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The effect of ontogeny, competition, site, and climate on background mortality for trees of nine species in Canadian boreal forest

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Abstract

Background tree mortality can be defined as the death of trees that naturally occurs as stands develop, in the absence of major or sudden stand disturbances. The phenomenon is often linked to ontogeny and competition and generally affects individual trees, unlike catastrophic mortality, which affects most trees in the stand. To forecast stand characteristics and to estimate how stand development could change in response to changing climate, it is necessary to quantify background mortality and to identify the most important factors involved. Using data from 10 045 permanent sample plots, we modeled background tree mortality for the nine most abundant tree species of the eastern Canadian boreal forest. We used explanatory variables related to stand and tree ontogeny, competition, site characteristics, and climate to calibrate the models. We found that an increase in age, competition, and the presence of partial cut increased the mortality risk. However, the effect of DBH and site-related variables varied among species. We also found that higher temperatures, less precipitation, and higher aridity index values increased background tree mortality. According to mortality simulations under different future climate scenarios, background tree mortality could increase in the next decades for six of the nine tree species studied.

Key words: mortality, climate change, Boreal forest, background mortality, climate variables

Résumé

La mortalité de fond peut être définie comme la mort naturelle au cours du développement des peuplements, en l'absence de perturbations majeures. Ce phénomène est souvent lié à l'ontogenèse et à la compétition. Il affecte généralement les arbres individuels, contrairement à la mortalité catastrophique, qui affecte simultanément une grande proportion des arbres du peuplement. Pour prévoir les caractéristiques des peuplements futurs et estimer comment leur développement pourrait changer en réponse aux changements climatiques, il est important de quantifier la mortalité de fond et d'identifier les principaux facteurs impliqués. En utilisant les données de 10 045 placettes-échantillons permanentes, nous avons modélisé la mortalité de fond des 9 essences les plus abondantes de la forêt boréale de l'est du Canada. Nous avons paramétré les modèles à l'aide de variables explicatives liées à l'ontogenèse des peuplements et des arbres, à la compétition, aux caractéristiques du site et au climat. Alors que l'augmentation de l'âge, de la compétition et la présence de coupes partielles augmentaient le risque de mortalité, l'augmentation du diamètre à hauteur de poitrine avait un effet variable d'une espèce à l'autre. De plus, des températures plus chaudes, des précipitations moins abondantes et un indice d'aridité élevé augmentent la mortalité de fond des arbres. D'après les simulations sous différents scénarios climatiques futurs, la mortalité de fond pourrait augmenter au cours des prochaines décennies pour 6 des 9 essences étudiées. [Ceci est une traduction fournie par l'auteur du résumé en anglais.]

Mots-clés : Mortalité de fond, Changements climatiques, Mortalité, Forêt boréale, Variables climatiques

Introduction

Quantifying tree mortality is necessary to accurately predict temporal changes in forest merchantable wood volumes, biomass, carbon content, and species composition. This highlights the importance of understanding how climate affects the occurrence of tree mortality, and eventually, how this phenomenon may change in the future. During the last decades, several studies have been conducted on tree mortality and its relationship with climate. These studies have been carried out in different forest biomes like the amazonian tropical forest (Brienen et al. 2015), North American temperate and boreal forests (van Mantgem and Stephenson

2007; Peng et al. 2011; Luo and Chen 2015; Hisano et al. 2019; Searle et al. 2022), or European temperate and boreal forests (Nothdurft 2013; Pretzsch et al. 2014*a*; Neumann et al. 2017). For most of the tree species studied, these authors found a trend of increasing mortality associated with the recent climate warming.

Given that the Canadian boreal forest region is expected to experience a large increase in temperature during the next decades (Wotherspoon et al. 2024), concerns about the impact of climate change on tree mortality rates in this region can be raised. The different growth conditions induced by climate change may lead to an increase in mortality rates for some tree species in this region (Peng et al. 2011;Yaussy et al. 2013; Sánchez-Pinillos et al. 2022; Liu et al. 2023).

Forest tree mortality can be classified as either catastrophic mortality or background mortality (Hember et al. 2017). While catastrophic mortality is generally related to punctual disturbances such as fire, blowdown, or severe insect infestation, background mortality is mainly driven by tree competition and stand ontogeny (Manso et al. 2015). Given their different effects on the growth of residual trees and regeneration patterns, these two types of mortality are generally treated and analyzed separately in forest growth models (Vanclay 1994).

Several factors have been found to influence background tree mortality. Among them, tree species is known to greatly influence background mortality because tree longevity differs among species (Vanclay 1994). For example, Mailly et al. (2009) found a higher rate of mortality for trembling aspen (*Populus tremuloides* Michx.) than for black spruce (*Picea mariana* (Mill.) B.S.P.) or jack pine (*Pinus banksiana* Lamb.) in Québec forests. In temperate mixedwood forests, Raymond et al. (2016) found that balsam fir (*Abies balsamea* (L.) Mill.) had a higher mortality rate than yellow birch (*Betula alleghaniensis* Britton), red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.), all other things being equal. Likewise, Fortin et al. (2008) found a significant effect of species on northern hardwood tree mortality. Among other tree-related variables that affect the probability of mortality, tree size, often described using diameter at breast height (DBH), as well as tree age have been reported (Chen et al. 2008; Peng et al. 2011).

Competition between trees is another major factor that influences tree mortality. Different variables have been used in mortality models to represent the effect of competition. Stand basal area (e.g., Fortin et al. 2008) and basal area of trees larger than the subject tree (Rathbun et al. 2010) or the ratio of the DBH of the subject tree over the mean quadratic diameter (Chen et al. 2008) are among the most frequent ones. Some authors separated the influences of intra- and interspecific competition (Luo and Chen 2015; Manso et al. 2015; Hisano et al. 2019) while, less frequently, others used distance-dependent competition indices (Bigler and Bugmann 2003; Luo and Chen 2015).

Anthropic disturbances, such as partial cutting, are known to affect the mortality rate of residual trees. Many authors have found an increase in tree mortality rates during the years following a partial cutting. This phenomenon is often explained by the damage caused to residual trees during the harvesting process or from a poor acclimation of residual trees to their new growth conditions. This has been observed in northern hardwoods (Martin et al. 2014; Brandeis and Brandeis 2021), and temperate mixedwoods (Prévost and Dumais 2013) as well as in boreal forest stands (Brais et al. 2019).

Over the last decades concerns regarding the potential effects of climate change on background mortality have also been raised (Allen et al. 2010). Many researchers found that limited water availability (van Mantgem and Stephenson 2007; Peng et al. 2011; Luo and Chen 2013) and drought (Breshears et al. 2005; Michaelian et al. 2011; Liu et al. 2023) were related with an increase in the occurrence of tree mortality. Drought indices were successfully used to model the background mortality rates of 64 North American tree species (Hember et al. 2017) and have also been associated with the decline of trembling aspen (Worrall et al. 2013), while sequential droughts of small amplitude have been related to an increase in background tree mortality in the Canadian boreal forest (Sánchez-Pinillos et al. 2022). An increase in air temperature is another factor that was associated with higher background mortality rate for the Canadian boreal forest (Hisano et al. 2019). This later element is consistent with what was reported by Allen et al. (2010) in their literature review on drought and heat-induced tree mortality. However, even without increasing water stress, Luo and Chen (2015) found an increase in mortality rates. They explained this increase in mortality by an increase in tree to tree competition and by heat stress. For black spruce stands in northern Manitoba, Bond-Lamberty et al. (2014) found that temperature increase was positively related to decreased stem growth and higher mortality risks, but that precipitation and moisture index had the opposite effect. All these factors underline the importance of the effects of climate on mortality and the possible impacts of climate change.

The main objective of this work was to assess the effects of ontogeny, competition, as well as topographic, edaphic, and climate-related variables on background mortality for nine of the most abundant tree species of the eastern Canadian boreal forest. By controlling for the effects of these variables, we also aim to derive indications as to how background mortality could change under future climate conditions. Based on previous studies, we hypothesized that an increase in DBH, age, and in competition will increase tree mortality rates. We also hypothesized that an increase in temperature and a diminution in water availability will increase the probability of mortality. Finally, based on our previous hypothesis, we hypothesized that we should expect an increase in background tree mortality under future climate for eastern Canadian boreal forest.

Methods

Data

Our study uses data collected from the permanent sample plot network of Québec's Ministry of Natural Ressources and Forests. The development of this network began in 1970 and over the years, more than 12 000 sample plots have been

established (DIF 2014). The network is composed of 400 m^2 circular plots that are measured at regular intervals (every 8 to 15 years) based on geographical location. Up to 6 measurements were available for some plots.

At the moment of plot establishment, all merchantable-size trees (DBH (measured at a height of 1.3 m) > 9.0 cm) were numbered to enable individual monitoring in subsequent measurements. For each numbered tree, DBH was measured with a diameter tape (to the nearest millimeter), and species was recorded. At each subsequent measurement, their status (dead, cut, or alive) was recorded. Recruits (i.e., trees that reached the DBH threshold of 9.1 cm during the interval) were added to the tree list, numbered, and their diameter recorded. The occurrence of a partial disturbance such as fire or cut, slope class (slope: <4%, 4%–8%, 9%–15%, 15%–30%, and >30%), soil texture (texture: fine, medium, coarse, and organic), and drainage (drain: xeric, mesic, subhydric, and hydric) were evaluated by the field crew at each measurement (Morneau et al. 2021). The DBH of living merchantable trees (DBH > 9.0 cm) in the plot was used to calculate plot basal area (BA) and, for each living merchantable tree located in the plot, the sum of the basal area of living merchantable trees with a larger diameter than the tree in question was also calculated (BAL).

We selected the nine most abundant tree species (balsam fir, black spruce, jack pine, paper birch (*Betula papyrifera* Marshall), tamarack (*Larix laricina* (Du Roi) K. Koch), trembling aspen, red maple, white spruce, and yellow birch) of Québec's boreal forest, which together, represent more than 99% of the merchantable-size tree abundance (Table 1, Fig. 1). Soil characteristics (proportion of sand (Sand), proportion of clay (Clay), pH, organic matter content (OM), and cation exchange capacity (CEC)) were retrieved from Québec's soil properties map for depths of 5–15 cm (Sylvain et al. 2021). The occurrence of a partial cut during the current growth interval (time elapsed between two consecutive measurements) (PCut0) or during the previous growth interval (PCut) was assessed by identifying the measurements where at least one tree had the status "cut". Two binary variables were created with the value of 1 (presence of cut in the plot) or 0 (absence of cut). The topographic wetness index (TWI) was computed for each permanent sample plot based on a 1 m resolution digital elevation model built from airborne acquired lidar data with the SAGA Wetness Index algorithm (Boehner and Selige 2006). TWI values for each 1 m^2 were averaged based on plot area. In each plot, nine sample trees were selected based on their species and on their crown class. For each softwood or intolerant hardwood sample tree, a wood core was taken at a height of 1 m, on which the annual growth rings were counted to estimate tree age. Plot age (Age) was computed as the mean age at a height of 1 m for dominant and codominant sample trees of the plot.

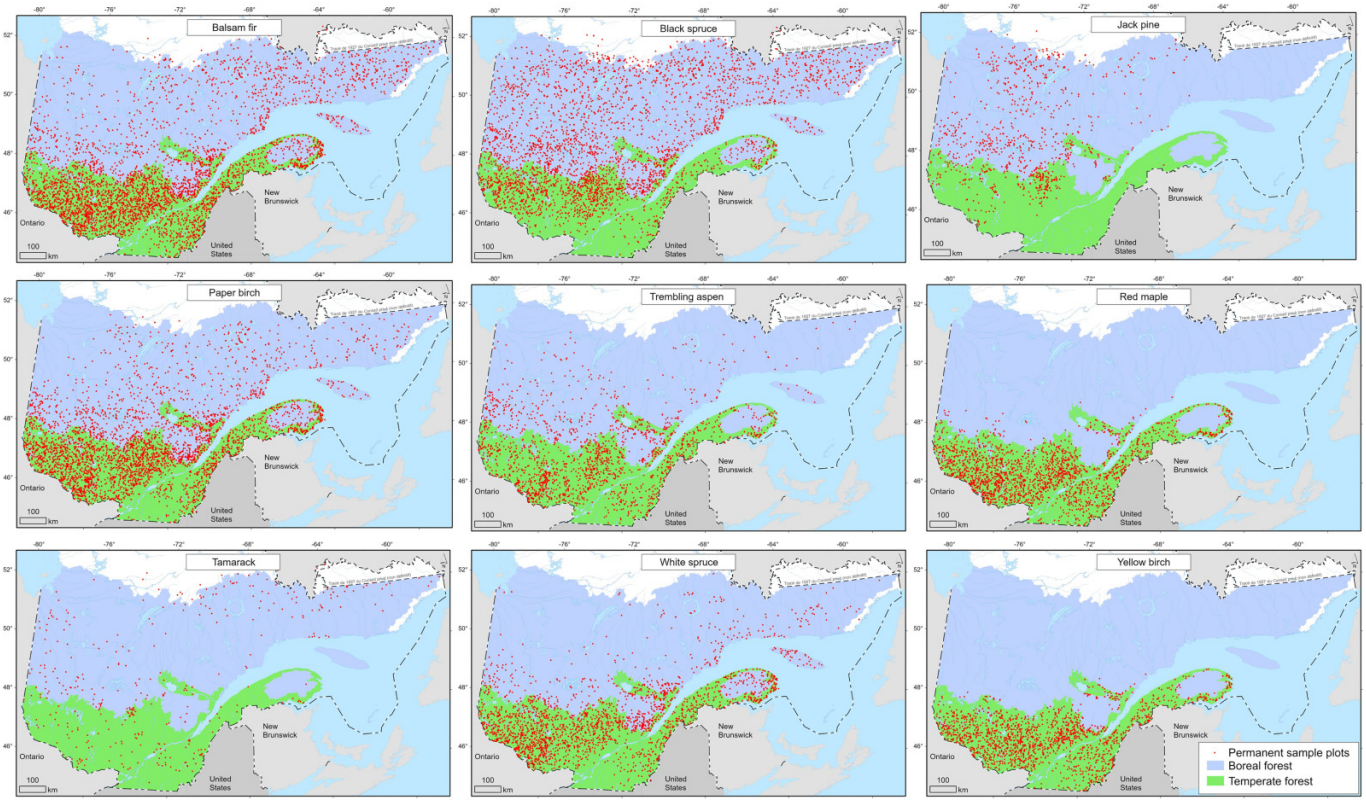
To remove the influence of disturbances on background mortality, we used annual aerial defoliation surveys to identify plots and growth intervals that were affected by defoliation attributed to the spruce budworm (*Choristoneura fumiferana* Clemens) or the forest tent caterpillar moth (*Malacosoma disstria* Hübner). For balsam fir and white spruce, we

Table 1. Description of the dataset.

Mortality equation	Number of trees	Number of plots	Latitude (decimal degrees)		Longitude (decimal degrees)		Mean annual temperature of the growth interval (°C)*	Mean annual total precipitation of the growth interval (mm)*	10 years mortality rate (%)
			Minimum	Maximum	Minimum	Maximum			
Balsam fir	67 300	6084	45.0	52.9	−57.3	−79.3	**1.7** (−4.3 – 7.3)	**1034** (663 – 1532)	17.5
Black spruce	100 819	5397	45.1	52.9	−57.3	−79.5	**0.0** (−4.6 – 6.3)	**942** (670 – 1609)	11.6
Jack pine	17 593	1217	45.7	52.6	−66.1	−79.5	**0.8** (−3.2 – 4.7)	**925** (690 – 1179)	14.0
Paper birch	36 347	5356	45.0	52.3	−58.0	−79.5	**1.8** (−3.7 – 7.3)	**1011** (698 – 1690)	19.1
Tamarack	1510	415	45.1	52.8	−57.3	−79.5	**2.2** (−4.6 – 6.3)	**970** (677 – 1441)	12.7
Trembling aspen	16 516	2255	45.0	51.8	−59.6	−79.5	**2.6** (−3.4 – 7.4)	**989** (745 – 1537)	25.7
Red maple	16 000	2712	45.0	49.5	−64.2	−79.5	**3.5** (−0.1 – 7.4)	**1042** (772 – 1535)	13.4
White spruce	10 244	3087	45.1	52.7	−58.2	−79.5	**2.4** (−4.2 – 6.3)	**1025** (717 – 1603)	10.9
Yellow birch	8177	2201	45.0	49.2	−64.3	−79.3	**3.0** (−0.5 – 7.5)	**1065** (795 – 1616)	11.3
All 9 species	274 506	10 045	45.0	52.9	−57.3	−79.5	**1.3** (−4.6 – 7.5)	**998** (663 – 1690)	15.1

*Mean values appear in bold, and minimum and maximum values are in parentheses.

Fig. 1. Distribution map of the permanent sample plots included in the dataset, for each of the nine tree species, throughout the boreal and temperate forests of Québec (Canada). The figure was created using Esri ArcGIS Pro version 3.2.1. Base maps: Ministère des Forêts, de la Faune et des Parcs du Québec (2020) and Commission de toponymie du Québec (2019). Coordinate system EPSG:32198—NAD83/Quebec Lambert.



excluded from the dataset the growth intervals corresponding to the presence of defoliation attributed to spruce budworm. For trembling aspen and red maple, we did the same when defoliation could be attributed to the tent caterpillar moth, and for all broadleaf tree species, we excluded the growth intervals that were affected by the major ice storm that occurred in southern Québec in 1998. Growth intervals of plots affected by forest fire were also removed from the dataset.

Climate variables for the period hereafter referred to as "current" (1991–2020) were estimated using the BioSIM 11 software (Régnière et al. 2017). We obtained climate variables for each month included between two consecutive measurements in each sample plot. The values of each climate variable were averaged over the growth intervals. The climate variables selected for the modeling procedure are listed in Table 2; these variables had already been identified as influent predictors of mortality rate (Park Williams et al. 2013; Hember et al. 2017; Sánchez-Pinillos et al. 2022) or growth (Wang et al. 2023), a characteristic that can be related to the probability of mortality (Weiskittel et al. 2011).

Analysis

We used a generalized linear mixed-effects model approach to fit a mortality model for each species. After experiencing convergence issues when fitting models including both plot and growth interval random effects, we randomly selected one growth interval for each plot where trees of the designated species were present, and included only a plot random effect.

We defined the status m_{ijk} of tree i in sample plot j as the dependent binary variable, setting its value at 0 when a tree survived and at 1 when it died during growth interval k. This variable follows a Bernoulli distribution, with parameter π_{ijk} as the probability of mortality (eq. 1) that is linearly related to explanatory variables via a complementary log–log link function (eq. 2), and with the natural logarithm of the length of the growth interval as an offset variable (Fortin et al. 2008). The models were fitted using the GLIMMIX procedure of the SAS statistical system (v. 9.4, SAS Institute Inc., Cary, NC, USA).

$$(1) \quad m_{ijk} \sim \text{Bernoulli}\left(\pi_{ijk}\right)$$

$$(2) \quad \pi_{ijk} = 1 - e^{-e^{x_{ijk}\beta + \ln\left(\Delta t_{jk}\right) + b_j}}$$

where x_{ijk} is a vector of explanatory variables, β is a vector of parameters, Δt_{jk} is length of the growth interval in years, and b_j is a plot random effect that is assumed to be normally distributed with mean 0 and variance σ^2_{plot}.

Table 2. List of the explanatory variables tested in the mortality models.

Group of variables	Variable (unit)	Abbreviation	Mean value (min – max)
Tree size	Diameter at breast height (cm)	DBH	14.7 (9.1 – 99)
	Squared diameter at breast height (cm^2)	DBH^2	216.1 (82.8 – 9801)
	Natural logarithm of DBH	lnDBH	2.69 (2.21 – 4.6)
Competition	Plot basal area ($m^2 \cdot ha^{-1}$)	BA	21.0 (0.2 – 66.8)
	Basal area of larger trees ($m^2 \cdot ha^{-1}$)	BAL	13.6 (0 – 63.1)
Site	Slope inclination	Slope	Class variable
	Soil texture	Texture	Class variable
	Soil drainage	Drain	Class variable
	Presence of a partial cut during the growth interval	PCut0	Binary variable
	Presence of a partial cut during the previous growth interval	PCut	Binary variable
	Topographic wetness index	TWI	5.4 (0.5 – 21.8)
	Plot age (years)	Age	73 (8 – 295)
	Potential hydrogen	pH	3.9 (3.5 – 5.7)
	Cation exchange capacity (mEq·100 g^{-1})	CEC	4.2 (0.3 – 29.9)
	Organic matter proportion (%)	OM	7.4 (1.5 – 12.5)
	Sand proportion (%)	Sand	65.4 (7.8 – 92.2)
	Clay proportion (%)	Clay	10.7 (1.7 – 78.1)
Climate	Aridity index (cm)*	Arid	26.6 (0.0 – 104.8)
	Natural logarithm of Arid + 1	lnArid	3.3 (0.0 – 4.7)
	Summer climate moisture index (mm)†	CMI	324 (−200 – 324)
	Degree-days (°C)‡	DD	1289 (619 – 2348)
	Natural logarithm of DD	lnDD	7.1 (6.4 – 7.8)
	Mean annual temperature (°C)	TMean	1.3 (−4.6 – 7.6)
	Natural logarithm of TMean + 5	lnTMean	1.8 (−0.9 – 2.0)
	July mean temperature (°C)§	TJuly	16.4 (11.9 – 21.7)
	Natural logarithm of TJuly	lnTJuly	2.8 (2.5 – 3.1)
	Summer mean temperature (°C)‖	TSummer	12.8 (8.3 – 18.4)
	Natural logarithm TSummer‖	lnTSummer	2.5 (2.1 – 2.9)
	Mean maximum daily temperature from June to August (°C)	TmaxUtil	21.2 (14.9 – 26.0)
	Natural logarithm of TmaxUtil	lnTMaxUtil	3.1 (2.7 – 3.3)
	Total precipitation (mm)	PTot	988 (663 – 1690)
	Natural logarithm of PTot	lnPTot	6.9 (6.5 – 7.4)

*Cumulative monthly water deficit (monthly Thornthwaite potential evapotranspiration—monthly precipitation; set to 0 if negative).
†Climate moisture index (sum of precipitation—sum of monthly potential evapotranspiration) from May to September.
‡Annual growing degree-day summation over 5 °C.
§Mean daily temperature for the month of July.
‖Mean daily temperature from May to September.

For each species, we used a sequential method to select the model's explanatory variables, sequentially adding variables from each group (tree size, competition, age, site, and climate; Table 2), variables from the group were first added individually to the model. The variable that produced the lowest Akaike information criterion (AIC) value was selected (Akaike 1973). Then, we added each of the remaining variables of the group individually to the model. Again, we selected the variable that produced the lowest AIC value. We repeated this process until no variable of the group further decreased the AIC. We then applied these same steps to the next group of variables. For climate variables, because temperature related variables were highly correlated, we only allow one temperature related variables to enter the model. The same rule was applied for precipitation and water availability related variables. To avoid high multicollinearity, at each step we checked that the variance inflation factor of the variables of the selected model did not exceed five units (James et al. 2013).

A non-trivial issue with mixed-effects logistic models is that population-averaged predictions are not obtained by setting the random effects to 0 (McCulloch et al. 2008, p.190; Meng et al. 2009; Fortin 2013). As a workaround, we used a Monte Carlo simulation, in which random deviates are drawn to account for the random effect. After copying the predicted values for each tree a thousand times, we added a simulated plot random effect to each model prediction. The average mortality probability of each tree was calculated after returning each prediction to its original scale. This step was performed to account for the nonlinearity of the random effect in the model (eq. 3):

$$Pm_{ijk} = \int \pi_{ijk} p\left(b_j\right) \mathrm{d}b_j \quad (3)$$

Table 3. Model cross-validation statistics.

Species	Observed 10-year proportion of mortality (%)	Predicted 10-year probability of mortality (%)	Area under the operator response curve (AUC)
Balsam fir	17.5	18.7	0.69
Black spruce	11.6	10.1	0.66
Jack pine	14.0	17.3	0.74
Paper birch	19.1	19.4	0.68
Trembling aspen	25.7	24.9	0.68
Tamarack	12.7	13.3	0.63
Red maple	13.4	13.4	0.64
White spruce	10.9	12.0	0.67
Yellow birch	11.3	11.6	0.60

where Pm_{ijk} is the population-averaged prediction of mortality and $p(b_j)$ is the probability density of the plot random effect b_j.

A 10-fold cross-validation (Hastie et al. 2009) was performed on the final models. For each species, we randomly divided the dataset in 10 groups of plots of equal size. We then estimated the model parameters with the plots from nine groups and, using these parameters, estimated the response variable for the 10th group. This operation was repeated for each group. Using the average prediction from the cross-validation for each tree, we calculated the area under the operator response curve (AUC) (Hosmer and Lemeshow 2000) based on these predictions. On the same basis, we compared the mean predicted mortality rate with the observed proportion of mortality on a 10-year period (eq. 4) based on the method presented by Crecente-Campo et al. (2009).

$$Pm_{10} = 1 - \left(\left(1 - Pm_{ijk}\right)^{\frac{1}{\Delta t}}\right)^{10} \quad (4)$$

where Pm_{10} is the population-averaged 10-year probability of mortality and Δt is the mean length of the growth interval.

To assess the importance of each explanatory variable that we retained in the mortality models we standardized the explanatory variable of each model to a mean value of 0 and a standard deviation of 1. After removing the variables that were not significantly correlated to the response variable (p-value > 0.05) we fitted the final models using the standardized explanatory variables according to the method proposed by Murray and Conner (2009). We then ordered the explanatory variables based on the value of their parameter, the most influent variable having the largest absolute value. We assessed the effects of these variables by plotting the 10-year predicted probability of mortality against each variable over its observed range, while keeping the other variables constant at their mean value.

For each species, we used the final model to contrast the predicted probability of mortality between two reference periods: 1991–2020 and 2041–2071. The climate values entering each model were simulated for the representative concentration pathway (RCP) 4.5 $W{\cdot}m^{-2}$ using BioSIM (Régnière et al. 2017) and three general circulation models (GCM4_ESM2, Hadley, RCM4_ESM2) for each permanent sample plot located in the boreal forest region (Morneau et al. 2021). We averaged three model forecasts for each reference period. For each species and reference period, the 10-year probability of mortality was predicted by setting the explanatory variables at their mean value.

Results

The cross-validation of the mortality models showed that AUC values varied from 0.60 for yellow birch to 0.74 for jack pine (Table 3). The mean observed 10-year probability of mortality varied from 10.9% for white spruce to 25.7% for trembling aspen, while the predicted 10-year probability of mortality varied from 10.1% for black spruce to 24.9% for trembling aspen (Table 3). In the nine species models, probability of mortality was related with DBH, which was significant in all models (Table 4). Tree DBH was the most (balsam fir) or the second most (tamarack, trembling aspen, and white spruce) important variable in four of the nine species models. (Table 5). DBH showed a monotonic positive relationship with 10-year probability of mortality for balsam fir, black spruce, paper birch, tamarack, white spruce, and yellow birch (Fig. 2). For the three other species, the relationship of DBH with the probability of mortality was negative indicating a larger probability of mortality for small trees (Fig. 2). The presence of a partial cut (PCut0 or PCut), BAL and Age were also important variables that contributed to explain the probability of tree mortality (Tables 4 and 5). The presence of a partial cut was retained in all mortality models, while BAL and Age were retained in 8 and 7 models, respectively (Table 4). The presence of a partial cut (PCut or PCut0) as well as BAL and Age had a positive effect on the tree-level probability of mortality (Table 4, Fig. 2), but the importance rank of these variables in the models varied among species. BAL was ranked first (jack pine, trembling aspen, and white spruce) to fourth, while Age was ranked first (black spruce and paper birch) to third in the different models. Partial cut was ranked first (tamarack) to last position for yellow birch and white spruce (Table 5). Among the other variables, tree mortality occurrence was higher on hydric or xeric than on mesic or subhydric soil drainage for balsam fir, black spruce, and paper birch (Table 4, Fig. 3), but lower on fine or coarse soil texture for jack pine or on fine and medium texture for trembling aspen. The proportion of sand in the soil had a negative effect on

Table 4. Mortality equations parameters.

Species	Parameter	Estimate	Standard error	*p*-value	Variance of the random effect
Balsam fir	Intercept	−7.2343	0.1754	<0.0001	1.0668
	DBH	0.0892	0.0029	<0.0001	
	BAL	0.0219	0.0020	<0.0001	
	Age	0.0084	0.0006	<0.0001	
	PCut0	0.8395	0.0609	<0.0001	
	Pcut	0.2444	0.0890	0.0060	
	CEC	−0.0137	0.0065	0.0345	
	DrainageCl	0.4678	0.0757	<0.0001	
	Slope (4%–8%)	−0.2953	0.0655	<0.0001	
	Slope (9%–15%)	−0.2743	0.0662	<0.0001	
	Slope (16%–30%)	−0.2183	0.0675	0.0012	
	Slope (>30%)	−0.1272	0.0817	0.1193	
	lnAridity	0.1710	0.0388	<0.0001	
	DD	0.0002	0.0001	0.0038	
Black spruce	Intercept	−7.8600	0.1961	<0.0001	1.0321
	DBH	0.0699	0.0034	<0.0001	
	BAL	0.0370	0.0020	<0.0001	
	Age	0.0102	0.0005	<0.0001	
	PCut0	1.1897	0.0944	<0.0001	
	Sand	−0.0046	0.0015	0.0017	
	Drain (hydric/xeric)	0.2020	0.0537	0.0002	
	lnTMean	0.3471	0.0690	<0.0001	
	lnAridity	0.1719	0.0435	<0.0001	
Jack pine	Intercept	2.4305	4.5399	0.5925	1.2946
	lnDBH	−0.6515	0.1417	<0.0001	
	BAL	0.0847	0.0050	<0.0001	
	Age	0.0279	0.0025	<0.0001	
	PCut0	0.5929	0.2280	0.0093	
	Texture (fine/coarse)	−0.5088	0.1092	<0.0001	
	Slope (4%–8%)	−0.1993	0.1276	0.1183	
	Slope (9%–15%)	−0.0453	0.1437	0.7526	
	Slope (16%–30%)	−0.1768	0.1749	0.3119	
	Slope (>30%)	0.7851	0.3352	0.0192	
	lnPTot	−1.0753	0.6641	0.1054	
Paper birch	Intercept	−6.4587	0.3573	>0.0001	1.2062
	DBH2	0.0003	0.0001	>0.0001	
	Age	0.0124	0.0009	>0.0001	
	BAL	0.0174	0.0023	>0.0001	
	PCut0	0.7926	0.0695	>0.0001	
	Pcut	0.6112	0.1118	>0.0001	
	Drain (hydric/xeric)	0.2631	0.0951	0.0057	
	TMax-Util	0.0476	0.0157	0.0024	
Trembling aspen	Intercept	−4.6329	0.3826	>0.0001	1.2326
	lnDBH	−0.7350	0.0999	>0.0001	
	BAL	0.0432	0.0041	>0.0001	
	Age	0.0191	0.0023	>0.0001	
	PCut0	0.4066	0.1189	0.0006	
	Texture (Fine/Average)	−0.2671	0.1054	0.0113	
	CEC	−0.0266	0.0117	0.0235	
	DD	0.0011	0.0002	>0.0001	

Table 4. (*concluded*).

Species	Parameter	Estimate	Standard error	*p*-value	Variance of the random effect
Tamarack	Intercept	−6.3376	0.3733	<0.0001	1.3513
	DBH^2	0.0014	0.0005	0.0046	
	BAL	0.0289	0.0156	0.0647	
	PCut0	1.6359	0.5260	0.0019	
Red maple	Intercept	−3.9961	0.3010	>0.0001	1.1409
	lnDBH	−0.3433	0.0990	0.0005	
	BAL	0.0156	0.0045	0.0005	
	Age	0.0068	0.0016	>0.0001	
	PCut0	0.4544	0.0921	>0.0001	
	Pcut	0.5054	0.1334	0.0002	
	CEC	−0.1330	0.0188	>0.0001	
White spruce	Intercept	−6.998	0.1947	>0.0001	2.3152
	DBH2	0.0010	0.0001	>0.0001	
	BAL	0.0476	0.0050	>0.0001	
	Age	0.0059	0.0018	0.0012	
	PCut0	0.5386	0.1564	0.0006	
	TMean	0.0955	0.0320	0.0029	
Yellow birch	Intercept	−6.1910	0.3694	>0.0001	0.9181
	DBH2	0.0002	0.00004	0.0003	
	PCut0	0.2516	0.1142	0.0277	
	DD	0.0008	0.0002	0.0005	
	CMI	0.0022	0.0006	0.0005	

Note: For variable definitions, see Table 2. CMI, climate moisture index; DD, degree-days; DBH, diameter at breast height; CEC, cation exchange capacity.

probability of mortality for black spruce (Fig. 3). CEC entered first in the mortality model for red maple, fifth for trembling aspen and last for balsam fir. Plots with high CEC values had a lower risk of mortality than plots with lower CEC (Table 5, Fig. 3).

Climate-related variables entered the mortality models for seven of the nine species (Table 4), the exceptions being red maple and tamarack. These variables can be grouped as temperature-related (TMean, DD, and TmaxUtil) and water availability-related (Aridity, climate moisture index (CMI), and Ptot). Temperature-related variables had a positive effect on probability of mortality risk for balsam fir, black spruce, white spruce, paper birch, yellow birch, and trembling aspen (Table 4, Fig. 4). Regarding water availability variables, Aridity (balsam fir and black spruce) and Ptot (jack pine) indicated that when the precipitation was more abundant or when the difference between potential evapotranspiration and precipitation was small, the risk of mortality decreased (Fig. 4). The opposite trend (increase of mortality with an increase in the difference between precipitation and potential evaporation) was found with CMI for yellow birch.

Compared with the 1991–2020 period, predictions for 2041–2070 period showed a greater 10-year probability of mortality for balsam fir, black spruce, paper birch, trembling aspen, white spruce, and yellow birch, when other variables than climate were fixed at their mean value. (Fig. 5). The trend showed a small decline of 10-year probability of mortality for jack pine. Trembling aspen and yellow birch present the strongest increase while balsam fir, black spruce, paper birch, yellow birch and white spruce show a milder increase in 10-year probability of mortality under RCP 4.5 $W{\cdot}m^{-2}$ for the period 2041–2070.

Discussion

Except for DBH for trembling aspen and red maple, our results corroborate our first hypothesis that ontogeny- and competition-related variables positively influence background tree mortality. However, the presence of recent partial cuts in the plot is also an important variable that increased the probability of tree mortality among the residual stems. Climate variables also influence tree mortality for seven of the nine species. Among these species, the temperature and water scarcity related variables always had a positive effect on background mortality, except for yellow birch where CMI had a positive effect on background tree mortality. Consequently, our results tend to support our hypothesis that the projected increase in temperature (+3.2 to +5.9 C) in the eastern Canadian boreal forests (Wotherspoon et al. 2024) could increase background mortality in most of the studied species. The moderate projected increase in precipitation under these scenarios (+75 to +225 mm per year) appears insufficient to offset the expected effect of rising temperatures on drought-related mortality.

Ontogeny, which was represented in our models by DBH and Age, has already been cited as an influent predictor of

Table 5. Fixed effects of the models ordered by the absolute value of their standardized parameters.

	Species (Standardized parameter)							
Balsam fir	Black spruce	Jack pine	Paper birch	Tamarack	Trembling aspen	Red maple	White spruce	Yellow birch
DBH (0.42)	Age (0.44)	BAL (0.77)	Age (0.27)	PCut0 (0.54)	BAL (0.33)	CEC (−0.28)	BAL (0.50)	CMI (0.15)
Age (0.27)	BAL (0.31)	Age (0.41)	PCut0 (0.22)	DBH2 (0.31)	lnDBH (−0.31)	PCut0 (0.17)	DBH2 (0.40)	DD (0.15)
PCut0 (0.22)	DBH (0.28)	Texture-Fine/Coarse (−0.25)	BAL (0.15)	BAL (0.23)	Age (0.31)	Age (0.15)	Age (0.16)	DBH2 (0.11)
BAL (0.22)	PCut0 (0.16)	PCut0 (0.11)	PCut (0.11)		DD (0.23)	BAL (0.13)	Mean (0.16)	PCut0 (0.09)
Slope 4–8% (−0.13)	lnTMean (0.14)	lnPTot (−0.11)	DBH2 (0.09)		CEC (−0.15)	PCut (0.12)	PCut0 (0.15)	
Slope 9–15% (−0.13)	lnAridity (0.10)	Slope > 30% (0.08) Slope 4–8% (−0.07)	TMaxUtil (0.07)		PCut0 (0.10)	lnDBH (−0.11)		
lnAridity (0.12)	Drainage-Hydric/Xeric (0.08)	DBH2 (0.02)	DrainageCl Hydric/Xeric (0.05)		Texture Fine/Average (−0.07)			
Drainage Hydric/Xeric (0.12)	Sand (−0.07)	Slope 9 – 15% (−0.01)						
Slope 16 – 30% (−0.11)								
CEC (−0.06)								
Slope > 30% (−0.05)								

Note: CMI, climate moisture index; DD, degree-days; CEC, cation exchange capacity.

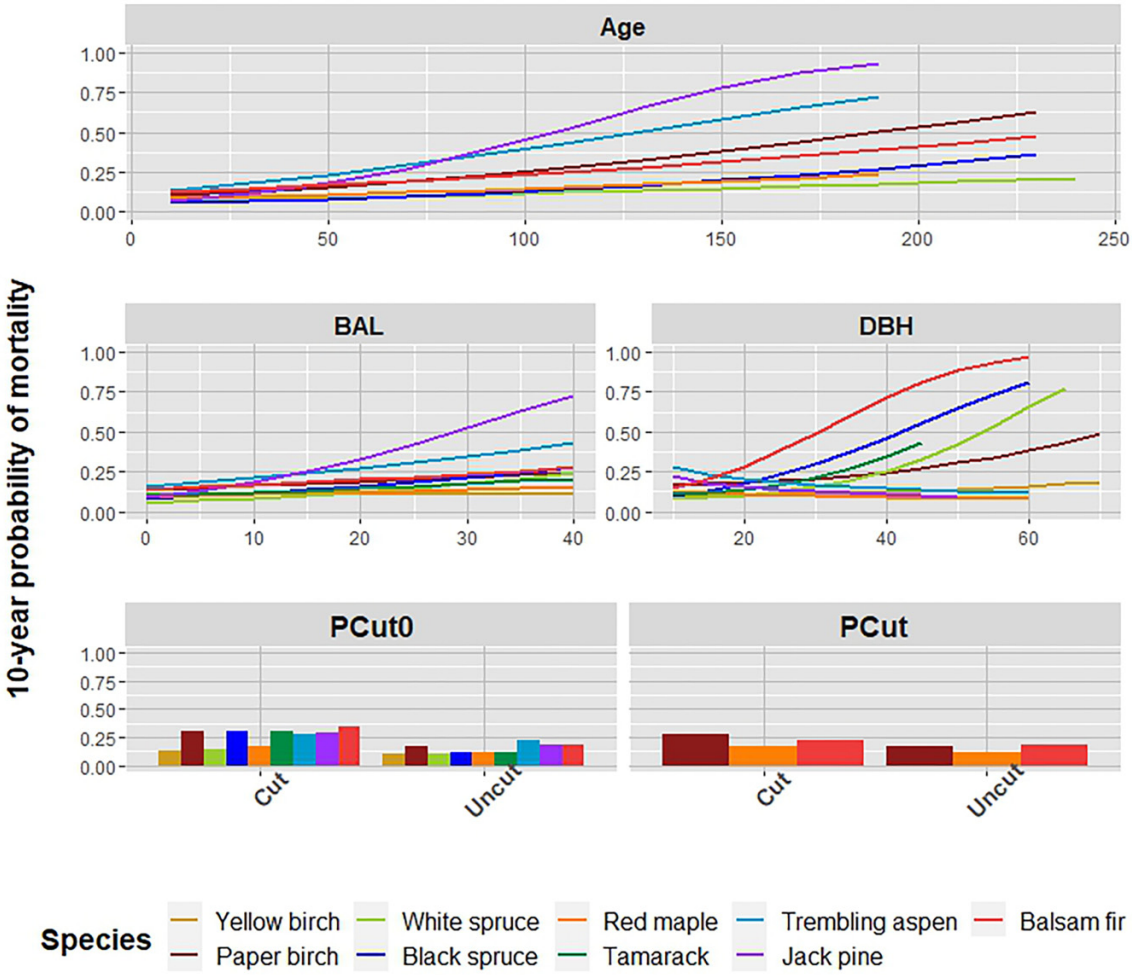
background tree mortality (Peng et al. 2011; Worrall et al. 2013). Most species in our study show an increase of mortality risk with DBH. Only trembling aspen and red maple presented a negative effect of DBH on mortality risk. For these shade-intolerant or mid-tolerant species, the decrease of mortality risk can reflect the difficulty for small trees to survive under a closed canopy cover (Côté and Blanchette 2013). As trees grow and age, the ratio between carbon assimilation and maintenance respiration diminishes, which affects tree vitality (Pretzsch 2009). Less vigorous trees can be more sensitive to damage due to biotic or abiotic stresses (MacLean 1980; Zhang et al. 1994). Moreover, tree size has often been reported to be a major factor promoting hydraulic failure and xylem embolism of trees, a phenomenon that can diminish their vitality and eventually contribute to their death (McDowell et al. 2002; Bennett et al. 2015). Our results regarding the influence of DBH and Age on mortality risk are consistent with these explanations.

BAL, a variable quantifying tree-level competition, a phenomenon often related to tree mortality, is present in all mortality models except for yellow birch. Within a stand, trees compete for limited resources, and individuals that are unable to capture enough resources are more prone to die (Bigler and Bugmann 2003). BAL, was the most influent variable in the jack pine mortality model (Table 5 and Fig. 2). This result is consistent with the results obtained on jack pine by Chen et al. (2008), who found that for this species relative tree size and age were the most influent variables to predict tree mortality. Since this species is shade-intolerant (Burns and Honkala 1990), it can be more vulnerable to competition-induced mortality, especially with respect to light (Luo and Chen 2011).

The recent occurrence of a partial cut was the most important variable to explain mortality for tamarack, and the second most influent variable for paper birch and red maple. An increase in residual tree mortality after a partial cut was also noticed by Brais et al. (2019) for black spruce in the eastern Canadian boreal forest. These authors related the increase in mortality rate to damages to the residual trees caused by harvest. Other authors have attributed higher mortality rates following partial cutting to windthrow (Thorpe et al. 2008) or to a greater evaporative demand (Bladon et al. 2006).

Edaphic variables entered the mortality models of some species. Less favorable drainage conditions (hydric and xeric) increased the probability of mortality for balsam fir, black spruce, and paper birch with. In addition, mortality probability decreased for jack pine on coarse-textured soils, for black spruce on soils with a higher proportion of sand, and for balsam fir, red maple and trembling aspen on soils with higher CEC values. A noticeable common trend for all these species is that less favorable growth conditions increase the tree-level probability of mortality. In this regard, a loss of growth or vigor can lead to an increase in the probability of mortality (Franklin et al. 1987). In boreal stands dominated by black spruce, sites with soils that contain a higher sand fraction are probably less subject to paludification than those with soils that contain less sand and a greater clay fraction (Fenton et al. 2005), the paludified soils being less favorable to tree growth, because of their limited nutrient availability.

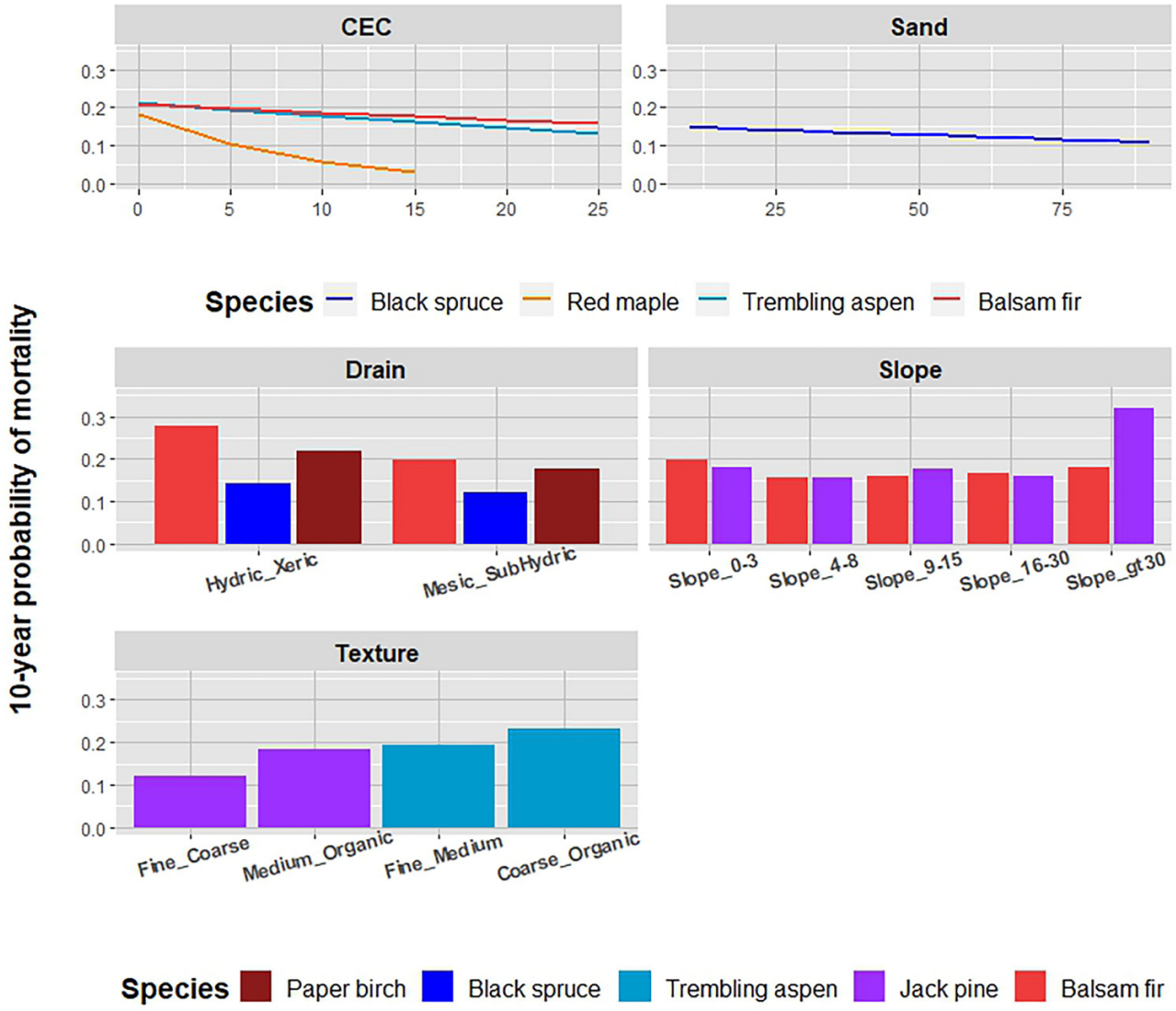
Fig. 2. Effect of plot age (in years), competition (basal area of trees larger than the subject tree (BAL, in $m^2 \cdot ha^{-1}$)), tree DBH at a height of 1.3 m (in cm), and partial cut (during the current (PCut0) or previous (PCut) growth interval) on 10-year probability of mortality, by tree species. Continuous variables of the model that do not appear on a plot were fixed at their mean value for a given species. When they do not appear on the figure, categorical variables were fixed at the following values: 0 for PCut and PCut0, 0%-4% for slope, medium for texture, and mesic for drainage.



Climate-related variables improved prediction of mortality for most tree species. Different variables contributed to explain tree probability of mortality. Among these, temperature-related variables were positively related to tree mortality risk for balsam fir, trembling aspen, black spruce, white spruce, paper birch, and yellow birch. The positive effect of temperature on mortality risk has also been reported for jack pine (Luo and Chen 2015), white spruce (Sánchez-Pinillos et al. 2022) and black spruce (Bond-Lamberty et al. 2014; Luo and Chen 2015). For other tree species, temperature also interacts with drought to increase mortality risk (Adams et al. 2009). For trembling aspen, Côté and Blanchette (2013) also reported a decrease of longevity as mean annual temperature rises. Moreover, for boreal stands, Hisano et al. (2019) found that the increase in temperature had the strongest effect on the increase of mortality rate.

High temperature can be involved in both carbon starvation (McDowell et al. 2008) and hydraulic failure (Brodribb and Cochard 2008), two causes of tree mortality. It is also known to interact with drought to increase mortality rates (Allen et al. 2015). We observed a positive relationship between Aridity (potential evapotranspiration–precipitation) and mortality probability for balsam fir and black spruce. In these 2 models, Aridity interacts with a temperature variable (DD for balsam fir and TMean for black spruce). When water availability is limited, trees can close their stomata to diminish evapotranspiration, thus reducing photosynthesis (McDowell et al. 2008). This in turn can lead to a loss in vigor and eventually, increase the risk of mortality (Bond-Lamberty et al. 2014). In addition, when evapotranspiration reaches critical values, air can enter the tree water conduction system, causing cavitation and loss of conductivity of conductive tissues. If this occurs on a large enough portion of sapwood, trees can lose vigor and eventually die from hydraulic failure (McDowell et al. 2008; Bennett et al. 2015). An opposite effect for yellow birch was found for summer climate moisture index were an increase in CMI, corresponding to more humid conditions, led to increased mortality rates.

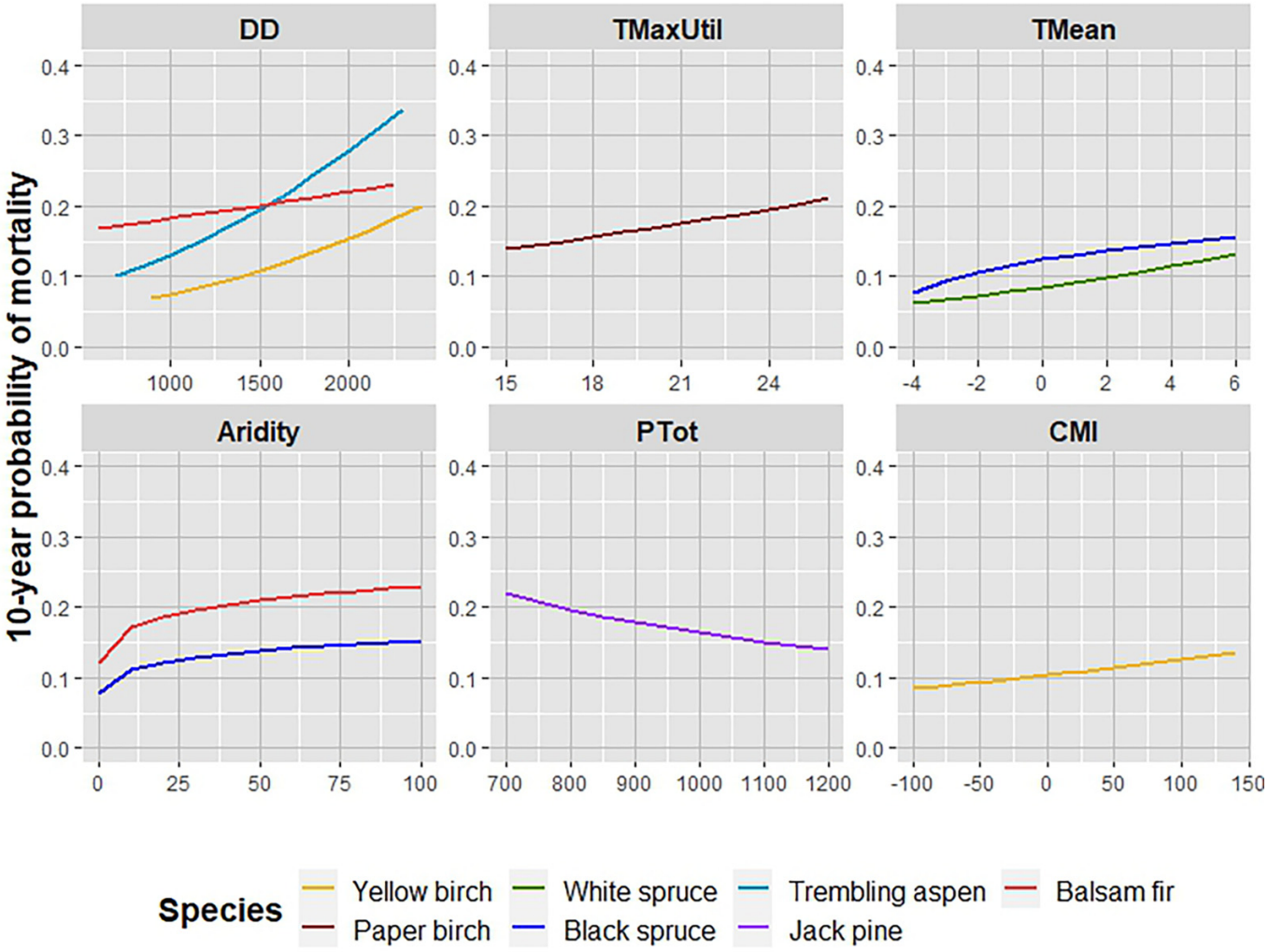
Fig. 3. Effect of site-related variables on the 10-year probability of mortality by tree species. Cation exchange capacity (CEC) is reported in mEq·100 g^{-1}, sand proportion of the soil (Sand) is reported in %. For categorical variables, drainage (Drain) is a categorical variable that groups hydric and xeric drainage against mesic and subhydric drainage. Slope is a categorical variable based on plot inclination (in %), while Texture groups fine, coarse, medium and organic soil texture. Continuous variables that do not appear on a plot were fixed at their mean value for a given species. When they do not appear on the figure, categorical variables were fixed at the following values: 0 for PCut and PCut0, 0%-4% for slope, medium for texture and mesic for drainage.



This effect seems counterintuitive. However, Sánchez-Pinillos et al. (2022) found the same effect for black spruce, trembling aspen, white birch and jack pine. They explained this phenomenon by the fact that soils with more precipitation can contain too much water and increase the mortality risk. This explaination is coherent with the positive effect on mortality risk of hydric soils for balsam fir, black spruce, and paper birch.

For six of the seven species for which climate variables were significant, our models predicted an increase in background tree mortality over the next decades. This projected increase in mortality rates is made under the assumption that the relationships between ontogeny, competition, site, and climate variables on the one hand and mortality on the other hand would remain the same in the future. However, factors that were not accounted for like genetic variation between the populations could modulate these relationships. Nevertheless, the projected increase in mortality rate is consistent with the recent observations in different ecosystems (Peng et al. 2011; Luo and Chen 2013, 2015; Pretzsch et al. 2014*b*), as well as with those anticipated for the future (McDowell et al. 2016). The anticipated increase in mortality could result from the increase in temperature (Luo and Chen 2015) or more frequent droughts (Sánchez-Pinillos et al. 2022). However, it could also reflect the reduced longevity and faster turnover rate of boreal forest trees exposed to warmer climates. Indeed, in the eastern Canadian boreal forest, tree growth is expected to increase in the next decades for most

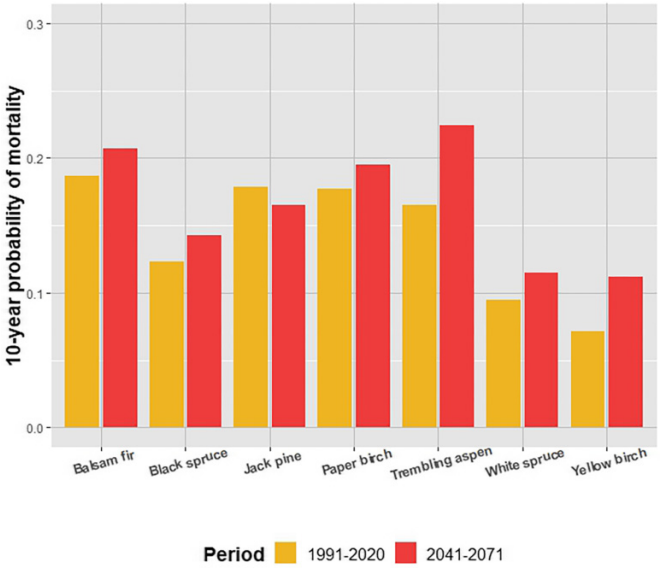
Fig. 4. Effect of various climate variables on the 10-year probability of mortality, by tree species. Aridity and climate moisture index (CMI) is reported in mm, degree-days (DD), mean maximum daily temperature for the month of June to August (TMaxUtil) and mean annual temperature (TMean) are in °C, while total annual precipitation (PTot) is in mm. Continuous variables of the model that do not appear on a plot were fixed at their mean value for a given species. When they do not appear on the figure, categorical variables were fixed at the following values: 0 for PCut and PCut0, 0%–4% for slope, medium for texture, and mesic for drainage.



of species (D'Orangeville et al. 2018; Wang et al. 2023). Over a large area, the turnover rate has been reported to increase with forest productivity and for a given species, to increase with temperature (Stephenson and van Mantgem 2005). This faster turnover rate, which can explain a higher background mortality, could also imply faster senescence of old stands. These higher expected background mortality rates are important considerations when forecasting the changes in stand growth rate under future climate. Indeed, many studies predict an increase of productivity at the tree level under future climate, for parts of the boreal forest (Chagnon et al. 2022; Wang et al. 2023). However, according to our results, this increase could be mitigated by higher tree mortality rates.

The dataset used in this study covers all the meridional parts of the boreal forest as well as the temperate forest of southern Québec. This large coverage of the province's territory enables us to monitor tree mortality over a relatively large temperature gradient. The actual annual mean temperature observed in the southern part of the province (6.8 C) could be analogue to the future climate of the boreal forest by the end of the century. However, for species such as jack pine, which is only sparsely present in southern Québec (Béland 2013), our dataset covers a smaller climate gradient. This could partly explain the absence of temperature-related variables and the weak effect of climate in the mortality model for this species. Also, because the time elapsed between 2 consecutive measurements averaged 10 years, our models were unable to account for the effect of isolated extreme events such as pronounced droughts, which are known to trigger mortality (Hember et al. 2017; Manso et al. 2015). Given these limitations, more work is needed to fully understand and

Fig. 5. Predicted 10-year probability of mortality by tree species under RCP 4.5 W·m^{-2} scenario, for both the 1991–2020 and 2041–2070 periods. Continuous variables of the model were fixed at their mean value for a given species. Categorical variable PCut and PCut0 where fixed to 0, slope was fixed at 0%–4%, texture to medium and drainage to mesic value.



estimate how climate change could impact background tree mortality.

Conclusion

Our results show that many factors influence background mortality of boreal tree species. Ontogeny and competition are well known factors, but others such as drainage, soil characteristics, and climate also play a role. While the effects of ontogeny and soil characteristics are expected to be constant or to change slowly in the next decades, climate is expected to change rapidly. According to our results, this should induce an increase in background mortality for most of the species, a change that should be considered when forecasting the effects of climate change on the boreal forest. Due to the temporal resolution of our dataset, we could not examine the effects of occasional extreme events on tree mortality. Since the occurrence of these events is expected to increase in the future, further work should be conducted to examine the effects of such events on the background mortality rate of boreal forest tree species.

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Data availability

The data generated or analyzed in this study are not publicly available due to their ownership by the Government of Québec. They can be obtained from the corresponding author upon reasonable request subject to a data sharing agreement.

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