditions and resource availability (Forrester 2015; Mina et al. 2017; Condés et al. 2018; Houpert et al. 2018) as well as in response to stand density (Condés et al. 2013; Brunner and Forrester 2020; Socha et al. 2023), which makes it challenging to generalize such effects (Forrester and Pretzsch 2015; Ammer 2019).

In this study we address background tree mortality in Central and Northern European continental (Poland) and boreal (NE Poland, Lithuania, Sweden and Norway) mixed forests, dominated by Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L. Karst), downy birch (*Betula pubescens* Ehrh.), and silver birch (*Betula pendula* Roth). These tree species are an important source of biomass both in the study region (occupying from 75% of forests in Poland up to 90% in Norway) and on a global scale. They are some of the most important tree species in Europe in economic and ecological terms (Drössler 2010; Bielak et al. 2014; Socha et al. 2023) and therefore research efforts are needed to quantify their sensitivity to climate conditions (Ruiz-Perez and Vico 2020). Data from the National Forest Inventories (NFI) of four different countries were used in this research, analysing individual tree mortality in small sample plots. Catastrophic mortality, destroying large parts of a plot or the entire plot, has been excluded from our data. Therefore, most of the observed mortality can be classified as background mortality. However, the remaining individual tree mortality is still composed of most of the classes described above, which cannot be separated in the NFI data. Increasing temperatures in the future is the most likely scenario for this biome. Positive growth trends linked to climate warming have already been observed in boreal forests (Pretzsch et al. 2023), which may result in more rapid forest dynamics (Stephenson et al. 2011), as well as higher mortality rates per unit of time and space (Senf et al. 2020). It is also expected that even if the amount of precipitation remains constant, the increase in temperature will accelerate mortality rates (Ruiz-Perez and Vico 2020). In this research we analyse not only how mortality varies but also how the effects of species mixture on this mortality vary with climate across a large geographic region, describing the way in which tree populations adapted to the local climate behave over the study period. Climate change can occur at a much faster rate than evolutionary adaptation, so established adaptation mechanisms might therefore be disrupted (Jump and Peñuelas 2005). Our space-for-time approach therefore mainly provides preliminary evidence for the effects of climate change on tree mortality. Although mortality models have already been developed for the main species in the Nordic countries (Eid and Tuhus 2001; Siipilehto et al. 2020), these models do not consider the inter-specific effects at tree level or their interaction with climate conditions.

Our main objective is to disentangle how climate modifies the effect of species interactions on the background mortality of individual trees in stands composed of mixtures of pine and birch and/or spruce along a climatic gradient in central and northern Europe. We posed the following specific questions:

Q1. Do species interactions modify the species-specific individual tree mortality?
Q2. Do climate conditions modify the species-specific individual tree mortality? and, if so,
Q3. Is the climate modifying the effects of species interactions on tree mortality?

Our main hypotheses are (1) The effect of competition on tree mortality is species-specific; (2) Temperature accelerates tree mortality in continental and boreal forests and modifies competition effects; and (3) The effects of temperature on tree mortality are species-specific.

Materials and methods

Data

Data from 6840 permanent sample plots belonging to the National Forest Inventories of four different countries in north-central Europe (Lithuania, Norway, Sweden, and Poland) were used in this research (Fig. 1). The selected plots were located in mixed stands of Scots pine and birch, and/or Norway spruce (Table 1), hereafter pine (Ps), birch (Bsp) and spruce (Pa), with sporadic presence of other species. A plot was considered to be within a mixture when the sum of the basal area of the studied species was greater than 95% of the total basal area and at least two of the species were present. Plots were re-measured at five-year intervals, either in one (Lithuania and Poland) or two periods (Norway and Sweden), recording dead trees at the end of each period. This resulted in a set of 10,396 surveys in 6840 plots embracing 188,405 sample trees of the main species, of which 4115 trees died between surveys. Typical low mortality rates associated with background mortality are 1.7% on average per year (Hulsmann et al. 2017), although can differ among species reaching higher values (Siipilehto et al. 2020; Searle et al. 2022). To avoid including catastrophic mortality caused by extreme events, the data considered were only taken from plots where the annual mortality rates, both in terms of basal area and number of trees per hectare, were less than 5%. Tables 2 and 3 summarize the main stand characteristics per species and the tree characteristics per species and mixtures respectively (see Sect. "Mortality models". For a more detailed description of species proportion and competition variables).

In addition, monthly data for mean temperature and precipitation were collected from the Climatic Research Unit (CRU) Time-Series (TS) Version 3.10 database (Harris et al. 2020). The mean annual temperature and annual precipitation were obtained by considering the coordinates of the plots and averaging the climatic variables for the inventory period. For the plots in the entire study region, the mean annual temperature ranges from – 3.0 to 10.3 °C and the annual precipitation from around 382 to 3666 mm (Table 2).

Studied mixtures

The basal area of pines was, on average, greater than that of birch and/or spruce. Furthermore, pines often had larger mean diameters (Table 2, Supplementary Fig. 1), reflecting the fact that the most common structures were stratified mixed stands dominated by pines, although other structures were also present. In the studied regions, typical sites for pine are often too poor for spruce. Pine-birch mixtures are frequently found on more fertile sites or where they are favored by silvicultural treatments (Hynynen et al. 2011). In the absence of young-stand management, the vigorous early growth of young birch, particularly sprouts, can easily outgrow the pines and begin to suppress them on sites with a milder climate, like in Poland (Jaworski 1988; Jakubowski and Sobczak 1999).

In the continental and boreal climates, as in Poland and Lithuania, pine and spruce can co-exist in a wide range of sites, but late-successional spruce prevails under moister conditions, while the pioneer pine dominates in drier and

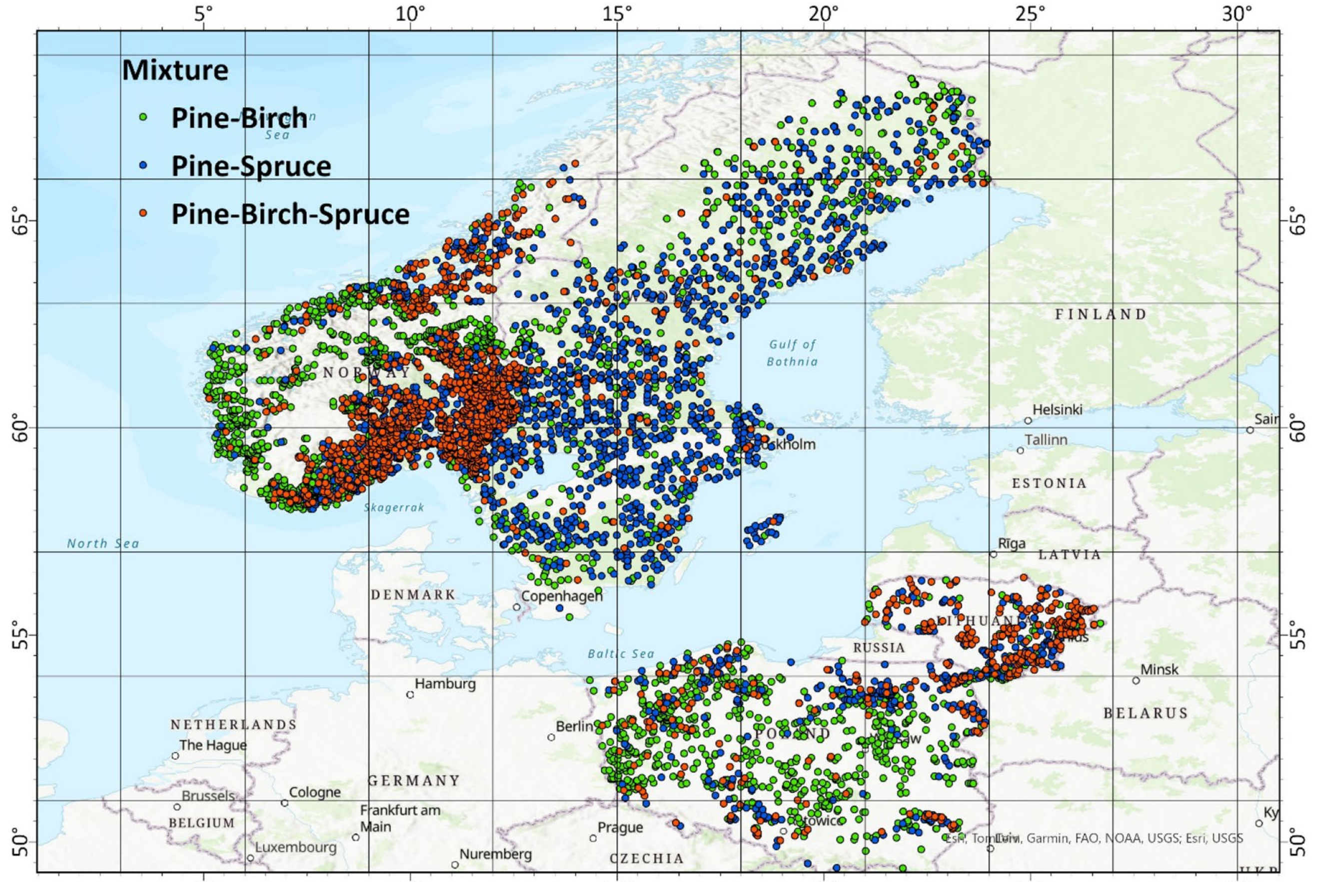

Fig. 1 Location of the plots in Lithuania, Norway, Poland and Sweden used in this study. Mixtures of pine and birch (green), pine and spruce (blue), and pine, spruce, and birch (orange). (Color figure online)

Table 1 Number of surveys per mixture and country and number of permanent sample plots. Survey years refer to the beginning of the 5 years period

Country	Pine-birch	Pine-spruce	Pine-birch-spruce	Periods	Total surveys	Total plots	Survey years
Lithuania	285	296	302	1	883	883	1998 to 2012
Norway	1880	1278	1467	2	4625	2646	1994 to 2012
Poland	707	294	143	1	1144	1144	2005 to 2012
Sweden	1261	2363	120	2	3744	2167	2003 to 2009
TOTAL	**4133**	**4231**	**2032**		**10396**	**6840**	**1994 to 2012**

Text is in bold font because is the total, the sum of the other rows

more nutrient-poor sites (Bielak et al. 2014; Drössler et al. 2018). Older pine stands in northern Europe are often open, allowing the establishment of younger cohorts in stratified mixtures, especially of the more shade tolerant spruce, although spruce is not well adapted to poorer sites.

Pine, birch, and spruce of differing age classes can coexist in humid sites with mesic, fertile soils (cf. Drössler 2010). Often, the upper layer is mainly occupied by light demanding pine and birch. Over the rotation period the admixture of short-lived pioneer birch is gradually decreased in this type of mixture through thinning. However, different stand structures can be found in the study areas.

Finally, it is important to note that silver and downy birch are recorded as *birch* in the NFI databases, as they coexist at some sites and are difficult to distinguish accurately. Silver birch is an essential component of continental (Poland) and boreal forests (NE Poland and the other countries), while downy birch is more frequent in colder and wetter areas. However, downy birch is generally more shade-tolerant than silver birch, so their behavior in mixtures can differ.

Table 2 Summary of main stand characteristics, total and by species, and of temperature and precipitation for the selected plots

	Total plot			*Pine*			*Birch*			*Spruce*				
	N	G	dg	N	G	dg	N	G	dg	N	G	dg	T	P
	stems/ha	m^2/ha	cm	stems/ha	m^2/ha	cm	stems/ha	m^2/ha	cm	stems/ha	m^2/ha	cm	ºC	mm
Mean	737	19.8	19.2	400	13.8	23.1	114	1.5	8.0	212	4.4	9.2	4.8	867
Sd	472	11.8	6.1	378	10.2	8.5	218	3.0	8.2	343	7.8	8.8	2.7	455
Min	64	0.6	7.2	20	0.2	7.0	0	0.0	0.0	0	0.0	0.0	−3.0	382
Max	5735	73.5	48.9	3600	62.3	67.8	4566	35.9	53.2	2840	58.8	52.9	10.3	3666

N is the number of trees, G is the basal area, dg the quadratic mean diameter, T the annual mean temperature and P the annual precipitation, sd is the standard deviation, min and max are minimum and maximum values, respectively

Table 3 Summary of main characteristics of the mixtures at stand and tree level

		G m^2/ha	P.Ps	P.Bsp	P.Pa	Pine		Birch		Spruce	
						d cm	RBAL	d cm	RBAL	d cm	RBAL
Pine-birch	Mean	16.5	0.77	0.23	–	19.0	0.32	12.8	0.33	–	–
nsurveys = 4133	Sd	10.5	0.24	0.24	–	8.4	0.24	5.8	0.23	–	–
ntrees = 47541/19049	Min	0.6	0.02	< 0.01	–	7.0	0.00	7.0	0.00	–	–
ndead = 995/646	Max	60.2	> 0.99	0.98	–	83.1	1.47	56.3	1.46	–	–
Pine-spruce	Mean	21.9	0.69	–	0.31	21.5	0.31	–	–	16.4	0.44
nsurveys = 4231	Sd	12.5	0.28	–	0.28	9.0	0.23	–	–	7.4	0.26
ntrees = 42632/34885	Min	0.6	0.02	–	< 0.01	7.0	0.00	–	–	7.0	0.00
ndead = 694/689	Max	73.5	> 0.99	–	0.98	66.4	1.27	–	–	74.5	1.48
Pine-birch-spruce	Mean	22.1	0.62	0.12	0.26	22.1	0.34	13.1	0.42	14.9	0.46
nsurveys = 2032	Sd	11.2	0.26	0.16	0.26	9.1	0.24	6.4	0.24	6.8	0.25
ntrees = 19331/7243/17720	Min	0.9	0.02	< 0.01	< 0.01	7.0	0.00	7.0	0.00	7.0	0.00
ndead = 446/291/354	Max	65.2	0.99	0.96	0.96	78.0	1.37	53.2	1.49	57.5	1.43

nsurveys is the number of surveys, ntrees is the number of trees of each species, and ndead the number of dead trees of each species, G is the stand basal area, P is the proportion by area of pine (Ps), birch (Bsp) and spruce (Pa) (Eq. 1), d is the breast height diameter and RBAL the relativized basal area of the larger trees (Eq. 2), sd is the standard deviation, min and max are minimum and maximum values, respectively

The mixing proportion of pine varied between 1.5 and 99.7%, and the mixing proportion of birch and spruce varied between 0.2 and 98.4%, and between 0.3 and 98.2%, respectively. The percentages of dead trees for pine and spruce were 2% on average over five years, while for birch it was almost twice that percentage (Table 3).

Mortality models

Tree-level mortality models, formulated as generalized linear mixed models following a binomial family, were developed for each species across all mixture types. The effect of tree size on mortality was described by the tree breast height diameter, *d*, and the second power of this variable, a transformation frequently included in mortality models to obtain the characteristic U-shape of the probability of mortality over tree diameter (Monserud and Sterba 1999; Jutras et al. 2003; Zhao et al. 2004).

To test the influence of the plot-level species composition on tree mortality, i.e., whether the presence of admixed species increases or decreases the probability of mortality, the proportion by area of each species P_{sp} was used (Eq. 1). The species proportion in the model may express the species admixture effect beyond the effect of size-asymmetric competition, that is, the symmetric competition and any potential facilitative effect.

$$P_{sp} = \frac{\frac{G_{sp}}{G_{\max sp}}}{\sum_{sp} \frac{G_{sp}}{G_{\max sp}}} \tag{1}$$

where G_{sp} is the basal area of the species *sp* in the plot and $G_{\max sp}$ is the maximum basal area that the species could occupy, estimated for each plot from the quadratic mean diameter of the species in the plot and the maximum density for that diameter, which was obtained from the size density equations proposed by Hynynen (1993). We used the species proportion by area to account for the differences in carrying capacities between species (del Río et al. 2016).

The effect of competition was analyzed using the basal area of the trees with a diameter larger than or equal to that of the target tree, *BAL* (Wykoff 1990), given that one-sided competition has proven to be a key variable when studying tree mortality, (e.g. Monserud and Sterba 1999; Eid and Tuhus 2001; Zhao et al. 2004; Condés and del Río, 2015). To study the effects of different inter-specific competition, this index was used in two ways: total BAL calculated by summing the basal area of all larger trees (in terms of breast height diameter), or splitting it up by species, i.e. BALpine + BALbirch + BALspruce. In any case, to take into account species-specific carrying capacities, these competition indicators were relativized considering the maximum basal area of each species (Hynynen 1993) as $RBAL_{sp}$ (Eq. 2). Total relativized basal area of larger trees, *RBAL* (Eq. 3), was then calculated as the sum of the three species.

$$RBAL_{sp} = \frac{BAL_{sp}}{G_{\max sp}} \tag{2}$$

$$RBAL = \sum_{sp} RBAL_{sp} \tag{3}$$

In addition, the possible effect of climate conditions was analyzed by including simple variables such as annual mean temperature (*T*), annual precipitation, or the Martonne aridity index (Martonne 1926), as they describe the variability of climates in the study area (Table 2), and are related to variation in mortality at large scales (Zhang et al. 2017).

After a preliminary exploration, the partitioning of competition into intra- and inter-specific competition was more significant than the total competition for the three species-specific models. Moreover, *T* was the significant climate variable resulting in the best models (Supplementary Table 2). Therefore, its effect was analyzed by including *T* as a single independent variable and as interactions with tree size and competition. This allows us to assess whether density-independent and density-dependent mortality respectively are modified by climate. The general expression of the logit function for each of the three species mortality models was:

$$\begin{aligned}\mathrm{logit}\left(m_{ij}\right) = {} & a_0 + a_1 \cdot d_{ij} + a_2 \cdot d_{ij}^2 + a_3 \cdot T_j \\ & + a_4 \cdot d_{ij} \cdot T_j + \sum_{sp} b_{sp} \cdot P_{spj} \\ & + \sum_{sp} c_{sp} \cdot RBAL_{spij} \\ & + \sum_{sp} e_{sp} \cdot RBAL_{spij} \cdot T_j + \varepsilon_{ijt}\end{aligned}$$

where m_{ij} is the probability that the tree *i* with d_{ij} dies in the plot *j* in a 5 years interval, P_{spj} are the proportion by area of the species *sp* in the plot j and $RBAL_{spij}$ are the relativized basal area of larger trees of species *sp* in the same plot, respectively. T_j is the mean annual temperature in the period. Even though periodical mean temperatures are used in the model, variation between periods is minimal (around 0.5 Celsius) compared with the variation in mean temperatures across the study area. Periods of high temperatures, low precipitation, or increased drought stress that cause episodic mortality are not described in detail by the five-year mean temperatures.

As tree mortality is a discrete event, and considering the possible correlation between trees measured in several surveys in the same plot, a generalized linear mixed model approach following a binomial family, i.e., logistic regression, was used. Random effects were included using an AR1 covariance structure and the plot as the grouping structure. Breast height diameter and mean annual temperature were rescaled, by dividing each variable by its root mean square, to ensure convergence of the models (Supplementary Table 3).

The mortality probability models were fitted using the "glmmTMB" function of the "glmmTMB" library (Brooks et al. 2017). As goodness-of-fit measures we used the ROC (Receiver operating characteristic) curve as well as the conditional and marginal area under curve (AUCc and AUCm), obtained using the "roc" function in the "pRoc" library (Robin et al. 2011). For all the models, a level of $p = 0.05$ was used for testing significance of the variables, and Akaike's information criterion (AIC) was used to compare results and to select from among different model structures.

Results

In the mortality models (Table 4), tree diameter and its quadratic form were significant, except for birch, for which the quadratic term was not significant. Thus, the effect of diameter, in general, presented the classic U-shape for pine and spruce while for birch the probability of mortality decreased consistently with increasing tree diameter (Fig. 2). This lack of the typical U-shaped mortality probability patterns over *d* for birches is probably due to the absence of large trees of this species, those present being smaller than the other tree species in the data set used (Table 3, Supplementary Fig. 1).

Figure 2 shows the interactive effects of diameter and temperature on the probability of mortality in stands in practically monospecific stands, i.e. where the proportion of the target species was Psp = 0.95. In general, birch showed the largest probabilities of mortality. In the range of diameters studied, the probability of mortality was greater for the smallest pine trees, while the increase in probability of mortality for the largest trees was only slight. In the case of

Table 4 Parameter estimates and p-values (Pr(>\|z\|)) for the mortality models

	Pine		Birch		Spruce	
	Value	Pr(>|z|)	Value	Pr(>|z|)	Value	Pr(>|z|)
Intercept	− 3.8434	0.0000	− 5.1913	0.0000	− 7.0072	0.0000
D	− 2.8483	0.0000	–	–	–	–
d*T	− 1.3351	0.0000	− 0.4663	0.0000	− 1.5965	0.0000
d^2	1.1908	0.0000	–	–	0.6571	0.0000
T	1.0611	0.0000	–	–	1.3481	0.0000
Ppine	− 1.1101	0.0000	1.5374	0.0000	1.2856	0.0002
RBALpine	2.5716	0.0000	− 1.3595	0.0067	− 1.8365	0.0063
RBALpine*T	1.0484	0.0005	1.3207	0.0001	1.8864	0.0001
RBALbirch	3.3819	0.0000	4.3894	0.0000	–	–
RBALbirch*T	–	–	–	–	1.5030	0.0306
RBALspruce	2.7974	0.0034	–	–	3.9905	0.0000
RBALspruce*T	2.7990	0.0057	4.0954	0.0000	–	–
StdRnd	1.2303		1.5230		1.6600	
AIC	17,751		7738		9405	
AUCm	0.7820		0.6169		0.6731	
AUCc	0.9093		0.9398		0.9364	

SdtRnd represents the standard deviation of the random effects associated with the intercept, AUCm and AUCc are the area under the ROC curve for the model, the former without and the latter with random effects, respectively

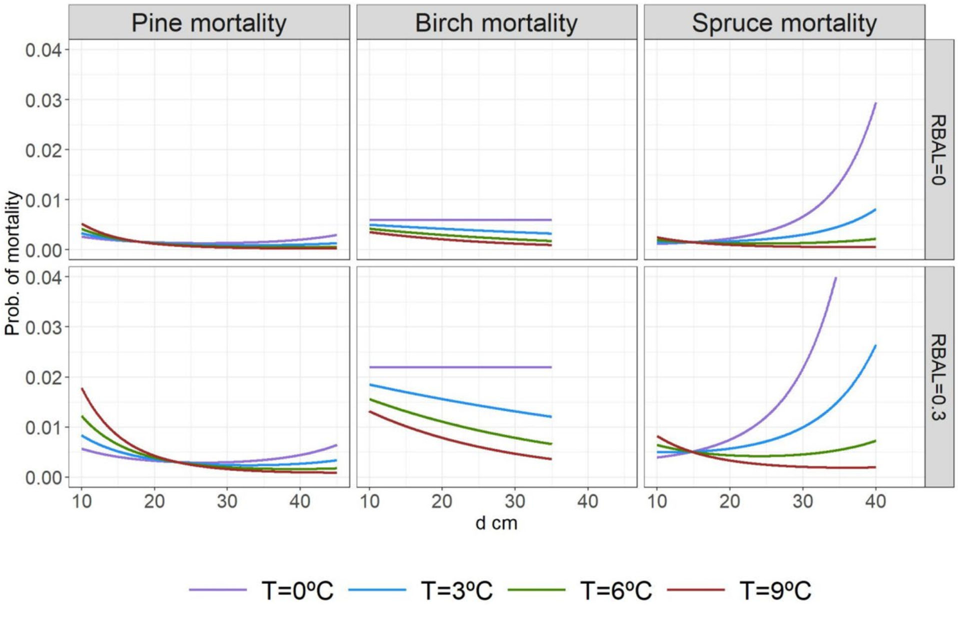

Fig. 2 Variation of the probability of tree mortality, according to the interacting effects of breast height diameter d and mean annual temperature T, in stands with clear dominance of the main species *sp* (monospecific composition: $P_{sp}=0.95$) for two degrees of intra-specific competition (dominant trees: $RBAL_{sp}=0$ and average degree of dominance: $RBAL_{sp}=0.3$). Lines are drawn for the inter-percentile range 5% to 95% of tree diameter for each species

spruce it was the opposite, low probability of mortality for the smallest diameters, only increasing notably at the lowest temperatures for the largest diameters. The aforementioned effects were modified by temperature and were more evident for trees that suffered greater competition. Thus, for pine and spruce, the higher the temperature, the greater the probability of mortality for smaller trees, while for larger trees, the probability of mortality was greater at lower temperatures, the latter effect being more evident for spruce than for pine.

Among the different species proportions, it was the proportion of pine that was always significant and resulted in better models in terms of AIC, although the parameter values were positive for the birch and spruce models and negative for the pine model (Table 4). In the studied mixed stands, the

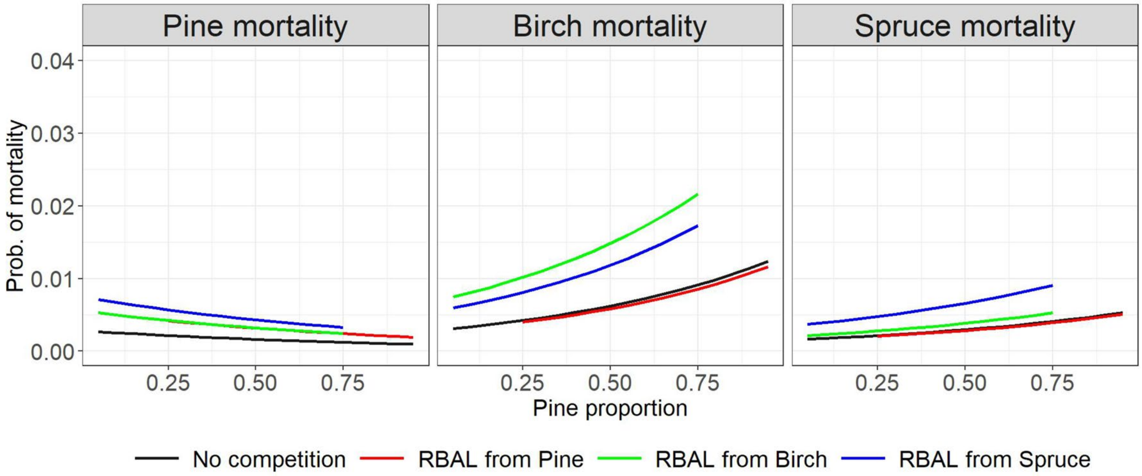

Fig. 3 Influence of the pine proportion and species composition of larger trees (RBAL) on the mortality of the three species for a tree with d = 25 cm and with T = 4.5 °C. Black lines for no competition from larger trees (RBAL = 0); colored lines for competition from pine, birch or spruce set to RBALsp = 0.2

presence of pine, measured by the pine proportion, increased the probability of mortality of the other species whereas its own mortality diminished (Fig. 3). Birch mortality was most affected by pine presence, whereas the effect on spruce was much smaller. However, the inter-specific effect of the competition from larger pines (pine *RBAL*) notably reduced the mortality of birch and spruce trees, which could result in a negative compound effect of pine (Figs. 3 and 4, Table 4).

The intra- and inter-specific competition, in terms of *RBAL*, i.e. caused by the larger competitors, was always significant, either on its own and/or interacting with temperature (Table 4). For the average temperature in the studied plots (T = 4.5 °C), the intra-specific *RBAL* competition had greater effects on the probability of mortality of birch and spruce than any inter-specific *RBAL*, although this intra-specific effect was much stronger for birch than for spruce (Fig. 4, T = 4.5 °C). For pine, the intra-specific effects were of similar magnitude to the inter-specific effects from birch, but the inter-specific competition from spruce resulted in higher mortality.

Temperature modified the effects of competition in different ways for the studied species (Table 4). For pine, the competition from spruce and the intra-specific competition increased the probability of mortality at the warmer sites, while the interaction of temperature and inter-specific competition from birch was not statistically significant. For birch, the temperature modified the inter-specific competition from pine and spruce, but not the intra-specific competition. For spruce, temperature also only modified the inter-specific *RBAL* effects (Table 4).

However, the effects of T on tree mortality are a combination of the individual T, and T interacting with diameter and RBAL, and must be considered together since they affect mortality in a multiplicative manner (as is inherent in the logit function formulation). In Fig. 4 for pine, the competition effects increased with temperature, especially for smaller trees, whereas for birch and spruce the changes in competition (mainly intra-specific competition) with temperature were greater for larger trees. For all three species, the effect of interaction between temperature and competition on the probability of mortality was always stronger in the case of competition with spruce.

When interpreting the species-specific effects, it must be considered that pine generally occupied the canopy layer in the studied mixtures and therefore the RBAL for pine was usually larger than those for the other species (Supplementary Table 1), and therefore the magnitude of the probability of mortality would be between the lines that represent the corresponding species (Fig. 4). The combined effect of pine presence (*Ppine*) and pine competition (*RBALpine)* depends on how much of the pine proportion corresponds to the upper canopy layer (*RBAL* competition). In general, it is expected that the presence of pine will reduce the probability of mortality in both birch and spruce trees, with higher mortality in stands which are almost monospecific than in mixtures (see the example in Supplementary Fig. 2). For the pines, however, the probability of mortality was greater in mixtures due to the stronger effect of inter-specific *RBAL* (Fig. 4, Supplementary Fig. 2).

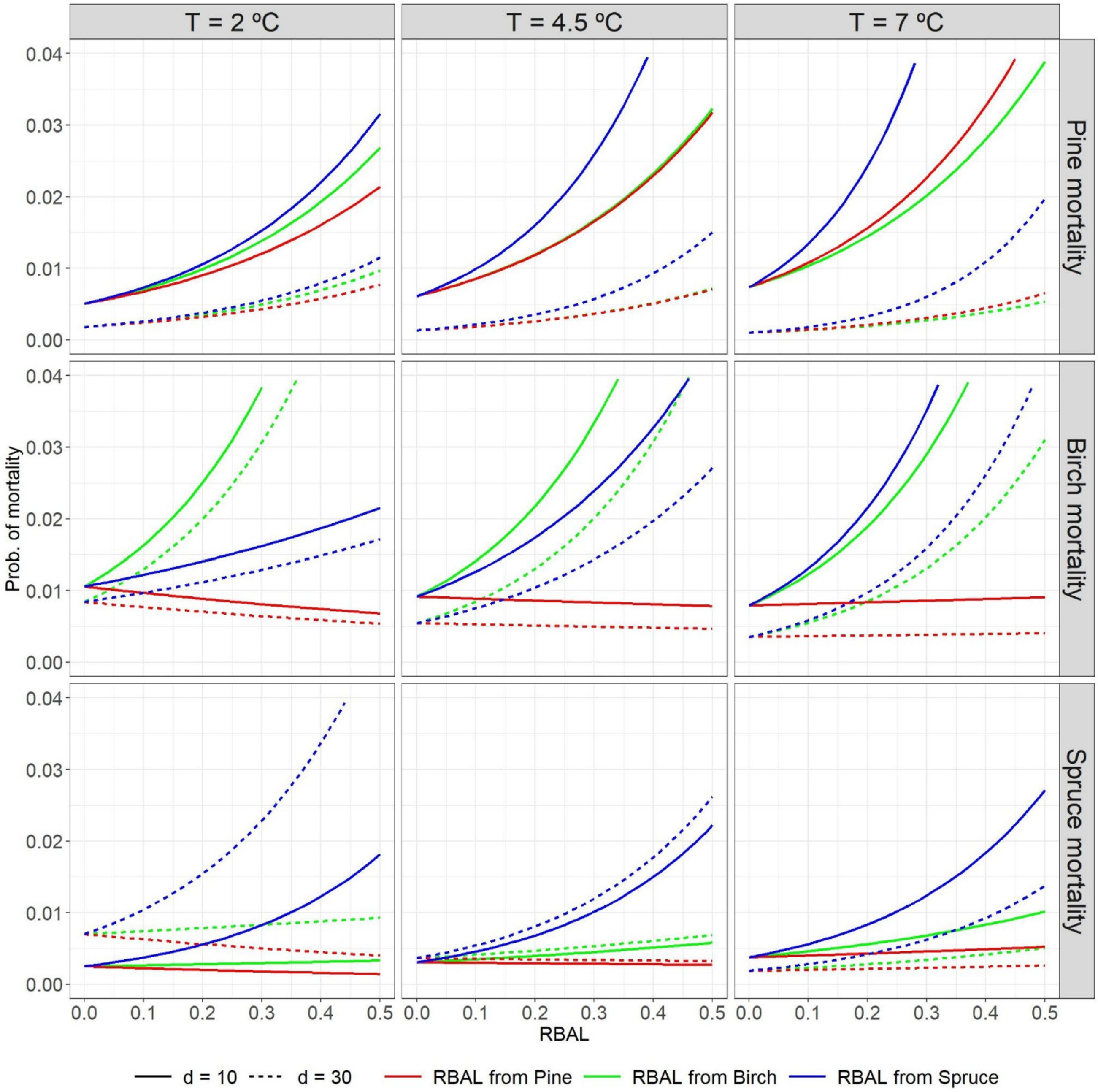

Fig. 4 Influence of the intra- and inter-specific RBAL competition on the mortality of the three species under different annual mean temperatures for trees with d = 10 cm (solid lines) and d = 30 cm (dashed lines) growing in mixed stands with pine species proportion of $P_{pine} = 0.5$. The colored lines denote that the RBAL corresponds to the species represented by that color

The goodness-of-fit of the mortality models differs among the species, the fixed-effects model being much more accurate for pine than for the other two species in terms of the marginal area under the ROC curve (AUC). For pine, the AUC was about 78%, while for spruce it was 67%, and only 62% for birch (Table 4). The complete model, including random effects, presented similar goodness-of-fit for the three species, with AUC over 90% for all three species (Table 4, Fig. 5).

Discussion

Species interaction effects on tree mortality

Competition terms in mortality models mainly reflect density-dependent mortality, with the effects of species-specific interactions having scarcely been explored. In our analysis, density-dependent mortality is explicitly modelled using species-specific RBAL to specify the competition level. We

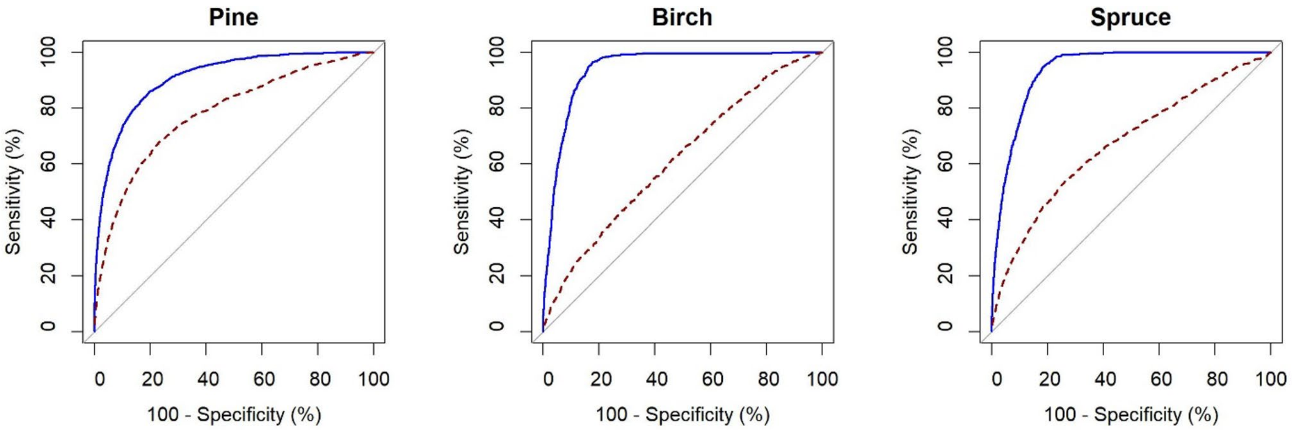

Fig. 5 Receiver operating characteristic (ROC) curves for the total and the fixed-effects models, solid blue lines and dashed red lines respectively

found that increasing competition from larger trees increased tree mortality in the three studied species. This finding agrees with the general assertion that mortality is lower in dominant canopy trees than in the trees occupying the understory. This is due to competition mainly for light, but also for belowground resources (Monserud and Sterba 1999; Wyckoff and Clark 2002; Pukkala et al. 2013; Ruiz-Benito et al. 2013). Eid and Tuhus (2001), using NFI data from Norway, found a similar competition effect from larger trees for both pine and spruce but not for birch. However, they did not consider that the effects of competition depend on species interactions, and thus the intensity of competition may vary markedly with species composition (e.g. Zhao et al. 2006; Pukkala et al. 2013; Condés and del Río, 2015; Hajek et al. 2022). In mixed stands, a reduction or an increase in tree mortality can be observed depending on species dominance and stratification. Moreover, tree mortality can increase in mixed stands due the stronger competitive pressure associated with their greater productivity in comparison to pure stands (Hajek et al. 2022; Searle et al. 2022).

According to our models, the mortality caused by competition from larger spruces was in general much higher than from larger pines and birches, although probably for different reasons. Spruce is a very strong competitor in terms of shade-producing capability due to their tightly packed pillar-like crowns (Pretzsch and Schutze 2005). As a result, large spruces have a strong impact on mortality of all three species. In contrast, competition from larger birch trees mainly affected birch mortality, as a light-demanding species, and mostly when the temperature is low, which is in line with findings reported by Maleki and Kiviste (Maleki and Kiviste 2016). Birch can also cause growth reduction and mortality in other trees, despite being a weak competitor allowing plenty of light to pass through the canopy (Fahlvik et al. 2005). Birch can suppress other species due to their rapid height growth (Hynynen et al. 2011) and occasionally by forming very dense shelters of birch in two-storied stands (Lundqvist et al. 2014). However, the most frequent situation according to our data is that birch trees were suppressed by other tree species (supplementary Fig. 1). Pines growing in the dominant canopy layer might not be strong competitors for spruces and birches (Fig. 4) probably because of their crown transparency (Hynynen et al. 2011; Bielak et al. 2014). Modelling the dynamics of boreal forests in Finland, Pukkala et al. (2013) also found better survival rates for the three species under pine cover than under spruce or birch cover. However, our results could be influenced by the inclusion of pine basal-area proportion in our models, as detailed below.

Beyond the effect of larger trees, the proportion of pine basal area significantly modifies tree mortality in the three species, underlining the relevance of species composition on tree mortality. Although we found that the greater the pine proportion the greater the probability of mortality for spruce and birch (Fig. 3), the combined effects of both pine proportion and species-specific competition from larger trees showed that, on average, spruce and birch survival was favored by the mixture while for pine trees the mortality was higher in mixtures than in near monospecific stands (Supplementary Fig. 2). As mentioned above, either the shade-producing spruce (Pretzsch and Schutze 2005) or the faster growing birch (Hynynen et al. 2011) might be stronger competitors for pine than pine itself. In Norway, Eid and Tuhus (2001) found that the presence of spruce increased its own probability of mortality and Taccoen et al. (2019) reported a similar effect for birch and spruce in France, both studies pointing to the positive effect of mixture for those species. Taccoen et al. (2019) also found that the probability of mortality in pine diminished with its presence and the same effect, although not statistically significant, was reported by Eid and Tuhus (2001). Jutras et al. (2003), using data from the Finnish NFI, also concluded that pine survival was negatively affected as the proportional basal area of birch increased. Similar results were found at stand level in Norway and Sweden by Siipilehto et al. (2020), who reported that increasing the proportion of pine decreased the probability of mortality in mixtures, whereas an increasing proportion of broadleaves had the opposite effect. However, these studies included the target species' basal area or basal area proportion in the mortality models without considering the social position of the different species, while in this research we show that species-specific effects on mortality also depend on canopy position of the subject tree.

Our data also suggest that mixed stands adapt better than pure stands to the diversity of site conditions at small spatial scales associated with the shallow soils of the boreal region. Spruce trees in the NFI plots may therefore, on average, display better site-adaption when growing in mixture with pine, compared with pure spruce stands at the same site. However, we are unable to quantify these effects due to a lack of data regarding the variation in soil depth. In contrast to spruce and birch, the more drought-tolerant pine does not benefit from the better site-adaptation of mixtures and is in fact negatively affected by the more rapid height growth of birch and the shade producing nature of spruce, which might explain the increase in pine mortality in mixed stands.

Climate effects on tree mortality

The effects of climate on density-dependent mortality are modelled as interactions with RBAL, given that more rapid development along the self-thinning line occurs at warmer sites, as indicated in previous studies (e.g.Pretzsch et al. 2014). Among the studied climatic variables, the effect of mean annual temperature was the most relevant for the three species. We found that temperature had a direct effect on tree mortality, this effect varying with tree size (Fig. 2), and that temperature modified the effect of competition with larger trees, generally intensifying this effect (Fig. 4). An increase in temperature was only found to result in increased mortality in small-diameter spruce and pine trees (Fig. 2), often growing under conditions of maximum stand density, especially in the commonly unthinned stands in Norway. The effect of temperature on competition-induced mortality was also reported by Taccoen et al. (2021), who observed higher sensitivity to temperature in suppressed trees, probably because of their shallower root system. The effect of the general interaction between climate and competition on tree mortality has previously been reported (Ruiz-Benito et al. 2013; Etzold et al. 2019; Taccoen et al. 2021). However, the interaction of climate with the species-specific effects of competition has frequently been ignored (e.g. Eid and Tuhus 2001; Eid and Oyen 2003; Jutras et al. 2003; Pukkala et al. 2013), and only recently being included in research aimed at developing mortality models for mixed stands (Condés and del Río, 2015; Looney et al. 2021; Condés et al. 2022). In the studied mixtures, temperature increased the effect of intra-specific competition on tree mortality in small pines and spruces, in accordance with our hypothesis. Small trees often grow at maximum stand densities with high competition levels, our findings suggesting less self-tolerance at warmer sites (Zeide 1985) or a more rapid development along the self-thinning line due to increased growth in warmer climate (Pretzsch et al. 2014). The same interaction between temperature and intra-specific competition was reported for Scots pine in the Iberian Peninsula (Ruiz-Benito et al. 2013), while Condés et al. (2022) also found the same effect on spruce in mixtures with fir and beech. However, in the case of birch, our model indicates the opposite trend, with greater mortality at colder sites as mentioned above. Temperature also increased the inter-specific competition for pine and birch when competing with spruce, which can be understood as a consequence of the more severe competition at better quality sites with higher growth rates (Bravo-Oviedo et al. 2006; Stephenson et al. 2011).

Density-independent mortality is that which affects trees and stands regardless of stand density and competition pressure. It often affects larger trees, which explains the higher mortality in large spruce trees compared with the other two species. This mortality is probably present in our data in the form of spruce trees dying due to bark beetle attacks (often at unsuitable sites or those which are no longer suitable for the species) and windthrow or snow breakage (Valinger and Fridman 1999). It is expected that climate will affect this type of mortality. For example, bark beetle attacks are much more severe in the south compared with latitudes north of about 60° (Marini et al. 2017). Hence, in this study the effects of climate on density-independent mortality are modelled as interactions between temperature and tree diameter. Furthermore, non-site-adapted use of spruce at many sites with shallow soils might contribute to increased drought stress and in turn bark beetle attacks (Löf et al. 2010). Spruce stands established at pine sites often develop without suffering damage or loss of significance over the first few decades, but they frequently become drought stressed and subsequently attacked by bark beetles after an age of about 50 years, leading to mortality of individual trees or groups of trees. The rapid increase in mortality with increasing diameter in the case of spruce compared with pine, especially in the colder regions, may point to spruce trees being poorly adapted to the conditions at some of the sites included in our data in Norway and Sweden. This type of mortality might also vary widely within a forest stand due to the small-scale variation in soil depth of the generally rather shallow soils in Fennoscandia. In warmer climates, such as Poland, with more balanced spruce and pine growth, background mortality is lower than at colder boreal sites, although more recently a catastrophic mortality problem in both species has been observed due to the frequent droughts over the last two decades (Brzeziecki and Zajaczkowski 2023; Socha et al. 2023). Nonetheless, our results about density-independent mortality may be influenced by the data selection criteria, as we avoided the inclusion of catastrophic events by limiting mortality rates to below 5%. However, due to the small plot size, individual trees within the plot may form part of adjacent catastrophic mortality events.

According to our results, an increase in temperature due to climate change would lead to higher mortality rates, especially in spruce and Scots pine. Forest management could help mitigate this effect by regulating species mixture, keeping pine trees and, to a lesser extent, birches, in the upper canopy layer.

Methodological approach

We developed empirical logistic models based on large inventory datasets that have proven suitable for describing the effects of tree size, competition, and climate on tree mortality in other studies (Lines et al. 2010; Hulsmann et al. 2017; Thrippleton et al. 2021).

We found a classic U-shaped mortality pattern on tree size (Monserud and Sterba 1999) for pine and spruce, while for birch there was only a negative effect of diameter related to higher mortality for suppressed trees. In the case of birch, the data contained few larger-diameter trees, probably because short-lived birch is frequently removed during the cleaning of young stands as it is a strong competitor or later during thinning treatments (Hynynen et al. 2011). Due to the lack of precise information on the identity of the birch species (downy or silver) in all NFI data, we have also pooled both species together, which may have slightly distorted the results obtained for this species. The data and models therefore need to be interpreted with caution, taking into consideration other potential effects.

As a measure of competition, we use an index that accounts for the species-specific basal area of larger trees, often related to competition for above-ground resources (Pretzsch and Biber 2010). To study species interactions, some authors recommend using distance-dependent competition indices because they better describe individual competition between species in mixed stands given their capacity to consider species intermingling and spatial arrangement of trees (Zhao et al. 2006; Hulsmann et al. 2018). However, the NFI data are limited in this regard by a lack of spatial information and/or by small plot sizes, so we had to use the distance independent RBAL calculated according to species identity.

Site conditions are also difficult to compare between national NFI plots. In our approach we focus on simple climate variables obtained from an external source. Among the basic variables, we found that temperature is the best explaining mortality (Supplementary Table 2). However, covariance among site variables frequently occurs. For instance, using the Norwegian NFI, Sharma et al. (2012) detected a negative effect of precipitation on site index for pine, caused by historical harvesting patterns rather than the effects of precipitation. Developing models that include more complex climate or drought indices as well as additional site variables could help us to better understand how climate mediates the species interactions in terms of mortality, thus avoiding flawed conclusions being drawn. Despite these limitations of NFI data for developing models (McCullagh et al. 2017; Pretzsch et al. 2019), the large area covered systematically by NFI data in our study means that our models represent a large gradient of site conditions across the region, which is one of the important requirements for obtaining models with wide applicability (Hulsmann et al. 2017).

Our results were statistically better for pine than for spruce or birch, when comparing exclusively the AUC obtained for the fixed effects of the logistic models, although they were similar when considering the complete model. Hulsmann et al. (2017) also reported low classification accuracy for spruce, probably because of the limited predictive power of diameter, which we found in the case of birch, or because of other agents such as insect attacks causing density-independent mortality. This could explain the higher accuracy when including the plot as a random factor in our models.

Our findings provide further evidence of the importance of studying species mixing effects on tree mortality and their interaction with climate conditions, while also highlighting the need to consider species composition and stratification (i.e. stand structure) when analyzing tree mortality. Understanding the dynamics of mixed forests requires the inclusion of species interactions through species-specific competition indices among the key factors when developing tree mortality models, as is common practice when studying tree growth (Brunner and Forrester 2020; Condés et al. 2022).

Conclusions

Understanding the effects of species composition, stratification and climate as well as their interactions on background tree mortality is essential for designing actions and policies aimed at preserving forests and the provision ecosystem services. We found that the occurrence of background mortality in mixed stands of pine, birch, and spruce across central northern Europe is mainly driven by tree size, intra- and inter-specific competition, and mean annual temperature.

Our results indicate that, for the mean temperatures of the studied area, the probability of mortality due to intra-specific competition is, on average, higher for birch and spruce than for pine. For pine, the mortality increased when mixed with spruce, while for birch and spruce the effects of mixture, especially with pine, result in lower mortality. This finding is in consonance with the hypothesis that the effect of competition on tree mortality is species-specific (H1).

Among the studied basic climatic variables, the effect of mean annual temperature was the most relevant, causing an increase in the probability of mortality of pine and spruce, while also magnifying the effects of intra- and inter-specific competition effects in different ways for the studied species, highlighting the complexity of species interactions. However, the variation in mortality with T is complex as it interacts not only with competition but also with tree diameter. In general, warmer temperatures exacerbated the differences caused by the effects of species interactions on spruce mortality, and colder temperatures had the same impact on pine. These findings support the hypothesis that the effects of temperature on tree mortality are species-specific (H3), but only partially sustain H2: Temperature accelerates tree mortality in continental and boreal forests and modifies competition effects.

It is important to consider that our models were developed from NFI data, which are limited by a lack of spatial information and by small plot sizes, together with simple climate variables. More complex indices and additional site variables could provide more accurate information about how climate mediates the species-specific interactions in tree mortality. Nevertheless, the identified patterns of species mortality with temperature should be considered in forest conservation and management as well as in forest carbon sink projections under climate warming.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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