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Can a multistage approach improve individual tree mortality predictions across the complex mixed-species and managed forests of eastern North America?

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ABSTRACT

Tree mortality plays a fundamental role in the dynamics of forest ecosystems, yet it is one of the most difficult phenomena to accurately predict. Various modeling strategies have been developed to improve individual tree mortality predictions. One less explored strategy is the use of a multistage modeling approach. Potential improvements from this approach have remained largely unknown. In this study, we developed a novel multistage approach and compared its performance in individual tree mortality predictions with a more conventional approach using an identical individual tree mortality model formulation. Extensive permanent plot data (n = 9442) covering the Acadian Region of North America and over multiple decades (1965–2014) were used in this study. Our results indicated that the model behavior with the multistage approach better depicted the observed mortality and showed a notable improvement over the conventional approach. The difference between the observed and predicted numbers of dead trees using the multistage approach was much smaller when compared with the conventional approach. In addition, tree survival probabilities predicted by the multistage approach generally were not significantly different from the observations, whereas the conventional approach consistently underestimated mortality across species and overestimated tree survival probabilities over the large range of DBH in the data. The new multistage approach also predictions of zero mortality in individual plots, a result not possible in conventional models. Finally, the new approach was more tolerant of modeling errors because it based estimates on ranked tree mortality rather than error-prone predicted values. Overall, this new multistage approach deserves to be considered and tested in future studies.

1. Introduction

Tree mortality is fundamental to forest dynamics, and as a result there is a long history of modeling efforts aimed at improving accuracy of mortality predictions (Hawkes, 2000; Weiskittel et al., 2011a). At the stand level, mortality generally is evaluated as mean basal area, volume, or number of trees, all of which have important implications for long-term forest projections (Wilson et al., 2019). Accurate stand-level predictions can be achieved with increasing sample sizes (i.e., the number of plots or size of each plot) or length of observational periods. Individual tree mortality, however, is difficult to predict due to its binary and stochastic nature (Weiskittel et al., 2011a). Increasing sample sizes improve accuracy of mean tree mortality predictions but not necessarily mortality probability of individual trees, because the probability of mortality does not always translate into the occurrence of tree death.

While both stand and individual tree-level mortality models can be applied in forest growth and yield projections, accuracy in predicting individual tree deaths are critical to understanding trajectories of forest development (Weiner, 1990). Mortality of specific trees rather than the total stand-level mortality is more indicative of successional changes in mixed forests like those in eastern North America (Franklin et al., 1987). Prediction errors associated with mortality of individual trees divert projections of forest structure and composition over time (due to the compounding nature of modeling errors (Gertner, 1989; Wilson et al., 2019).

Given the prevalence of individual tree mortality predictions in current forest growth models (Weiskittel et al., 2011a), a number of modeling strategies have been developed to improve their accuracy. These strategies include.

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1) selecting influential predictors of tree mortality such as tree size (e.g., diameter at breast height (DBH) and its transformations; Wykoff et al., 1982), one-sided competition (e.g., basal area of trees larger than the subject tree (BAL)) and two-sided competition (e.g., total basal area; Hamilton, 1986; Hann and Wang, 1990), species composition (e.g., the percentage basal area of a species; Eid and Tuhus, 2001), and site condition (e.g., climate site index; Weiskittel et al., 2011b);
2) arranging predictors in suitable functional forms for regression models, e.g., logistic transformation (Monserud, 1976; Hartmann et al., 2007) and Gompit functions (Chen et al., 2017a; Salas-Eljatib and Weiskittel, 2020);
3) utilizing measurements of varying intervals through the annualization technique (Weiskittel et al., 2007; Chen et al., 2017b); and
4) estimating optimal thresholds to translate the 0–1 probability prediction into a dichotomous mortality event (Hein and Weiskittel, 2010; Chen et al., 2018).

A less explored strategy in modeling individual tree mortality is the use of a multistage approach, where models for additional stages (e.g., at stand-level) are developed to adjust tree mortality predictions. For example, in some variants of the widely used Forest Vegetation Simulator (FVS; Dixon, 2002), the total number of trees that die in a stand is predicted in the first stage and distributed among individual trees according to their predicted mortality probabilities in the second stage. Though applied mostly in stand-level models (e.g., Woollons, 1998; Álvarez González et al., 2004; Pothier and Mailly, 2006), strategies similar to Dixon's (2002) have also been proposed for individual tree mortality models by Pretzsch et al. (2006), Pukkala and Miina (2006), and Le Moguédec and Dhôte (2012). Their focus is on disaggregating stand mortality among individual trees to create compatibility between stand- and tree-level mortality predictions (e.g., Qin and Cao, 2006; Hevia et al., 2015; Cao, 2021). In addition, Fridman and Ståhl (2001) developed a three-stage approach to modeling individual tree mortality where the binary response of whether a plot has observed mortality is modeled in the first stage. Then, mortality as a proportion of total basal area of a plot is modeled in the second stage using data from plots with observed mortality. Finally, individual tree mortality probabilities are predicted in the third stage and multiplied by a plot-specific constant so that the sum of these modified probabilities equals to the proportion of basal area mortality predicted in the first two stages.

A multistage approach adds considerable complexity to tree mortality modeling, and errors from various stages are potentially compounded. Existing (e.g., Johnson and Dixon, 1986; Fridman and Ståhl, 2001) have not provided detailed evaluations of whether the multistage approach improves predictions of individual tree mortality (e.g., in terms of accuracy and bias) compared to a more conventional approach (i.e., a single-stage approach), particularly across species in mixed forests. Given the inherent challenges of accurately predicting individual tree mortality (e.g. Hülsmann et al., 2017; Thrippleton et al., 2020, 2021), a comprehensive assessment of complex approaches to mortality modeling is necessary.

In this study, we tested whether adopting a multistage approach can improve individual tree mortality predictions. Identical individual tree mortality models (with the same regression model, predictors, and annualization technique) were applied alone and as a part of a multistage approach, with the only difference being that the tree mortality model was constrained by additional stages in the multistage approach. Performances of these two approaches were evaluated and compared using extensive permanent plot data covering the Acadian Region of the State of Maine in the US and the provinces of New Brunswick, Nova Scotia, and Quebec in Canada. Specific objectives of this study were to: 1) develop a new multistage approach for individual tree mortality modeling; 2) compare the behavior of the multistage approach with a conventional tree mortality model; 3) evaluate whether this approach improves mortality predictions based on data from the Acadian Region; and 4) assess differences in mortality predictions by region, species, DBH, and plot size.

2. Materials and methods

2.1. Study area

The Acadian Forest region resides in the transition zone between the softwood-dominant boreal forests to the north and the broadleaf forests to the south (Braun, 1950; Rowe, 1972). Three Canadian Maritime provinces (New Brunswick, Nova Scotia, and Prince Edward Island) are found in the region, along with southern portions of Québec, and much of the US state of Maine. Across the region, climate estimates indicate an average annual precipitation of 1130 mm with a range of 870 to 1750 mm, with mean growing degree days (sum of temperatures >5 °C) of 1625 d fluctuating between 726 and 2292 d (Rehfeldt, 2006). Glacial till is the principal soil parent material with soil types ranging from well-drained loams and sandy loams on glacial till ridges to poorly and very poorly drained loams on flat areas between low-profile ridges.

The majority of the Acadian Forest is dominated by naturally-regenerated, mixed stands that primarily display mixed-cohort stand structures. Amongst the more than 60 tree species that occur in the region are coniferous evergreen species such as red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* L.), eastern white pine (*Pinus strobus* L.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.) as well as deciduous hardwood species such as red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), paper birch (*Betula papyrifera* Marsh.), and northern red oak (*Quercus rubra* L.). Common forest types are described in Eyre (1980) as well as in Gawler and Cutko (2010), while the general information on prevailing environmental conditions is available in more detail in Bose et al. (2016).

2.2. Data

Data for this study were obtained from a network of permanent sample plots across New Brunswick, Nova Scotia, and Quebec as well as from four sources in Maine including the permanent plots of US Forest Service Forest Inventory and Analysis (FIA; Bechtold and Patterson, 2005), the Penobscot Experimental Forest (PEF; Kimball, 2014), the Ecological Reserve Monitoring of Maine (ERM; Kuehne et al., 2018), and the Commercial Thinning Research Network from the Cooperative Forestry Research Unit of the University of Maine (CTRN; Seymour et al., 2014). The plots spanned the State of Maine and provinces of New Brunswick and Nova Scotia, but were restricted to the southern portion of Quebec. Data from the Canadian provinces were based on single 400 m^2 plots, while FIA plots comprised a cluster of four 168 m^2 sub-plots, and PEF, ERM, and CTRN plots were 810, 168, and 810 m^2 in size, respectively. There were 9442 plots in the data and were established between 1965 and 2014 with measurement intervals ranging from 1 to 15 years. The longest measurement history was 40 years.

The individual tree data used in this study are typical of the type collected on permanent sample plots. Each individual tree was tagged with a plot-unique ID number, and, at minimum, species and DBH were recorded. Minimum threshold diameters and plot sizes varied from each study. Total heights were measured on at least a subset of trees on each plot for each measurement period. Tree status also was recorded for each measurement period (live, dead, and cut), and new trees exceeding the minimum threshold diameter were added to the tree list. This study focused on plots without human-induced disturbances during the measurement periods. Therefore, plot measurements, in which any cutting occurred, were removed from the dataset resulting in a final record of 495,286 trees and 2,954,235 measurements (Table 1).

There were 66 tree species recorded in the dataset. Balsam fir was the most abundant in each region with a total population of 168,947. Red spruce was the second most abundant tree species with a total population

Table 1
Numbers of trees and plots in the data and summaries of tree sizes and plot-level forest characteristics by region.

Attributes	Maine	New Brunswick	Nova Scotia	Quebec	Overall
No. of plots	3417	1398	2288	2339	9442
No. of trees	213,238	108,927	76,209	96,912	495,286
No. of trees of the most abundant species					
Balsam fir	71,366	31,301	29,487	36,793	168,947
Red spruce	26,448	11,568	13,507	2218	53,741
Red maple	25,118	10,183	8888	6508	50,697
Black spruce	3842	19,655	4961	10,910	39,368
Paper birch	12,398	6377	2966	11,989	33,730
Plot-level mean					
Mortality ($m^2 \cdot ha^{-1} \cdot yr^{-1}$)	0.14	0.32	0.17	0.28	0.18
Density ($trees \cdot ha^{-1}$)	3153	1678	770	845	2061
Basal area ($m^2 \cdot ha^{-1}$)	22.90	31.57	17.56	17.40	21.75
% basal area of balsam fir	19.6	19.1	19.9	25.8	20.0
% basal area of shade-intolerant hardwood	10.6	12.8	7.3	22.3	10.5
Quadratic mean DBH (cm)	17.0	16.6	17.1	16.2	17.0
Relative density	0.41	0.64	0.41	0.41	0.44
Climate site index	14.6	11.9	12.9	12.3	13.6
Tree-level mean					
DBH (cm)	13.4	13.5	15.8	15.0	14.3
Height (m)	15.2	16.1	13.0	14.6	14.8

of 53,741 followed by red maple, black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg) and paper birch with varying abundance across the regions (Table 1).

2.3. Individual tree and plot summaries

Plot data were standardized to values on hectare basis by measurement periods (Table 1). The following plot-level summaries were obtained: stem density (trees·ha^{-1}), total basal area (m^2·ha^{-1}), and percent basal area of both balsam fir and shade-intolerant hardwood. In addition, quadratic mean DBH (cm) and relative density were derived. Relative density was expressed as the ratio between observed stand density index (Reineke, 1933) and the theoretical maximum stand density index calculated using the method proposed by Woodall et al. (2005). Finally, a climate-based site index was estimated for each plot based on mean temperature of the warmest month, temperature difference between the warmest and coldest month, and the ratio of precipitation during the growing season to total annual precipitation (Weiskittel et al., 2011b).

In addition to the stand-level summaries described above, several variables for individual tree competition were calculated or estimated for each individual tree. Preliminary screening of variables indicated that basal area per ha of trees with DBHs greater than the subject tree was the best measure of the local competition.

2.4. A new multistage approach to tree mortality modeling

The new multistage approach has three stages in model development: 1) the annual probability that a plot will experience mortality (p) is modeled based on all available plot observations; 2) per ha basal area mortality (m; m^2·ha^{-1}·yr^{-1}) is modeled using data only from plots with observed mortality; and 3) annual tree survival probabilities (s) are predicted for each tree within a plot.

The procedure to apply the multistage approach uses four steps: 1) the second stage model, though developed using data only from plots with observed mortality, is applied to predict m in all plots; 2) p from the first stage model is multiplied by an indicator variable I such that $I = 0$ if $p < v$ or $I = 1$ otherwise, where v is a threshold constant to be estimated (a universal v is used in this study, but v may take specific values for different regions and/or forest types); 3) m is multiplied by $p \times I$; and 4) trees are ranked by s predicted by the third stage model from low to high in each plot, and trees with the lowest predicted survival probabilities are sequentially “killed” until basal area mortality predicted in the first two stages is achieved. The four steps are iterated to determine the value of v that minimizes root mean squared error (RMSE) of mortality predictions across all plots by the multistage approach. While modifying plot mortality predictions by taking into consideration plot mortality probabilities has been proposed (e.g., Woollons, 1998; Álvarez González et al., 2004), the addition of an indicator variable to reduce potential noises in stand-level mortality probability predictions has not been evaluated before to our knowledge. Predictions of plot mortality probabilities are always nonzero whether or not mortality occurs in a given plot. The threshold value, v, and the resulting indicator value, I, provide for zero plot-level mortality predictions. Finally, the fourth step is a new mortality disaggregation technique different from existing ones (e.g., Ritchie and Hann, 1997; Qin and Cao, 2006; Hevia et al., 2015; Cao, 2021).

Measurement intervals varied across data sources in this study, so annualization techniques were needed. The recursive annualization technique proposed by Cao (2000) and Weiskittel et al. (2007) in the form of Eq. (1) was used for plot mortality predictions in the first two stages:

$$x_j = x_i + \sum_{t=i}^{j-1} f(x_t, w) \tag{1}$$

where x_j is the value of the variable of interest (e.g., DBH, height, or observed mortality) at the end (year j) of the measurement cycle; x_i is the corresponding value at the beginning (year i) of the cycle (which is zero for mortality); and $f(x_t, w)$ is the predictive model, which utilizes x along with some other variables w as predictors. This technique recently has shown successes in predicting tree diameter and height increments in the same region included this study (Kuehne et al., 2022). Tree survival probabilities were annualized using the compound interest formula (Monserud, 1976) in the third stage because attributes of dead trees were not recorded and hence cannot be interpolated for the recursive annualization technique. Since the data were also collected from a number of jurisdictions using different plot sizes and measurement protocols, plots were grouped into regions of Maine, New Brunswick, Nova Scotia, and Quebec. Random effects were tested on selected parameters across the regions in each stage to account for unspecified regional variations. Random effects on survival of various tree species were also included in the third stage.

While logistic regression is the usual choice for tree mortality modeling, there are debates over whether it is the optimal method (Weiskittel et al., 2011a). Comparisons provided in Salas-Eljatib and Weiskittel (2020) suggest that Gompit regression outperforms logistic regression in many aspects, while Chen et al. (2017a) found that the asymmetric Gompit model probably is more suitable to account for the relatively rare event of tree mortality. Consequently, both logistic and Gompit models using identical linear functions of predictors were developed and tested in the first and third stages, while the models with lower RMSE were applied in the multistage approach.

Based on prior model development and assessment, the following logistic and Gompit models were used to predict annual plot mortality probability p in the first stage:

$$p = \frac{1}{1 + e^{f(x)}} \tag{2}$$

$$p = 1 - e^{-e^{f(x)}} \tag{3}$$

where $f(x) = p_0 + p_1\mathrm{ba} + p_2\mathrm{CSI} + p_3\mathrm{qDBH} + p_4\mathrm{baBF} + p_5\mathrm{baIH}$; ba is basal area of a plot (m^2·ha^{-1}); CSI is climate site index (Weiskittel et al., 2011b); qDBH is quadratic mean DBH (cm); baBF and baIH are percent basal area of balsam fir and shade-intolerant hardwood in a plot, respectively; and p_0 to p_5 are parameters. Random effects across the regions were included on p_0. Preliminary results showed that the fixed effect for p_0 was not significantly ($p > 0.05$) different from zero so it was not included in the final model.

Annual per ha basal area mortality (m, $\mathrm{m^2 \cdot ha^{-1} \cdot yr^{-1}}$) was predicted using data from plots with observed mortality in stage two. Cumulative basal area mortality $\sum m$ shows sigmoidal patterns over time t, and was predicted using a three-parameter logistic model with the following form:

$$\sum m = \frac{\mathrm{ba}_0 k}{\mathrm{ba}_0 + (k - \mathrm{ba}_0)e^{-rt}} \tag{4}$$

where ba_0 is initial basal area of a plot ($\mathrm{m^2 \cdot ha^{-1}}$); and k and r are parameters to be estimated representing the asymptotic and rate constants of mortality, respectively. Differentiating $\sum m$ with respect to t provides annual basal area mortality in the following form:

$$\frac{d\sum m}{dt} = r\left(1 - \frac{\sum m}{k}\right)\sum m \tag{5}$$

where $k = q_0 + q_1\mathrm{CSI} + q_2\mathrm{baBF} + q_3\mathrm{baIH}$ and $r = q_4 + q_5\mathrm{qDBH}$; q_0 to q_5 are parameters. Random effects across regions were tested on q_0 and q_4. Preliminary results showed that the fixed effect for q_4 was not significantly ($p > 0.05$) different from zero so it was not included in the final model.

The logistic model (Eq. (2)) and Gompit model (Eq. (3)) were used to predict annual tree survival probability s in the third stage using individual tree predictors $g(x) = b_0 + b_1\mathrm{DBH} + b_2\mathrm{DBH}^2 + b_3\mathrm{BAL} + b_4\mathrm{qDBH} + b_5\mathrm{CSI}$, where b_0 to b_5 are parameters. Random effects across tree species were included on b_0 and b_1, while those across regions on b_0.

2.5. Comparisons with a conventional tree mortality model

Single-stage and multistage approaches were compared using the same individual tree mortality models to control potential prediction biases resulting from applying different regression models and predictors between the two approaches. The third stage logistic (or Gompit) model (Eqs. (2) and (3)) from the multistage approach is the stand-alone individual tree mortality model in the single-stage approach. The multistage approach uses models from all three stages described above (Section 2.4). The comparisons were based on three statistics: 1) accuracy in classifying live/dead trees, 2) true positive rate (the number of observed dead trees predicted as dead/the number of observed dead trees; sensitivity), true negative rate (the number of observed live trees predicted as live/the number of observed live trees; specificity), receiver operating characteristic (ROC) curves, and areas under curves (AUC) in classifying dead trees, and 3) RMSE in annual plot basal area mortality predictions. These comparisons were made across regions and plot sizes using the same models (i.e., subset model output by region and plot size). Numbers of dead trees by species and 95% confidence intervals of mean annual survival probabilities by 0.5-cm DBH classes from observations and predictions by the two modeling approaches were compared. Statistics for each stage of the multistage approach were presented along with the above overall statistics to show potential effects of compounding error.

All analyses were conducted in R v3.6.3 (R Core Team, 2020). R packages “nlme” (Pinheiro et al., 2022) and “lme4” (Bates et al., 2015) were used to fit nonlinear mixed effects models.

3. Results

Cumulative tree mortality rates over the course of the study period varied from 7.5% in Maine to 20.4% in Quebec and averaged at 10.1% across the four regions. Percentages of plots with observed mortality exhibited a similar pattern with the lowest in Maine at 40.6% and the highest in Quebec at 82.8%. Observed mean annual basal area mortality was 0.18 $\mathrm{m^2\ ha^{-1} \cdot yr^{-1}}$ across all regions, ranging from 0.14 in Maine to 0.32 $\mathrm{m^2\ ha^{-1} \cdot yr^{-1}}$ in New Brunswick (Table 2). Balsam fir, red spruce, red maple, paper birch, and black spruce had the highest observed mortality of 60,679, 11,183, 11,115, 10,097, and 9160 trees, respectively (Fig. 1), and accounted for 35.9%, 20.8%, 21.9%, 29.9%, and 23.3% of trees within each species, respectively. Trees in the 46.0–46.5 cm DBH class had the highest annual survival probability of 99.3% (i.e., an annual mortality probability of 0.7%; Fig. 2).

RMSEs of the logistic (Eq. (2)) and Gompit (Eq. (3)) models were 0.4493 and 0.4497 in the first stage, and 0.2906 and 0.2909 in the third stage. All parameter estimates for both models were significantly different from zero ($p < 0.05$, Tables 3 and 4). The ROC curves of these models largely overlapped (Figs. 3 and 4). The logistic models (Eq. (2)) were selected in the multistage approach and reported in detail below. The optimized threshold value v for classifying plots with and without mortality in the first stage using the logistic model was estimated to be 0.72.

3.1. Stage-specific performance in the multistage approach

All parameter estimates in each stage from the multistage approach were significantly different from zero ($p < 0.05$, Tables 3–5). Summary statistics of the three stages are presented in Table 6. Accuracies in classifying plots with and without mortality in the first stage were between 63.6% and 83.0% across the regions when the classification cutpoint was 0.57 (stage-specific and not optimized for the whole approach), maximizing the differences between true and false positive rates. Accuracies were higher in regions where mortality occurred more frequently (Tables 2 and 6). However, higher accuracies were generally associated with higher true positive rates (28.4%–99.9% across the regions). Few plots without observed mortality were largely misclassified as having mortality (Tables 2 and 6).

RMSEs of plot basal area mortality predicted in the second stage were between 0.29 and 0.48 $\mathrm{m^2\ ha^{-1} \cdot yr^{-1}}$ across the regions (Table 6). Overall RMSE was 2.2 times of the mean observed mortality (note that the latter was calculated including plots without observed mortality, while the former is from a model fitted only using plots with observed mortality), and there was no clear relationship between the RMSEs and observed mortalities within each region (Tables 2 and 6). Accuracies in classifying live/dead trees in the third stage ranged from 79.7% to 92.6% and were higher in regions with lower observed tree mortality rates. Between 27.9% and 50.9% of dead trees were correctly classified by the third stage model across regions (Tables 2 and 6).

3.2. Comparisons of performances of single-versus multistage approaches in mortality prediction

With the multistage approach, individual trees were correctly classified as live or dead 72.7%–88.4% of the times; however, only 8.5%–17.8% of dead trees were correctly identified across regions (i.e., high true negative rates with low true positive rates; Table 2). These results were lower than those obtained directly from the third stage model (Table 6). RMSEs in plot basal area mortality predictions were greater by 0.37 to 0.54 $\mathrm{m^2\ ha^{-1} \cdot yr^{-1}}$ than those in the second stage model, which were already greater than the mean observed values (Tables 2 and 6). Accuracies of the single-stage approach in classifying live or dead trees ranged from 77.3% to 92.2%; however, similar to the multistage approach, only 2.4%–28.7% dead trees were correctly identified across regions based on a classification cut-point of 0.67 that minimize RMSEs for plot-level basal area mortality predictions. RMSEs ranged from 0.39 to 0.58 $\mathrm{m^2\ ha^{-1} \cdot yr^{-1}}$ across regions and were similar to those observed in the multistage approach (Table 2).

The multistage approach overestimated mortality for several most abundant species (including all spruce species) and underestimated for

Table 2
Summary statistics for observed mortality and comparisons of evaluation statistics for the single-stage and multistage approaches by region, where true positive rate is defined as the number of observed dead trees predicted as dead/the number of observed dead trees, and true negative rate is defined as the number of observed live trees predicted as live/the number of observed live trees.

Item	Statistics	Region				
		Maine	New Brunswick	Nova Scotia	Quebec	Overall
Observed mortality	% plot observations	40.8	78.2	67.1	82.8	56.2
	% tree observations	7.5	8.0	12.6	20.4	10.1
	RMSE ($m^2 \cdot ha^{-1} \cdot yr^{-1}$)	0.14	0.32	0.17	0.28	0.18
Multistage approach	Tree-level accuracy (%)	88.4	83.2	82.4	72.7	84.3
	Tree-level true positive rate (%)	12.0	17.8	8.5	16.9	12.5
	Tree-level true negative rate (%)	94.6	88.9	93.1	87.0	92.4
	RMSE ($m^2 \cdot ha^{-1} \cdot yr^{-1}$)	0.48	0.54	0.37	0.45	0.45
Single-stage approach	Tree-level accuracy (%)	92.2	91.7	86.0	77.3	89.2
	Tree-level true positive rate (%)	17.1	2.4	8.0	28.7	12.8
	Tree-level true negative rate (%)	98.4	99.5	97.3	89.8	97.8
	RMSE ($m^2 \cdot ha^{-1} \cdot yr^{-1}$)	0.42	0.58	0.39	0.44	0.43

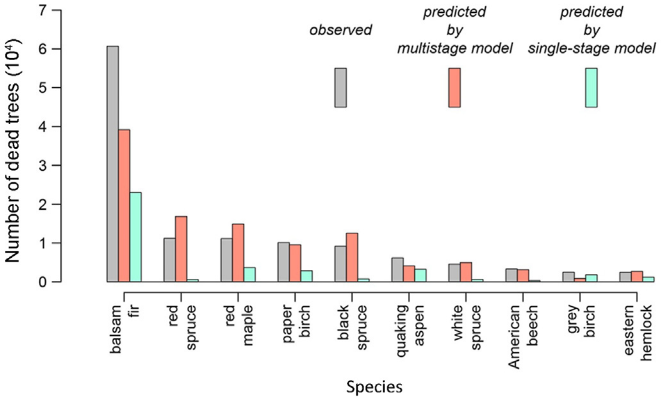

Fig. 1. Numbers of dead trees observed and predicted by the single-stage and multistage approaches of species that have the highest numbers of observed mortality.

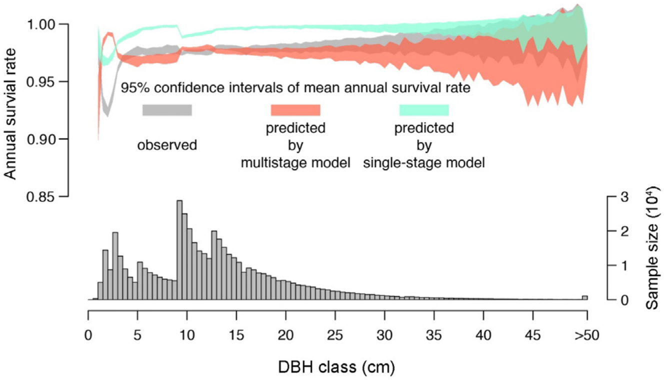

Fig. 2. Ninety-five percent confidence intervals of mean annual survival probabilities of trees and their associated sample sizes by 0.5-cm DBH classes from observations and predicted by the two modeling approaches.

the others, while the single-stage approach underestimated mortality for all species (Fig. 1). For most species, both overestimates and underestimates from the multistage approach generally occurred at smaller scales than those from the single-stage approach, except for grey birch (*Betula populifolia* Marshall; Fig. 1). The total number of dead trees observed in the data was 138,206, and the predicted numbers were 132,820 using the multistage approach and 44,638 using the single-stage approach. Annual tree survival probabilities were generally underestimated with the multistage approach and overestimated with the

Table 3
Parameter estimates, standard errors, and *p*-values of the logistic and Gompit models for annual plot mortality probabilities in the first stage of the multistage approach.

Predictor	Logistic model		Gompit model	
	Parameter Estimate	Standard error	Parameter estimate	Standard error
Fixed effect				
p_1: Basal area ($m^2 \cdot ha^{-1}$)	–0.054	<0.001	0.036	<0.001
p_2: Climate site index	–0.047	0.004	0.031	0.002
p_3: Quadratic mean DBH (cm)	0.065	0.001	–0.044	<0.001
p_4: % basal area of balsam fir	0.230	0.027	–0.115	0.018
p_5: % basal area of intolerant hardwood	–0.811	0.037	0.474	0.024
Random effect				
p_0: intercept				
Maine	1.441		–1.352	
New Brunswick	–0.135		–0.331	
Nova Scotia	–0.170		–0.225	
Quebec	–0.839		0.151	

Table 4
Parameter estimates, standard errors, and *p*-values of the logistic and Gompit models for annual tree survival probabilities in the third stage of the multistage approach. The first number in the parentheses is random effect from the logistic model, and the second number is from the Gompit model.

Predictor	Logistic model		Gompit model	
	Parameter estimate	Standard Error	Parameter estimate	Standard error
Fixed effect				
p_0: intercept	–3.4250	0.0141	1.2171	0.0037
p_1: DBH (cm)	–0.1358	0.0008	0.0417	0.0002
p_2: DBH^2 (cm^2)	0.0035	<0.0001	–0.0008	<0.0001
p_4: Basal area of trees larger than the subject tree ($m^2 \cdot ha^{-1}$)	0.0400	0.0002	–0.0092	<0.0001
p_5: Quadratic mean DBH (cm)	–0.0530	0.0005	0.0118	0.0001
p_6: Climate site index	0.0319	0.0008	–0.0071	0.0002
Random effect				
p_0: intercept				
Maine	–0.2134		0.0080	
New Brunswick	–0.6260		0.1018	
Nova Scotia	0.0845		–0.0550	
Quebec	0.5464		–0.1702	
p_0: intercept				
See Supplemental materials Table S1				
p_1: DBH (cm)				
See Supplemental materials Table S1				

Table 5
Parameter estimates, standard errors, and *p*-values of the second stage annual plot basal area mortality (m^2·ha^{-1}·yr^{-1}) model.

Predictor	Parameter estimate	Standard error
Fixed effect		
p_0: intercept	84.2843	12.9514
p_1: Climate site index	–1.1754	0.2436
p_2: % basal area of balsam fir	83.4725	6.8540
p_3: % basal area of intolerant hardwood	13.3258	3.2133
p_5: Quadratic mean DBH (cm)	0.0005	<0.0001
Random effect		
p_0: intercept		
Maine	44.8462	
New Brunswick	–8.2982	
Nova Scotia	–17.6687	
Quebec	–11.9457	
p_4: intercept		
Maine	0.0009	
New Brunswick	0.0012	
Nova Scotia	–0.0018	
Quebec	0.0028	

single-stage approach. Predictions from the multistage approach generally were not significantly different from observations across the DBH classes (Fig. 2). RMSEs in plot basal area mortality predictions decreased with increasing plot size in both approaches, whereas inverse patterns were found in true positive rates of tree mortality (Table 7).

Quebec was predicted to have the highest plot mortality probabilities and annual basal area mortalities as well as the lowest tree survival probabilities compared to the other regions, consistent with the observations (Tables 3–5). Tree survival probabilities varied by species as estimated by random effects (Table S1). Among the most abundant species, red maple and eastern hemlock had the highest predicted survival probabilities, while balsam fir and grey birch had the lowest predicted survival probabilities (Table 8).

4. Discussion

The single-stage and multistage approaches had similar RMSEs and true positive rates in mortality predictions. The overall differences were 0.02 m^2 ha^{-1}·yr^{-1} in basal area mortality and 0.3% in tree mortality, respectively (Table 2). However, the patterns in both predicted tree survival probabilities and distributions of mortality across species were distinct between the two approaches (Figs. 1 and 2). The accuracy of individual tree mortality predictions was 4.9% higher in the single-stage approach than in the multistage approach (Table 2). Given the similar low true positive rates, a higher accuracy indicates that more trees, including more dead trees, were classified as live in the single-stage approach. The underlying causes were tree mortality being relatively rare and thresholds for DBH measurements were relatively large in the data. The model optimization process lowered mortality predictions to reduce errors from the majority of zero-mortality observations. This resulted in consistent underestimation of tree mortality across species as shown in Fig. 1 and general overestimation of individual tree survival probabilities across the range of DBH classes (Fig. 2).

Consequently, the model behavior in the multistage approach better depicted observed mortality and showed a notable improvement over the single-stage approach despite slightly inferior fit statistics. For example,

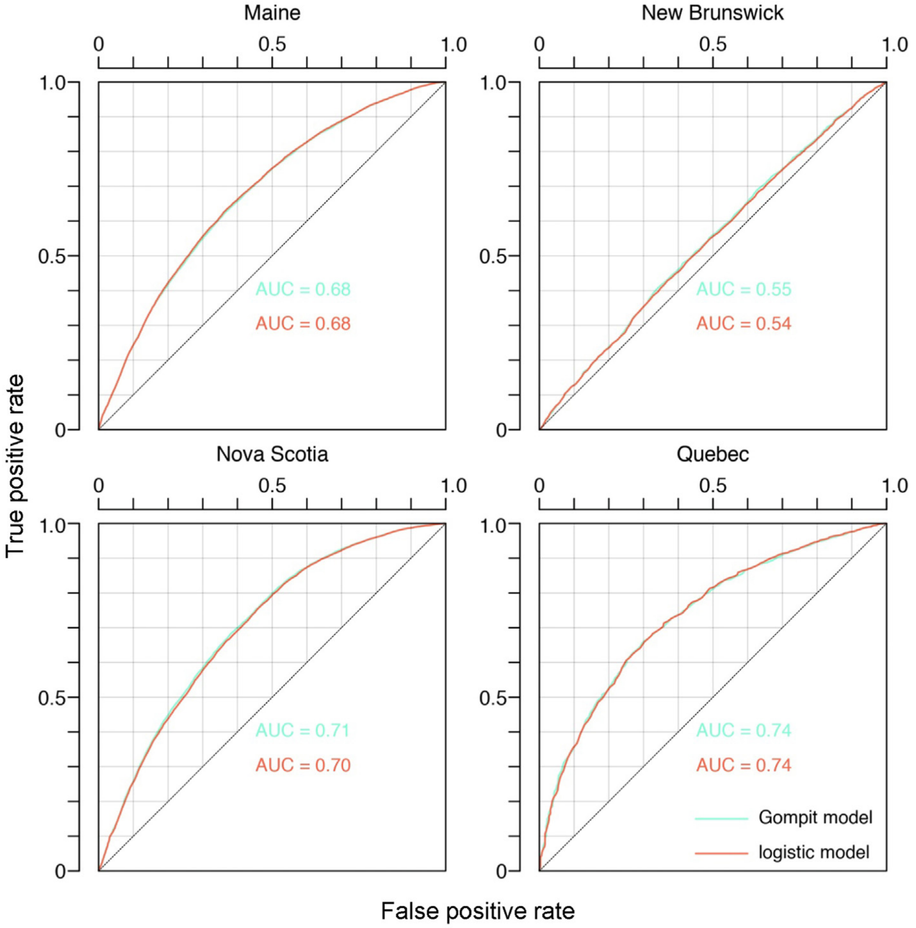

Fig. 3. Receiver operating characteristic (ROC) curves and areas under curves (AUC) of predicted annual plot mortality probabilities using logistic (Eq. (2)) and Gompit (Eq. (3)) models by region.

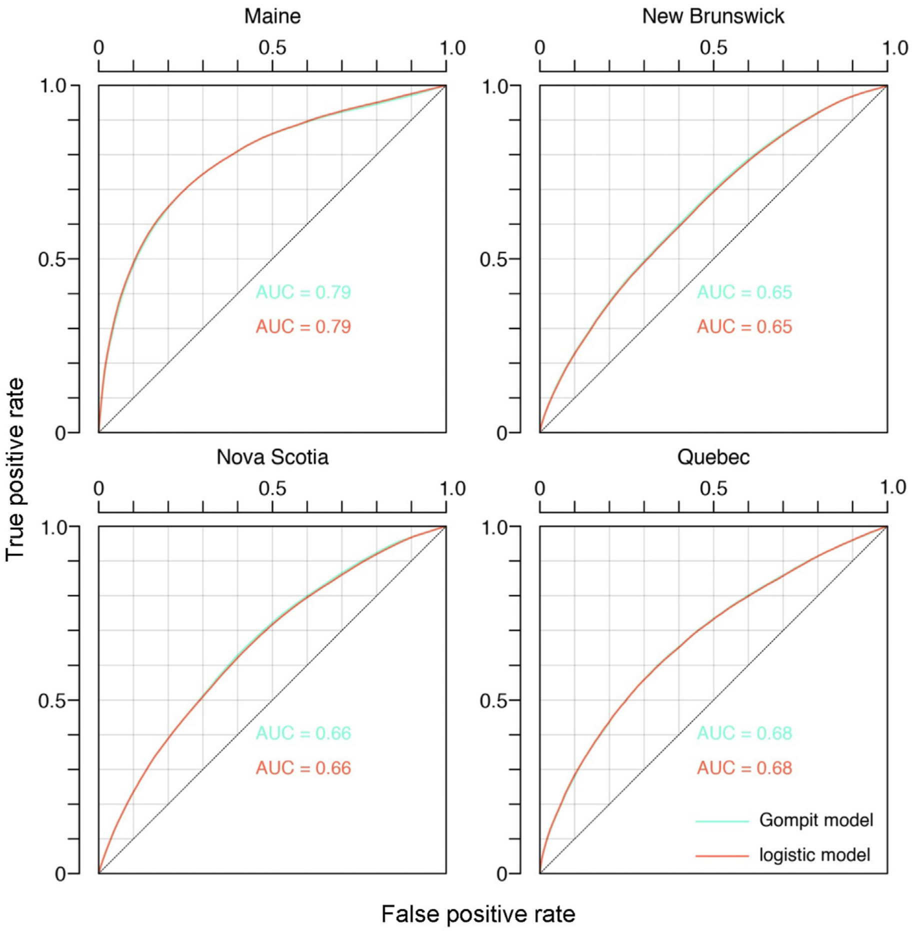

Fig. 4. Receiver operating characteristic (ROC) curves and areas under curves (AUC) of predicted annual individual-tree survival probabilities using logistic (Eq. (2)) and Gompit (Eq. (3)) models by region.

Table 6
Evaluation statistics of each stage in the multistage approach developed in this study by region.

Region	Stage 1			Stage 2	Stage 3		
	Accuracy (%)	True positive rate (%)	True negative rate (%)	RMSE ($m^2 \cdot ha^{-1} \cdot yr^{-1}$)	Accuracy (%)	True positive rate (%)	True negative rate (%)
Overall	69.1	69.4	31.2	0.40	88.9	45.2	93.9
Maine	63.6	28.4	12.2	0.46	92.6	50.9	96.0
New Brunswick	78.0	99.4	98.8	0.48	88.5	27.9	93.8
Nova Scotia	71.9	88.3	61.6	0.29	86.6	46.9	92.3
Quebec	83.0	99.9	98.6	0.34	79.7	50.4	87.3

the difference between the numbers of observed and predicted dead trees from the multistage approach was 5,386, compared to 93,568 from the single-stage approach. In addition, tree survival probabilities predicted by the multistage approach generally were not significantly different from observations across the range of DBH (Fig. 2). Nevertheless, the multistage approach slightly overestimated mortality as a result of the sequential "killing" of trees with lower predicted survival probabilities.

The multistage approach developed in this study was an improvement over the Forest Vegetation Simulator (FVS) approach (Johnson and Dixon, 1986; Dixon, 2002), which predicted stand mortality in one stage before distributing it among trees. Tree mortality does not occur frequently and may not be observed for years in any given plot (Eid and Tuhus, 2001). While mortality is an intrinsic part of forest development, nil observations of mortality from small sample plots and/or short durations of observations are sampling errors that will be passed on to mortality predictions (Curtis and Marshall, 2005). Consequently, basal area mortality will be underestimated if all plots, including those without mortality observations, are used in model development. Likewise, using only plots where mortality occurred would overestimate mortality since plot mortality probabilities are ≤ 1 but inflated to one when zero mortality plots are censured. The multistage approach takes plot mortality probabilities (predicted by the first stage model) into consideration and uses them to adjust plot basal area mortality predictions from the second stage. This strategy is similar to that of Woollons (1998) and Álvarez González et al. (2004).

The multistage approach used here advances one step further from the above strategy of using plot mortality probabilities to adjust plot basal area mortality. A limitation of stand-level mortality models is that there is always some level of mortality predicted, even if no mortality occurred (Weiskittel et al., 2011a). This also is the case for the second stage plot mortality model in the multistage approach used here. Solely multiplying mortality predictions by predicted plot mortality probabilities cannot overcome this limitation because predicted probabilities also are nonzero. The introduction of an indicator variable and an optimized

Table 7
Statistics of observed mortality and comparisons of statistics of the two modeling approaches by plot size, where true positive rate is defined as the number of observed dead trees predicted as dead/the number of observed dead trees, and true negative rate is defined as the number of observed live trees predicted as live/the number of observed live trees.

Item	Statistics	Plot size (m^2)			
		128	400	810	Overall
Observed mortality	% plot observations	42.3	71.4	32.7	56.2
	% tree observations	8.8	11.8	6.8	10.1
	RMSE ($m^2 \cdot ha^{-1} \cdot yr^{-1}$)	0.16	0.21	0.04	0.18
Multistage approach	Tree-level accuracy (%)	82.6	81.5	92.0	84.3
	Tree-level true positive rate (%)	21.8	12.7	4.0	12.5
	Tree-level true negative rate (%)	98.3	90.8	88.5	92.4
	RMSE ($m^2 \cdot ha^{-1} \cdot yr^{-1}$)	0.51	0.42	0.23	0.45
Single-stage approach	Tree-level accuracy (%)	90.7	87.1	93.2	89.2
	Tree-level true positive rate (%)	7.0	11.0	25.2	12.8
	Tree-level true negative rate (%)	98.1	97.3	98.8	97.8
	RMSE ($m^2 \cdot ha^{-1} \cdot yr^{-1}$)	0.45	0.44	0.14	0.43

threshold in the first stage of the multistage approach extends the range of predicted probabilities to zero. Consequently, plot mortality predictions of zero can be achieved, and this reduces the number of false positive plot mortality predictions.

The most notable difference between the multistage approach and the approach of Fridman and Ståhl (2001) as well as other various mortality disaggregation techniques (e.g., Ritchie and Hann, 1997; Qin and Cao, 2006; Hevia et al., 2015; Cao, 2021) is in how predicted plot mortality is distributed among trees in a plot. Fridman and Ståhl (2001) distribute plot mortality across trees proportional to their predicted mortality probabilities similar to the strategy used in FVS (Dixon, 2002). Many mortality disaggregation techniques rely on this strategy and various equations were developed to build quantitative relationships between predicted mortality probabilities of individual trees and total plot mortality. In these applications, a portion of a tree is "killed" by modifying the tree's expansion factor (i.e., the ratio in a ratio estimator in sampling; Thompson, 2012). As a result, stand composition remains somewhat stable, and successional changes are not effectively articulated.

An obvious limitation of the disaggregation technique is that errors in the nonzero tree mortality probability predictions are generally ignored. In reality, a large portion of the nonzero predictions actually are zero since tree mortality is not frequent. In the multistage approach, trees are ranked by their predicted survival probabilities, and those with the lowest survival probabilities are sequentially "killed" until predicted plot mortality in the first two stages is achieved. Consequently, the multistage approach is more tolerant of errors in mortality probability predictions because only trees with the highest mortality probabilities are "killed" regardless of specific predicted values and their associated errors. This is the case provided these errors are commensurate with predicted values and do not change tree ranks in survival. Overall, our multistage approach may better represent the binary nature of tree mortality and be in agreement with the stochastic occurrences of mortality across species (Fig. 1).

Predicted tree survival probabilities from the third stage were a peak function of DBH, in agreement with general ecological expectations (Monserud and Sterba, 1999; Coomes and Allen, 2007; Weiskittel et al., 2011a). Climate site index was positively related to mortality probabilities at both stand- and tree-levels, while increased basal area of trees larger than the subject tree (BAL) lowers tree survival probabilities. In addition, tree survival probabilities increased with quadratic mean DBH likely because most DBH observations were <50 cm in the data (Tables 3–5). Regional variations in mortality were related to differences in forest management as well as large-scale disturbance events like past spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks (e.g., Chen et al., 2017a, b). For hardwood species, variation may also be related to species-specific differences in stem form and risk (e.g., Castle et al., 2017) and susceptibility to internal decay (Frank et al., 2018). Finally, caution is needed in comparing non-annual statistics across regions because they are affected by various measurement intervals and plot sizes across data sources.

Some important limitations persistent in single-stage tree mortality modeling are also found in the multistage approach. First, there is no easy way to determine the exact year of tree mortality in plots of multiyear measurement intervals (Salas-Eljatib and Weiskittel, 2020). Tree mortality generally is assumed to have occurred at the end of a multiyear measurement period, which is not always true. Annual tree mortality probability will likely be underestimated in these plots with the application of annualization techniques. Greater underestimation comes with longer measurement intervals since observed mortalities are more deeply discounted. The longest measurement interval was 15 years in the data used in this study. Second, the data do not cover life spans of most trees despite a measurement history up to 40 years (most tree life spans range from 60 to 500 years in the region; Burns and Honkala, 1990). The observed mortality is certainly right-censored. There were only 1066 trees having >50 cm initial DBH with 495,286 trees in the data and hence large trees were scarce in the region. It is unlikely that including additional data would increase the numbers of large trees, and hence improve accuracies of large tree mortality predictions. Records of champion trees (American Forests, 2020) were initially considered to constrain survivals of large trees in this study given their successful use in other studies (e.g. Bragg, 2008). This strategy made practically no difference in survival predictions because only 15 trees reached the DBH of champion trees, and height measurements were not available in many tree records. Besides, champion trees likely grow in the open, and are not comparable to trees in forest stands.

Finally, much effort has been put into identifying core drivers and influential predictors of tree mortality (Poorter et al., 2008; Weiskittel

Table 8
Predicted percent annual survival probabilities of the most abundant species by DBH and region using the multistage approach developed in this study.

Species	Maine				New Brunswick				Nova Scotia				Quebec			
	Annual survival prob. at DBH (cm) of				Annual survival prob. at DBH (cm) of				Annual survival prob. at DBH (cm) of				Annual survival prob. at DBH (cm) of			
	10	20	30	40	10	20	30	40	10	20	30	40	10	20	30	40
Balsam fir	98.7	98.0	93.9	70.5	99.0	98.5	95.4	76.2	98.7	98.0	93.8	70.2	97.9	96.8	90.4	59.3
Red spruce	99.5	99.7	99.6	99.0	99.6	99.8	99.7	99.3	99.4	99.7	99.6	99.0	99.1	99.5	99.3	98.4
Red maple	99.5	99.9	100.0	100.0	99.6	99.9	100.0	100.0	99.5	99.9	100.0	100.0	99.2	99.9	100.0	100.0
Paper birch	99.1	99.5	99.4	98.5	99.3	99.6	99.5	98.8	99.1	99.5	99.4	98.4	98.6	99.1	99.0	97.5
Black spruce	99.3	99.0	97.2	85.8	99.5	99.3	97.9	89.0	99.3	99.0	97.2	85.7	98.9	98.4	95.5	78.7
Quaking aspen	98.3	99.0	98.8	97.3	98.7	99.2	99.1	98.0	98.3	99.0	98.8	97.3	97.2	98.4	98.1	95.6
White spruce	99.1	99.3	99.0	96.9	99.3	99.5	99.2	97.7	99.1	99.3	99.0	96.9	98.6	98.9	98.3	95.0
American beech	99.1	99.3	99.0	96.8	99.3	99.5	99.2	97.6	99.1	99.3	98.9	96.8	98.6	98.9	98.3	94.8
Grey birch	97.5	96.3	89.7	58.7	98.1	97.2	92.1	65.6	97.5	96.3	89.6	58.4	96.0	94.1	84.1	46.4
Eastern hemlock	99.8	100.0	100.0	100.0	99.8	100.0	100.0	100.0	99.8	100.0	100.0	100.0	99.6	100.0	100.0	100.0

et al., 2011a), but successes seem to be largely dependent on specific aspects of each study and availability of specific data. For example, costs associated with measuring tree heights and spatial locations have limited their applications in tree mortality modeling. Height and crown ratio were measured for a subset of the trees, while spatial locations were not available at all in the data. None of these factors were applied in the models developed in this study. Such limitations in the data may affect model performances, but comparisons between the single-stage and multistage approaches are still valid since identical tree mortality models were used in both approaches. In addition, prior analyses found no substantial differences in predicting individual tree mortality using contrasting distance-independent and -dependent competition metrics (Kuehne et al., 2019). This suggests the continual need to better develop and identify measures that simultaneously reflect both tree vigor and competitive status.

This study evaluated the performance of a new multistage approach on tree mortality predictions and demonstrated some improvements compared to a conventional tree mortality model. The evaluation was believed to have a significant level of general validity based on the sample size and spatio-temporal scale of the data. Modifying tree mortality predictions with constraints such as multistage equations has opened up the utilization of information of various sources and scales. It is a strategy that requires further refinement, and there are other techniques in this direction that are worth exploring. One is the use of piecewise functions to predict mortality of trees in various ranges of DBH. It is similar to the practice of predicting DBH increments separately for large and small trees (Crookston and Dixon, 2005), and some studies have found that such discontinuous methods provided better long-term projections (Weiskittel et al., 2016). Another technique is relating tree mortality to growth (Hartmann et al., 2007), which, however, has been considered challenging (Wunder et al., 2008) because of data availability and robustness of implementation. Regardless, due to its importance, continued exploration of alternative approaches for modeling tree mortality across contrasting species and broad regions is critical.

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Authors' contributions

Cen Chen: Methodology, Software, Validation, Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing, Visualization. John Kershaw Jr.: Conceptualization, Methodology, Investigation, Resources, Data Curation, Writing - Original Draft, Writing - Review & Editing, Supervision, Project administration, Funding acquisition. Aaron Weiskittel: Methodology, Investigation, Resources, Data Curation, Writing - Review & Editing, Supervision, Project administration, Funding acquisition. Elizabeth McGarrigle: Conceptualization, Methodology, Investigation, Writing - Original Draft.

Data availability

Data are available upon request sent to cen.chen@maine.edu.

Declaration of competing interest

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Appendix A. Supplementary data

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