Forest Ecology and Management 475 (2020) 118369

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

On studying the patterns of individual-based tree mortality in natural forests: A modelling analysis

Christian Salas-Eljatib[a,b,*], Aaron R. Weiskittel[c]

[a] Centro de Modelación y Monitoreo de Ecosistemas, Facultad de Ciencias, Escuela de Ingeniería Forestal, Universidad Mayor, Santiago, Chile
[b] Laboratorio de Biometría, Vicerrectoría de Investigación y Postgrado, Universidad de La Frontera, Temuco, Chile
[c] Center for Research on Sustainable Forests, University of Maine, Orono, ME 04469-5755, USA

ARTICLE INFO

Keywords:
Competition
Survival
Forest dynamics
Logistic regression
Nothofagus
Temperate forest
Gompit
Logit
Multi-level, mixed-effects model

ABSTRACT

Tree mortality is a critical ecological phenomenon shaping forest ecosystem dynamics, structure, and composition, while its effects are of global relevance due to its relationship with forest conditions and environmental changes. There are several challenges associated with individual-based mortality data, particularly observations with uneven measurement intervals. Here, we develop and examine several common individual-based mortality modelling strategies that simultaneously account for unequal measurement lengths and the hierarchical structure of the data in long-term, permanent plot data from the mixed *Nothofagus* forests in south-central Chile. These strategies depend on: (a) the functional model form (logit and Gompit), (b) the period length adjustment method (annualized, covariate, and exposure), and (c) the data structure used (traditional or all multiple combinations of the time series). Our findings indicated that the Gompit functional form outperformed the commonly used logit link function. Furthermore, considering the period length as exposure in a generalized linear mixed-effects model offered better goodness-of-fit than the other examined period length adjustments. Using all the possible combinations of the dynamic data did not improve the prediction capabilities of the model variants, but important differences were found in the statistical inferences of the fitted models. Our results highlighted that understanding tree mortality strongly relies on using a suitable modelling strategy that is capable of both capturing and assigning the sources of variation to the corresponding variables, which was best accomplished using a multi-level, binary, and Gompit-exposure modelling framework in this analysis.

1. Introduction

Individual-based, tree-level mortality has been traditionally classified as either density-dependent or density-independent (Dennis and Taper, 1994; Dennis et al., 2006), which have also been termed as regular and irregular, respectively (Weiskittel et al., 2011). The former is related to the general tree growing conditions within a specific forest, while the latter is more related to stochastic natural disturbances or site factors. Potentially, a new class of mortality should be included and would better reflect the intra- and inter-annual environmental factors that influence mortality (e.g., drought-driven mortality). Regardless, understanding and predicting tree mortality is critical in both basic and applied ecology (Franklin et al., 1987), as well as its long-term influence on forest composition, structure, and sustainability, which becomes even more relevant at the global scale given changing environmental conditions.

Mortality of individuals is highly uncertain and difficult to model. Among the forest dynamics phenomenon typically modelled, tree-level mortality predictions are the most complicated and least accurate, while generally having the largest effects on long-term simulation uncertainty (Wilson et al., 2019). In particular, environmental change plays an increasingly important role in intensifying the complexity and uncertainty on tree mortality patterns (Herr et al., 2016). Furthermore, as pointed out by Dennis et al. (1985), life is stochastic and uncertain. Consequently, there will always be high level unexplained variation in individual-based mortality models, but the use of contrasting approaches to modelling mortality may create additional, unnecessary, and poorly quantified sources of variation.

By far, binomial logistic regression is the most widely used statistical model for studying mortality (Weiskittel et al., 2011). The wide use of logistic regression is likely due to the fact that it offers a sound body of theory for hypothesis testing, and directly predicts the probability of occurrence, which can be used in a variety of individual-based modelling applications. In fact, tree mortality is most likely one of the

* Corresponding author at: Centro de Modelación y Monitoreo de Ecosistemas, Campus Alameda, Universidad Mayor, Santiago, Chile.
E-mail addresses: cseljatib@gmail.com (C. Salas-Eljatib), aaron.weiskittel@maine.edu (A.R. Weiskittel).

https://doi.org/10.1016/j.foreco.2020.118369
Received 8 April 2020; Received in revised form 30 May 2020; Accepted 25 June 2020
0378-1127/ © 2020 Elsevier B.V. All rights reserved.

most suitable ecological phenomena for being modelled as a probabilistic process given its general stochastic and uncertain behavior over time and space.

Given the use of mortality data on individual-based observations from repeated measurements on permanent plots, three additional major concerns arise, namely: (1) determining the exact timing of death; (2) effectively standardizing and accounting for observations with varying remeasurement period length intervals; and (3) properly quantifying the influence and statistical significance of the potential primary drivers of mortality. We further elaborate on each of these issues below.

The length of the remeasurement interval must be accounted for when modelling mortality as the probability of tree mortality effectively increases with the length of the interval. Although mortality is a phenomenon that relatively easy to conceptualize, several critical misinterpretations of mortality rate measures are commonly found in the ecological literature, which Sheil et al. (1995) highlighted a few examples. Individual-based tree mortality data is often obtained from different sources, where the measurement interval or period length varies considerably (Weiskittel et al., 2011). Even within a given dataset, remeasurements on sample plots can vary due to fluctuations in available funding (a frequent issue in developing countries) or simple logistics. In the statistical literature, this phenomenon is known as observations differing in their time of exposure (Gelman and Hill, 2006). Therefore, the vast majority of mortality studies must rely on data collected with unequal measurement intervals (i.e., unequal period lengths). Besides, given that tree mortality is a rare event, the length of the observation period needed for detecting mortality must be long enough (aside of fast-growing species) to minimize false negatives. In addition, as noticed by Sheil et al. (1995), more complex model formulations are required to allow comparison over varying time periods because these measures require core knowledge or key assumptions on how individual-based probabilities of death change through time. Regardless, effective methods for addressing data from varying period lengths in modelling mortality is an open topic of research, especially within a climate change framework and more comprehensive methodological comparison studies need to be conducted.

Identifying the fundamental core drivers of mortality has been a long endeavor in ecological research. Although some causes of tree mortality are evident (e.g., insect outbreaks, wildfires, and hurricanes), the patterns and causes of tree death are complex and often interactive (Franklin et al., 1987; Nyland, 1996). Several studies have been conducted on identifying the most important variables influencing tree mortality, which likely depend heavily on the actual methods being used to assess mortality. Poorter et al. (2008) and Weiskittel et al. (2011) provided a review on some common predictor variables of individual-based tree-level mortality. Here, we offer a classification of these predictors depending on the main drivers being represented (Table 1).

However, disentangling the density-dependent and environmental effects on tree mortality is not as straightforward or obvious as one might think. This is because tree mortality has been primarily modeled based on simple, theoretical assumptions that lack a physiological and/or empirical basis (Lutz and Halpern, 2006; Bircher et al., 2015). Although tree mortality can be predicted using tree growth data (Hartmann et al., 2007; Hülsmann et al., 2018), It is a remarkable challenge to find reliable approaches for modelling the growth-mortality relationship due to variation in the available data sources, modelling approach used, and contrasting sample sizes across species as well as length of the observation (Wunder et al., 2008). In the last decade, several studies have attempted to determine the most important variables, i.e. drivers, of tree mortality. Among them, we highlight a few key illustrative examples (Hartmann et al., 2007; Das et al., 2011; Cailleret et al., 2014; Anderegg et al., 2015; Cailleret et al., 2016; Cailleret et al., 2017; Hülsmann et al., 2018), but all differ in their key methodological assumptions.

In this paper, we examine and evaluate different alternatives for individual-based modelling of tree-level mortality from data having highly unequal period length of measurements, while simultaneously accounting for the hierarchical nature and contrasting structures of the available data. Therefore, we aimed at: (1) developing a new statistical strategy for effectively modelling tree mortality and its relationship with an array of density-dependent and environmental factors; (2) evaluating various approaches for accounting of unequalness of period length remeasurements and the implicit hierarchies in the data; and (3) exploring contrasting data structures to leverage the available data and better identify key drivers.

2. Materials and methods

2.1. Data

We use individual-based data measured within permanent sample plots with at least two measurement occasions. The permanent sample plots were established between 37° and 41° S. in south-central Chile where the species *Nothofagus obliqua, N. alpina*, and *N. dombeyi* conform the most abundant forest type (Donoso, 1995). These three species are the most important for commercial and cultural purposes, usually growing on the most productive sites in the Central Depression and foothills of the Andes (Salas et al., 2016). Furthermore, these forests are part of the temperate rainforests of Chile, which represents the second largest remaining area of this type in the world (Donoso, 1995; Veblen et al., 1996).

At each measurement of the permanent sample plots, conventional tree-level variables (e.g., tree diameter and species) were measured as well as the status (live or dead) of each tree. From these measurements, we computed several stand variables at the plot-level (e.g., density N, basal area G, and the diameter of the mean basal area tree $d_{\bar{g}}$). The sample plots areas ranged from 500 to 10,000 m^2, but most of them are of 1,000 m^2. We computed the relative tree population density (*RD*), as a variable representing site occupancy, following the models provided by Salas-Eljatib and Weiskittel (2018). The site productivity of each plot was estimated from the model of Salas (2011), which estimates dominant-trees height growth at age of 50 years depending on variables representing climate, topographic, and habitat type features.

For each tree, we computed basal area in larger trees (*BAL*) as a proxy for tree competition status, and its representation as a percentile too (Wykoff et al., 1982). We deliberately avoided the use of a diameter increment variable, because low growth rates do not necessarily result in high mortality rates (Martínez-Pastur et al., 2007; Cailleret et al., 2014; Bircher et al., 2015). We again want to indicate that our study is not aiming at providing the best model for predicting mortality in this particular analysis, but primarily want to assess the influence of various modelling strategies for studying this complex ecological phenomena. Regardless, we believe that the use of a variable representing competition helps to represent the growth effect on mortality without including an additional source of potential measurement error (Peet and Christensen, 1987; Bottero et al., 2017; Gleason et al., 2017; Lorimer et al., 2001).

The sample data provided a good approximation to individual-based mortality of native species of south-central Chile, spanning a full range of tree sizes and competition, as well as stand density and site productivity (Table 2). We used remeasurements from 49 permanent sample plots, which had been remeasured between two and four times, gathering a total of 88 plot-level measurements. The period length ranged between 2 and 20 years, with an median value of 7 years. On average, alive trees have larger diameter than trees that died, while trees that died were subject to higher levels of competition than living trees. In addition, the distribution of the variable percentile of *BAL* enhances the differences between living and dead trees.

Table 1
Classification of predictor variables in individual-based tree-level mortality studies.

Group	Variables	References
Size	Tree diameter (d), height (h), basal area (g)	Monserud (1976), Hamilton (1986); Monserud and Sterba (1999), Eid and Tuhus (2001); Groom et al. (2012), Hülsmann et al. (2018).
Growth	Diameter increment (pai_d), crown ratio (cr) stability (h/d)	Monserud (1976), Monserud and Sterba (1999); Pretzsch et al. (2002), Hartmann et al. (2007); Wunder et al. (2008), Cailleret et al. (2016), Cailleret et al. (2017).
Competition		
Asymmetric	Basal area in larger trees (BAL), spatial configuration	Monserud (1976), Das et al. (2011); Gonzalez-Akre et al. (2016), Hülsmann et al. (2018).
Symmetric	Stem density (N), basal area	Temesgen and Mitchell (2005), Young et al. (2017).
Composition	Species diversity, proportion of basal area in hardwoods or pioneer species	Bravo et al. (2001), Yang et al. (2003). Crecente-Campo et al. (2009), Yang and Huang (2013)
Productivity	Site index, elevation dominant height	Bravo et al. (2001); Yao et al. (2001), Pretzsch et al. (2002); Groom et al. (2012)
Environment	Long-term climate, drought climate sensitivity	Suarez et al. (2004), Bigler et al. (2006); Anderegg et al. (2015), Young et al. (2017); van Mantgem et al., 2009
Traits	Wood density, specific leaf area, leaf water potential	Baltzer et al. (2008), Poorter et al. (2008); Wright et al. (2010), O'Brien et al. (2017);

Table 2
Summary of individual-level and plot-level attributes. The variables d and $p.BAL$ are tree diameter at breast-height and percentile of basal area in larger trees, respectively. Meanwhile G, RD, and SI are stand basal area, relative density, and site index, respectively.

Statistics	Tree-level (n = 13, 482)				Plot-level (n = 88)		
	Alive		Dead				
	d (cm)	$p.BAL$ (%)	d (cm)	$p.BAL$ (%)	G (m^2 ha^{-1})	RD (%)	SI (m)
Minimum	5.00	0.10	5.00	0.20	4.10	8.80	21.60
Maximum	155.90	100.00	100.30	100.00	126.60	101.60	71.00
Mean	18.30	46.00	11.70	68.60	49.40	59.90	44.20
Median	15.10	43.20	9.90	72.50	47.20	59.90	44.40
Std.Dev.	12.90	28.60	7.70	22.70	18.80	16.90	12.70
CV (%)	70.50	62.30	65.70	33.10	38.10	28.30	28.70

2.2. Modelling approaches

2.2.1. The functional form of a generalized linear model

As explained above, logistic regression is the most widely used statistical model for studying tree- and stand-level mortality (Monserud, 1976; Hamilton, 1986; Temesgen and Mitchell, 2005; Hartmann et al., 2007; Wunder et al., 2008; Groom et al., 2012; Cailleret et al., 2016; Young et al., 2017; Hülsmann et al., 2018), as well as for mortality of vascular epiphyte (Zuleta et al., 2016) and individual tree branches (Hein and Weiskittel, 2010). A logistic regression model belongs to the group of generalized linear models ("GLM", Schabenberger and Pierce, 2002). A GLM consists of the following three components: (a) *random component* or response distribution, a set of observations $y_1, y_2, \cdots, y_n$, sample size n, that are independently distributed with mean $E(y_i) = \mu_i$; (b) *systematic component*, which refers to the quantity $\mathbf{X}\boldsymbol{\beta}$, called the linear predictor; and (c) *the link function*, which is a transformation of the mean response so that covariate effects are additive and range restrictions are ensured (Schabenberger and Pierce, 2002). For instance, if the random component is Bernoulli, and the probability of the event of interest ($\pi_{y|x}$) is modelled by the function

$$\pi_{y|x} = \frac{1}{1 + e^{-\mathbf{X}\boldsymbol{\beta}}}, \quad (1)$$

we have a logistic regression model, because the functional form resembles a logistic function (see further details in Appendix A).

If some of the various components of the GLM were modified, an alternative to logistic regression model could be developed. In this regard, we can assume the same random component as above, but change the link function. A particularly appealing alternative, as is going to be shown later, for the link function is the Gompertz model (Gompertz, 1825). Then, the probability is modelled by

$$\pi_{y|x} = 1 - e^{(-e^{\mathbf{X}\boldsymbol{\beta}})}. \quad (2)$$

To the best of our knowledge, we believe the only study of tree mortality that had previously used the Gompit functional form was conducted by Fortin et al. (2008) in Canada. From above, we have defined two functional forms that can be used as link expressions in a GLM framework.

2.3. Period length adjustments

Although the period length must be considered in mortality studies, consensus on the best approach to address data with varying period length when modelling mortality remains to be determined. In general, there are four alternatives that can be used: (a) utilize only fixed period lengths observations (e.g., Monserud and Sterba, 1999; Groom et al., 2012); (b) estimate an annualized mortality rate before fitting a model (e.g., Flewelling and Monserud, 2002); (c) include the period length as

a covariate in the model (e.g., Mugasha et al., 2017); and (d) incorporate Δt as an exposure directly into the statistical model to be fitted. Alternative (a) would greatly reduce the amount of observations available for fitting a model, which is even more critical for mortality data that must be obtained from long-term sample plots and it still remains a relatively rare event. Furthermore, given the current sparseness of available data on this ecological phenomenon, particularly in developing countries, we do not consider it as a viable method. In addition, option (c) does not accommodate the period length effectively as it limits flexibility by assuming a linear or curvilinear relationship. On the other hand, alternatives (b) and (d) appear to be more appropriate, but contrasting approaches have used to achieved it. Therefore, we refer to the three selected alternatives henceforth as "annualized", "covariate", and "exposure", which we explain further below.

(i) *Annualized*. Here an annual mortality model is fitted iteratively, therefore, there is no need for incorporating Δt into the mortality expression. The approach of Flewelling and Monserud (2002) relies on annually interpolated predictor values between t_o and t_1. Within a specific time interval step, from each annualized value of $\mathbf{X}$, the linear predictor η and the annual probability of mortality (using either of the functional forms, Eq. (1) or (2)) are computed. The annual probabilities of survival (P_s) are obtained by subtracting them from 1, and the probability of survival at the end of the period (Ps_{t_1}) by

$$Ps_{t_1} = Ps_{(t_0)} \times Ps_{(t_0+1)} \times Ps_{(t_0+2)} \times \cdots \times Ps_{(t_0+\Delta t).} \quad (3)$$

As Monserud (1976) highlighted, mortality is not a Markov process, therefore, survival is the process to be handled as such (Eq. (3)). Later, the probability of mortality at the end of the period (Pm_{t_1}) is obtained by

$$Pm_{t_1} = 1 - Ps_{t_1}, \quad (4)$$

and accordingly for each observation. Finally, based on theses probabilities, and using a functional form such as logit or Gompit, a model can be fitted using an iterative fitting approach. Therefore, we assess both the logit–annualized and Gompit–annualized approaches.

(ii) *Covariate*. In this approach, we directly include an additional term for the period length Δt. Therefore, we assess both the logit–covariate and Gompit–covariate approaches.

(iii) *Exposure*. For a dynamic phenomenon, such as mortality and other like processes in ecology (e.g., germination), it is important to consider the period length of exposition to certain conditions. Shaffer (2004) proposed a logistic-exposure model for representing the nest success of animals having different period of exposure to wild conditions. He proposed the following link function

$$\ln\left[\frac{(\pi_{y|x})^{1/\Delta t}}{1-(\pi_{y|x})^{1/\Delta t}}\right] = \mathbf{X}\boldsymbol{\beta} = \eta, \quad (5)$$

which is similar to the logit model (Eq. (A.7)), but including the effect of Δt. Shaffer (2004) refer to (5) and the prediction function (A.4) as the logistic–exposure model, which we shall used here as well. Yang and Huang (2013) provided additional details on this expression too.

we can extend the Gompit regression model to accommodate for unequal period lengths, as full explained in Appendix B, up to obtain

$$\ln[-\ln(1-\pi_{y|x})] = \mathbf{X}\boldsymbol{\beta} + \ln(\Delta t). \quad (6)$$

From (6), we can see that to the previously defined linear predictor $\mathbf{X}\boldsymbol{\beta}$, we just have to add $\ln(\Delta t)$. Accordingly, we now have the following GLM,

$$\mathbf{X}\boldsymbol{\beta} + \ln(\Delta t) \quad (7)$$

$$\ln[-\ln(1-\pi_{y|x})] \quad (8)$$

$$\pi_{y|x} = 1 - \exp[-\exp(-\mathbf{X}\boldsymbol{\beta})\Delta t] \quad (9)$$

where (7)–(9) are the linear predictor, the link function, and the inverse function, respectively. Eqs. (7)–(9) define a Gompit regression mortality model for varying period lengths, and we will refer to it as the Gompit–exposure model. Notice that Δt does not affect the parameters and acts as an offset, i.e., a variable without a coefficient. Gelman and Hill (2006) explained an offset as equivalent to including the variable as a predictor, but with its coefficient fixed to the value 1.

2.4. Data structure

Given that mortality is a dynamic phenomenon, we have complex time-series data with a specific structure. Contrasting data structures can influence the amount of available data and the final derived model behavior (Wang et al., 2007). There are several alternative data structures that can be used in time series modelling. We will focus here on two of them, the first is the most traditional, which uses non-overlapping and non-descending pairs of observations (Fig. 1a). This data structure greatly limits the amount of data available for modelling. The second one is to use all possible combinations of observations pairs (Fig. 1b). As noted by Wang et al. (2007), this might offer advantages as it greatly increases the number of observations and effectively extends the remeasurement length interval. In Wang et al. (2007), only the non-overlapping and all possible combinations data structures were able to produced unbiased predictions of dominant height growth. However, to our knowledge, the effects of alternative data structures has yet to be tested on a binary variable like mortality rather than purely continuous variables as in Wang et al. (2007).

2.5. Statistical models

Base model. We start by defining a reference model for individual-based mortality, that will be used as a baseline model for the linear predictor of our analyses. It is important to highlight that constructing the best mortality model is beyond the scope of the present research as we focus here instead on assessing alternative approaches on statistical inference and on general model behavior. Several predictor variables have been used in previously developed mortality models, but they can be segregated in variables representing the factors given in Table 1. From the cited studies, we fit several model alternatives (i.e., a logistic model having different predictor variables, and/or transformations of them), and we choose the following functional form for the linear predictor (η) of a GLM after extensive analyses,

$$\eta = f(d, d^2, perc.\ BAL, G \times RD, SI), \quad (10)$$

where: d is diameter at breast-height and *perc. BAL* is the percentile of basal area in larger trees of a given tree; while G, RD, and SI are stand basal area, relative density, and site index of the plot to which the given tree belongs, respectively. Notice that the results were not qualitatively affected by the choice of base model.

Fitting. Based on the previous sections, we have defined 12 alternative modelling strategies (Table 3), or model variants, depending on: (1) the functional form to be used (logit vs. Gompit); (2) the period length adjustments (iterative, covariate, and exposure); and (3) the data

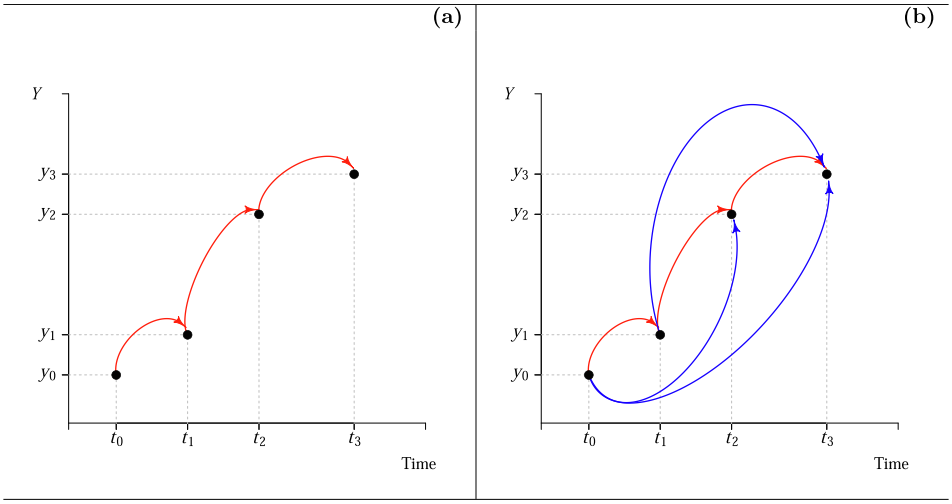


Fig. 1. Data structures in time series. The plots show measurements of the state variable Y at four different times (t_0, t_1, t_2, and t_3). In the traditional data structure approach (a), pairs of non-overlapping and non-descending observations are used, i.e., using the following periods $t_0 - t_1$, $t_1 - t_2$, and $t_2 - t_3$, which are joined by red arrows. In the all combinations data structure approach (b), all overlapping observations are also used, i.e., considering as well the following periods $t_0 - t_2$, $t_0 - t_3$, and $t_1 - t_3$, which are joined by blue arrows.

Table 3
Alternative modelling strategies evaluated in this analysis. They are a result of combining the different levels of: (1) the underlying functional form for the generalized linear mixed-effects model, (2) the period length adjustment method, and (3) the data structure used in model fitting.

Data structure	Functional form	Period length (Δt) adjustment	Model variant (Eq. number)
Traditional (n = 16, 998)	Logit	Annualized	(11)
		Covariate	(13)
		Exposure	(15)
	Gompit	Annualized	(12)
		Covariate	(14)
		Exposure	(16)
All combinations (n = 25, 717)	Logit	Annualized	(11)
		Covariate	(13)
		Exposure	(15)
	Gompit	Annualized	(12)
		Covariate	(14)
		Exposure	(16)

structure (non-overlapping forward-only combinations vs. all possible combinations).

In the previous sections, we have defined different functional forms, period length adjustments, and data structures. Fitting a model in a GLM framework is straightforward, but statistical inference on coefficients of variables measured at higher hierarchical levels than the observed phenomena will not be efficient because the variance component will be affected by pseudoreplication. For overcoming this issue, we fit each model as a multi-level, mixed-effects model (Wong and Mason, 1985; Guo and Zhao, 2000), by adding random-effects to the fixed-effects parameters of the model.

The annualized-based variants are effectively non-linear mixed-effects models. For instance, the logit–annualized model variant is

$$\begin{aligned}&(Y|X)\sim\mathcal{N}(\pi_{(y|x;\Delta t=1)},\ \sigma_y^2),\\&\pi_{(y|x;\Delta t=1)} = [1 + \exp(-\mathbf{X}\boldsymbol{\beta} - \mathbf{Z}\boldsymbol{\gamma})]^{-1},\\&\boldsymbol{\gamma}\sim\mathcal{N}(0,\ \sigma_\gamma^2),\end{aligned} \tag{11}$$

where: $\mathbf{X}\boldsymbol{\beta}$ is the linear predictor having the variables specified in (10); $\mathbf{Z}$ and $\boldsymbol{\gamma}$ are the design matrix and vector for the random-effects, respectively; meanwhile σ_y^2 and σ_γ^2 are the variances for the response variable Y and the random-effects, respectively. Notice that the probability of mortality here ($\pi_{(y|x;\Delta t=1)}$) is annualized as explained above using the approach of Flewelling and Monserud (2002). Meanwhile, the Gompit–annualized model variant is

$$\begin{aligned}&(Y|X)\sim\mathcal{N}(\pi_{(y|x;\Delta t=1)},\ \sigma_y^2),\\&\pi_{(y|x;\Delta t=1)} = 1 - \exp[-\exp(\mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\gamma})],\\&\boldsymbol{\gamma}\sim\mathcal{N}(0,\ \sigma_\gamma^2).\end{aligned} \tag{12}$$

All the terms had been already defined, and the main difference with the previous model is the functional form for the probability of annual mortality.

The covariate-based GLM variants were as follows. For instance, the logit–covariate model variant is

$$\begin{aligned}&(Y|X)\sim\text{Bernoulli}(\eta)\\&\pi_{(y|x;\Delta t)} = [1 + \exp(-\mathbf{V}\boldsymbol{\beta} - \mathbf{Z}\boldsymbol{\gamma})]^{-1}\\&\eta = \mathbf{V}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\gamma}\\&\boldsymbol{\gamma}\sim\mathcal{N}(0,\ \sigma_\gamma^2),\end{aligned} \tag{13}$$

where: $\pi_{(y|x;\Delta t)}$ is the probability of mortality in Δt years; $\mathbf{V}$ is a matrix of predictor variables such as in (10) but also including Δt; and the rest of terms were already defined. Meanwhile, the Gompit-covariate model variant is

$$\begin{aligned}&(Y|X)\sim\text{Bernoulli}(\eta)\\&\pi_{(y|x;\Delta t)} = 1 - \exp[-\exp(\mathbf{V}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\gamma})]\\&\eta = \mathbf{V}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\gamma}\\&\boldsymbol{\gamma}\sim\mathcal{N}(0,\ \sigma_\gamma^2),\end{aligned} \tag{14}$$

where all the terms had been already defined. Finally, the exposure-based GLM variants were as follows. The logit-exposure model variant is

$$\begin{aligned}&(Y|X)\sim\text{Bernoulli}(\eta)\\&\pi_{(y|x;\Delta t)} = 1 - [1 + \exp(-\mathbf{X}\boldsymbol{\beta} - \mathbf{Z}\boldsymbol{\gamma})]^{-\Delta t}\\&\eta = [\mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\gamma}]^{\Delta t}\\&\boldsymbol{\gamma}\sim\mathcal{N}(0,\ \sigma_\gamma^2);\end{aligned} \tag{15}$$

where all terms had been already defined. Notice that for fitting this model we had to provide a custom link function as in Shaffer (2004). Meanwhile, the Gompit-exposure model variant is

Table 4
Goodness-of-fit and prediction capabilities by the various modelling strategies of mortality examined in this analysis. LogLik is the maximized log-likelihood, AIC is the Akaike's information criterion, BIC is the Bayesian information criterion, AUC is area under the receiver operation characteristic curve, MCE is misclassification error. Est., low.CI, and upp.CI represents the estimated, lower confidence interval at 95% (or the 2.5% percentile of the empirical distribution of the statistics), and upper confidence interval at 95% (or the 97.5% percentile of the empirical distribution of the statistics), respectively.

Data structure	Model	Δt adjustment	LogLik	AIC	BIC	AUC			MCE		
						Est.	low.CI	upp.CI	Est.	low.CI	upp.CI
Traditional	Logit	Annualized	−5588.970	11197.940	11275.349	0.643	0.631	0.649	0.357	0.360	0.377
		Covariate	−7392.652	14802.586	14869.508	0.802	0.801	0.815	0.198	0.192	0.206
		Exposure	−6850.522	13719.044	13788.711	0.652	0.647	0.664	0.348	0.344	0.362
	Gompit	Annualized	−5517.574	11055.149	11132.557	0.643	0.633	0.651	0.357	0.358	0.375
		Covariate	−6616.188	13252.377	13329.785	0.802	0.798	0.813	0.198	0.195	0.208
		Exposure	−6600.963	13219.927	13289.594	0.805	0.804	0.818	0.195	0.189	0.204
All combinations	Logit	Annualized	−10768.051	21556.101	21637.651	0.684	0.676	0.693	0.316	0.316	0.333
		Covariate	−11401.862	22821.308	22893.024	0.798	0.783	0.799	0.202	0.209	0.224
		Exposure	−12804.314	25626.628	25700.022	0.625	0.626	0.645	0.375	0.365	0.385
	Gompit	Annualized	−10707.494	21434.988	21516.537	0.683	0.679	0.696	0.317	0.313	0.329
		Covariate	−10596.099	21212.198	21293.747	0.798	0.801	0.815	0.202	0.192	0.207
		Exposure	−10589.159	21196.318	21269.712	0.799	0.791	0.806	0.201	0.202	0.218

$$
\begin{aligned}
&(Y|X) \sim \text{Bernoulli}(\eta)\\
&\pi_{(y|x;\Delta t)} = 1 - \exp[-\exp(\mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\gamma})\Delta t]\\
&\eta = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\gamma} + \ln(\Delta t)\\
&\boldsymbol{\gamma} \sim \mathcal{N}(0, \sigma^2_{\gamma});
\end{aligned} \tag{16}
$$

All the model variants were fitted by maximum likelihood using the `lme4` package (Bates et al., 2015) implemented in R (R Core Team, 2017). Random-effects were allocated depending on the data structure. Most studies have added plot-level random intercepts into the fitted models (Shaffer, 2004; Rose et al., 2006; Fortin et al., 2008; Groom et al., 2012; Yang and Huang, 2013). Aside of the sample-plot hierarchy, we also considered random effects due to the species and the measurement period.

2.6. Model assessment

We assessed all of the defined model variants in the following three aspects, namely: (a) statistical inference, (b) prediction capabilities, and (c) biological behavior. For the first, we analyzed the significance and signs of the estimated coefficients, as well as comparing the maximum likelihood-based statistics Akaike's information criterion (AIC) and the Bayesian information criterion (BIC).

For prediction purposes, we first computed the optimal cutoff (i.e., threshold) for assessing whether the event (i.e., mortality) occurs following the recommendations of Hein and Weiskittel (2010). We used the package `InformationValue` (Prabhakaran, 2016) of R for computing the optimal threshold and then determined the area under the receiver operation characteristic curve (AUC), as well as the misclassification error (MCE, Hein and Weiskittel, 2010). To this effectively, we conducted $1,000$ bootstrapping samples of size $5,000$ observations, in order to compute the empirical 95% confidence intervals of both AUC and MCE. Mixed-effects models can produce population-averaged predictions, as well as, subject-specific predictions (Pinheiro and Bates, 2000). We use the species-level random-effects only, because in any forest sampling efforts, the species is a variable generally measured.

The biological behaviour of each model variant was analyzed by evaluating the expected mortality trends across the various predictor variables. To do this, the marginal predicted probabilities versus each predictor variable were computed and plotted. That is, across all the groups in our sample (which is generally representative of our population of interest), plot the average change in probability of the outcome across the range of some predictor of interest. We show here the behavior versus tree diameter only to allow for easier interpretation.

Finally, we assess the prediction of annual probability of mortality of each modelling strategy by comparing it against the observed relative frequency of mortality at diameter classes (class size of 10 cm). We computed the following statistics recommended for comparing relative frequencies in modelling studies (Reynolds et al., 1988), such as the root-mean-square deviation,

$$
\text{RMSD} = \sqrt{\frac{\sum_{k=1}^{m} (\hat{\pi}_{y|x,k} - \pi_{y|x,k})^2}{m}}, \tag{17}
$$

the mean bias

$$
\text{Bias} = \frac{\sum_{k=1}^{m} (\hat{\pi}_{y|x,k} - \pi_{y|x,k})}{m}, \tag{18}
$$

and the combined error index

$$
\text{CEI} = \sum_{k=1}^{m} d_k \ |\hat{\pi}_{y|x,k} - \pi_{y|x,k}|, \tag{19}
$$

where: $\hat{\pi}_{y|x,k}$ and $\pi_{y|x,k}$ are the predicted and observed probability of mortality for the k-th diameter class, respectively; m is the number of diameter classes; and d_k is the diameter for the k-th diameter class. The lower the value of RMSD and CEI, the better, while the closer to zero is better for bias. As pointed out by Pogoda et al. (2019), implications of an error of one tree will substantially differ depending on whether that error arose in a small or large diameter class. A statistic which accounts for this additional criterion is the combined error index (Eq. (19)) of Reynolds et al. (1988). Finally, we compute a rank index for each modelling strategy depending on the goodness-of-fit statistics (Table 4) and these derived tree-level prediction statistics. Notice that we assign the goodness-of-fit statistics within each data structure because of the effect of sample size. The lower the value of this rank index, the better the strategy.

3. Results

Two primary patterns were obtained when comparing the goodness-of-fit statistics among modelling strategies. The Gompit functional form generally outperformed the logit for both data structures (Table 4). The annualized period length adjustment offered the best fit only for the traditional data structure, but the exposure and the covariate based on the Gompit model had a better fit (Table 4). Regarding the predictive abilities of the mixed-effects models, the Gompit-exposure strategy had the largest AUC and lowest MCE, regardless of the data structure being considered. Overall, there were no clear differences in the general predictive capabilities between the logit and Gompit model forms when

Table 5
Parameter estimates, standard errors, and *P*-values for the different individual-based mortality modelling strategies examined in this analysis.

Model	Δt adjustment	Statistics	Simple increment data							Multiple increment data						
			$\widehat{\beta_0}$	$\widehat{\beta_1}$	$\widehat{\beta_2}$	$\widehat{\beta_3}$	$\widehat{\beta_4}$	$\widehat{\beta_5}$	$\widehat{\beta_6}$	$\widehat{\beta_0}$	$\widehat{\beta_1}$	$\widehat{\beta_2}$	$\widehat{\beta_3}$	$\widehat{\beta_4}$	$\widehat{\beta_5}$	$\widehat{\beta_6}$
Logit	Annualized	Est.	24.308	−1.114	0.010	−0.121	−0.001	−0.033		0.876	−0.403	0.003	−0.022	0.001	0.036	
		Std.Err.	1.956	0.029	0.000	0.004	0.000	0.035		1.303	0.014	0.000	0.002	0.000	0.023	
		P-value	0.000	0.000	0.000	0.000	0.000	0.355		0.501	0.000	0.000	0.000	0.000	0.119	
	Covariate	Est.	−5.403	−0.030	0.000	0.038	0.000	−0.000	0.141	−4.815	−0.041	0.000	0.034	0.000	0.006	0.058
		Std.Err.	0.582	0.013	0.000	0.002	0.000	0.008	0.022	0.606	0.011	0.000	0.002	0.000	0.009	0.004
		P-value	0.000	0.019	0.009	0.000	0.002	0.951	0.000	0.000	0.000	0.000	0.000	0.001	0.530	0.000
	Exposure	Est.	−1.095	−0.002	0.000	0.024	0.000	0.005		1.313	−0.020	0.000	0.017	−0.000	−0.011	
		Std.Err.	0.612	0.005	0.000	0.001	0.000	0.011		0.695	0.003	0.000	0.000	0.000	0.013	
		P-value	0.073	0.739	0.012	0.000	0.413	0.609		0.059	0.000	0.000	0.000	0.000	0.370	
Gompit	Annualized	Est.	6.842	−0.309	0.002	−0.033	−0.000	−0.008		−0.504	−0.124	0.001	−0.006	0.001	0.015	
		Std.Err.	0.673	0.009	0.000	0.001	0.000	0.012		0.544	0.005	0.000	0.001	0.000	0.010	
		P-value	0.000	0.000	0.000	0.000	0.000	0.488		0.355	0.000	0.000	0.000	0.000	0.128	
	Covariate	Est.	−4.652	−0.035	0.000	0.029	0.000	0.000	0.109	−3.800	−0.048	0.000	0.026	0.000	0.001	0.049
		Std.Err.	0.537	0.013	0.000	0.002	0.000	0.007	0.018	0.796	0.009	0.000	0.002	0.000	0.011	0.003
		P-value	0.000	0.006	0.010	0.000	0.002	0.985	0.000	0.000	0.000	0.000	0.000	0.086	0.946	0.000
	Exposure	Est.	−5.652	−0.036	0.000	0.029	0.000	0.002		−5.799	−0.043	0.000	0.027	0.000	0.004	
		Std.Err.	0.612	0.005	0.000	0.001	0.000	0.011		0.695	0.003	0.000	0.000	0.000	0.013	
		P-value	0.073	0.739	0.012	0.000	0.413	0.609		0.059	0.000	0.000	0.000	0.000	0.370	

the same period length adjustment and data structure combinations were considered (Table 4). Based on the boostrapped-determined confidence intervals of both AUC and MCE, it was observed that Gompit–exposure, Gompit-covariate, and logit–covariate were generally superior, but were not statistical different than the other approaches at $\alpha = 0.05$.

Statistical inference of models was strongly influenced by the examined modelling strategies. As expected, the standard errors of coefficient estimates were much lower for the all combinations data structure than the traditional one (Table 5). The annualized period length adjustment offered quite different parameter estimates than the exposure method for both functional forms and data structures (Table 5). Overall, the model variants based on the exposure period length adjustment were more robust in the parameter estimates between the traditional and the all combinations data structure, particularly for the Gompit functional form.

Simply adding Δt to the models altered the variance components of the remaining predictor variables for both data structures and functional forms. Therefore, caution must be taken for mortality models that include period length as a covariate because it can result in misleading statistical inference and the determined relationships are highly dependent on the actual measurement interval, which are often relatively arbitrary.

Model functional form (logit or Gompit) influenced both the magnitude and shape of the marginal predicted probabilities of annual mortality from the fitted models (Fig. 2). For instance, the annualized period length adjustment produced the expected U-shaped of probability of mortality (Monserud and Sterba, 1999; Foster et al., 2014), but tended to reach rather unrealistic levels of mortality too rapidly. However, the Gompit model form produced more realistic levels of mortality when using all the combinations data. Furthermore, the logit model always produced higher mortality rates than the Gompit model, especially when the exposure alternative was used. Consequently, the predicted mortality patterns will depend heavily on the selected modelling strategy and is an important source of consideration when determining the final selected model. Indeed, the period length adjustment produced different marginal probabilities of mortality. The annualized alternative always resulted in a more pronounced U-shaped mortality curve, but the predictions do not appear to be rather reliable in practice (Fig. C.1). This trend is even more drastic for the logit model. The covariate and exposure adjustments produced distinct shapes of mortality rates for the logit model, but maintained almost the same trend when the Gompit model form was used. In general, the data structure used did not drastically influence the marginal probabilities of mortality as much as the other factors examined in this study (i.e., the functional form and the period length adjustments). Regardless of the data structure, the annualized method produced relatively unrealistic mortality predictions (Fig. C.2). In particular, the all combinations data structure predicted mortality to be higher than when using the traditional data structure, but smaller differences were observed for the Gompit model, indicating that it behaved more independently of the data structure.

The predictive ability of the models by tree size class also highlighted important differences among the examined modelling strategies. Regardless of the statistics being used here, the Gompit model form always was among the top three rankings (Table 6). The all combinations data structure did not offer better prediction capabilities than the traditional data structure, therefore, the larger the sample size of this method implies also creating more variability in the predictions too. The precision of the model variants, measured by the RMSD, was lower for the annualized alternatives, especially when the logit model form was used. A similar trend was observed when analyzing the bias, but the Gompit annualized had the lowest bias in the traditional data structure. The combined error index (Eq. (19)), which gives extra weights to larger trees, indicated that Gompit–covariate variant was the best on this metric, although closely followed by Gompit–exposure. Overall, we ranked the different variants according the goodness-of-fit and prediction capabilities performance statistics and the best ones were, in order, Gompit–exposure and Gompit–covariate using the traditional data structure, and Gompit-exposure using the all combinations data structure.

4. Discussion

Mortality is a highly dynamic phenomena that varies both temporally and spatially. Individual tree mortality occurs when a tree goes from living to dead, but determining the exact time and cause of tree death is difficult to do at scale, which complicates understanding and interpretation of key factors influencing it. In order to effectively capture mortality, longitudinal studies often using dendrochronological records are common, which can be highly time-consuming to reconstruct, rely on numerous assumptions, and is often limited in scale. If a more refined and robust understanding at the forest-level is required, the repeated remeasurement of tagged individuals located on permanent sample plots over time and space is needed.

However, most of our knowledge on forest dynamics (where

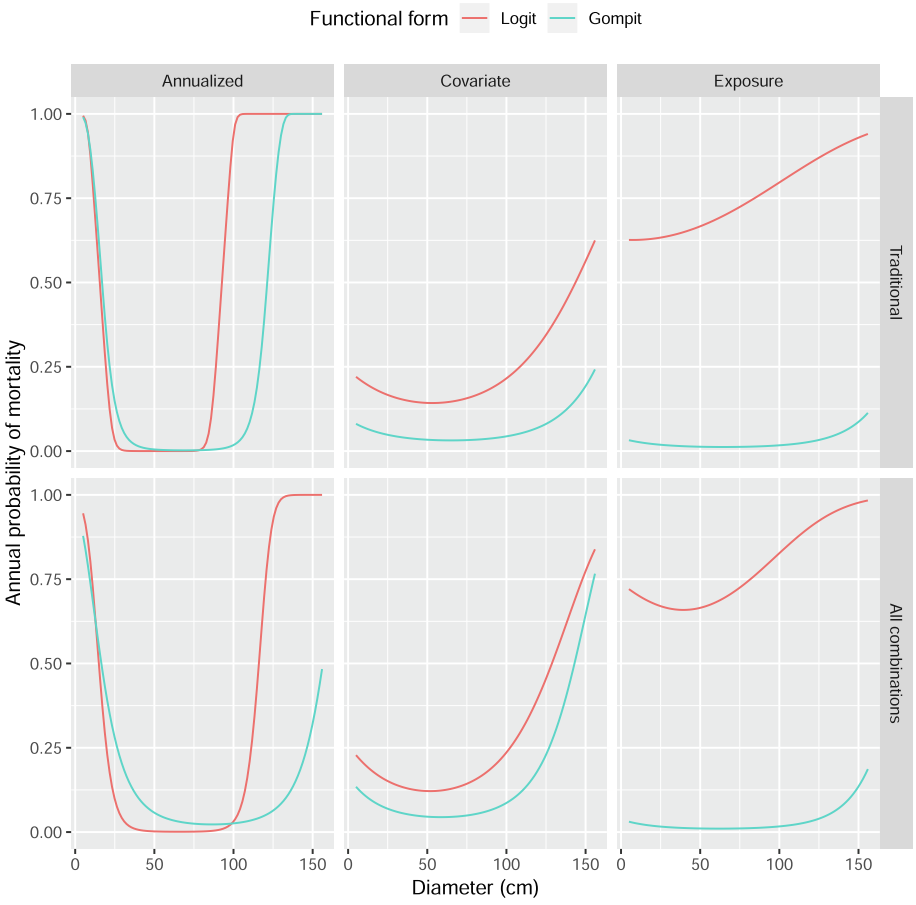


Fig. 2. Average marginal predicted probability of annual individual tree-level mortality by functional form used for the link function of the generalized linear mixed-effects model.

Table 6
Evaluation statistics for predicted annual tree-level mortality rates using diameter size class as a proxy for tree size. RMSD is the root-mean-square deviation (Eq. (17)), bias is computed as in Eq. (18), and CEI is the combined error index (Eq. (19)). The rank index is the mean ranking based on model goodness-of-fit (Table 6 and the prediction statistics shown in the current table, with the lower the value the better.

Data structure	Model	Δt adjustment	RMSD	Bias	CEI	Rank index
Traditional	Logit	Annualized	0.5758	0.3743	506.4973	12
		Covariate	0.0632	0.0509	49.6720	5
		Exposure	0.2724	0.2061	228.8960	9
	Gompit	Annualized	0.2437	0.0973	118.0520	8
		Covariate	0.0512	0.0430	37.9547	2
		Exposure	0.0543	0.0451	38.3852	1
All combinations	Logit	Annualized	0.4257	0.2766	357.1129	10
		Covariate	0.0941	0.0677	76.0140	6
		Exposure	0.2612	0.1927	214.5742	11
	Gompit	Annualized	0.1302	0.0884	71.8614	7
		Covariate	0.0666	0.0509	52.2050	4
		Exposure	0.0728	0.0580	52.2760	3

mortality is crucial) is based on the chronosequence assumption (i.e., space substituted for time). For instance, the forest dynamics studies summarized by Veblen et al. (1996), rely heavily on the chronosequence assumption as static data on forest structure and composition was combined with dendrochronologically derived data on individual tree age and radial growth. Nevertheless, this critical assumption is now highly questioned in several ecological disciplines (e.g., Johnson and Miyanishi, 2008; Damgaard, 2019). Besides, Norden et al. (2015) highlighted that successional trajectories vary widely, even among nearby stands with similar environmental conditions and disturbance histories. In fact, Norden et al. (2015) called into question the premise that successional processes are consistent over space and time. This finding suggests the need to develop more effective methodologies that can utilize and leverage repeated individual-based observations.

In addition, pseudoreplication is common in ecological research, particularly studies on tree-level mortality. In most individual-based mortality studies, trees are observed within sample plots, being located within stands or forests, and so on. This hierarchical structure of the data implies in practice that we have to use a unique value of stem density and stand basal area within a sample plot but for different trees (the same applied to other variables). In statistics, this sort of structure is known as clustering data though hierarchical random processes (Schabenberger and Pierce, 2002). If the hierarchical structure of the data is not taken into account for statistical inference, the hypotheses testing of the fitted model are not fully valid, because the variance estimation is imprecise. It is common when assessing the effects of forest structure and composition as well as environmental factors on tree mortality to observe the pseudoreplication issue (e.g., Hartmann et al., 2007; Young et al., 2017; Hülsmann et al., 2018), as well as in vascular epiphyte mortality (e.g., Zuleta et al., 2016). A more suitable statistical approach for overcoming the pseudoreplication issue is to fit models in a hierarchical mixed-effects framework for directly accounting for the structure of the data (Pinheiro and Bates, 2000). The vast majority of applications of mixed-effects models in forest ecology has been related to continuous variables, such as: height-diameter allometry (Temesgen and von Gadow, 2004); stem shape (Leites and

Robinson, 2004); and growth modelling (Salas et al., 2008). However, relatively fewer studies have used mixed-effects models applied to binary responses (Fortin et al., 2008; Groom et al., 2012; Yang and Huang, 2013; Zhang et al., 2017). Finally, the methodology to effectively disentangle the density-dependent and environmental effects on tree mortality remains a poorly explored research topic, particularly in highly productive, species rich forests in the Southern Hemisphere. Therefore, our study provides some important insights into this issue.

As previously highlighted, evaluating long-term trends in individual-based tree mortality poses several important challenges. Mortality is clearly a key ecological process, but the inherent challenges for examining it have only been recognized in relatively few studies (Monserud, 1976; Zens and Peart, 2003). First, mortality is generally represented as a dichotomous variable in mathematical models, which relies on a relatively small subset of suitable statistical approaches capable of handling data of this nature. In addition, mortality is a very rare event that is rather difficult to sample for effectively, particularly for trees because of their temporal scale when compared to other organisms (Pretzsch, 2009). This feature is even more pronounced if the focus is on long-lived species similar to the ones in this study, which are an important contrast to the fast growing species in even-aged plantations (Li et al., 2015; Thapa and Burkhart, 2015). Consequently, the available data for dynamically examining tree mortality are rather limited and difficult to identify than many other tree ecological features such as static variables at the individual tree- (e.g., height in Fajardo et al., 2019) and stand-levels (e.g., tree stem density in Crowther et al., 2015). The use of different types of time series data for tree modelling had been rarely examined, and if so, only focused on continuous random variables (Wang et al., 2007). To our knowledge, this is the first study revealing the importance of leveraging all of the available data on a binary variable. In addition, our results suggest the need to addtionally consider a relatively novel framework like the Gompit exposure in future studies of individual-based mortality.

Overall, our analysis highlighted the rather strong influence of alternative modelling strategies on individual-based mortality trends, statistical inference, and model performance. In particular, we found that adding the period length as a covariate alters the resulting parameter standard errors and p-values of the remaining predictor variables. It is relatively evident that the period length influencing the probability of mortality, therefore, Δt must be considered when modelling this phenomenon, but this is likely too obvious to draw any real statistical inference on it. Consequently, we argue that the period length must be taken into account when modelling mortality, but it is not done effectively as a simple new and often linear predictor.

Tree mortality is one of the critical ecological phenomenons that requires the most empirical evidence for improving our understanding of the process (Cailleret et al., 2016; Hülsmann et al., 2018). The lack of a strong connection between theory and empiricism is a common problem in many ecological disciplines (Rossberg et al., 2019). Much previous work has been focused on finding the best predictors for mortality analysis, but very few studies have questioned the widespread use of the logit model form. In this vein, Cailleret et al. (2016), Hülsmann et al. (2017), Hülsmann et al. (2018) compared several predictor variables for predicting tree mortality using the logit model, and various specific recommendations were determined based on these analyses. Although we do not question those specific recommendations here with our analysis, we do raise the important and rather critical question whether the logit model form was actually the most appropriate for the analyses being conducted. We tried to advance our ability to model individual-based mortality by considering a different functional form, the Gompit. In our analysis, we consistently showed that any mortality pattern to be described based on the models being determined will depend heavily on the modelling strategy selected. Therefore, we recommend the need to assess alternative modelling strategies before making any further conclusions.

Although we developed a Gompit-exposure, multi-level model to facilitate the rather difficult modelling of individual-based mortality data, we would also suggest this approach for more simplistic analyses. The primary advantages of our approach are that it is: the most amenable way of taking into account the unequal period length of the data, utilizes the full extent of the data available, and offer a rather suitable way of statistical hypothesis testing. For instance, Hülsmann et al. (2018) made a pattern of conclusions on individual-based mortality models determined for several European species. However, they did not directly take into account the hierarchical structure of the data and as pointed out before, relied on a logit model form. Besides, several other recent studies have examined the influence on climate and individual-based mortality pattern with differing conclusions yet nearly all have relied on the logit model form.

In general, our analysis indicated the underlying data structure did not greatly influence the marginal probabilities of mortality. However, using all combinations of the data helped us for appropriately assessing the statistical importance of potential drivers of mortality as well as for detecting general patterns that would not have been possible when only using simple forward steps of the available time series data. Furthermore, regarding the importance of the three major factors under study on the behavior of the fitted models, we found that the data structure was the least important followed by the functional form and the period length adjustment being the most important.

5. Conclusions

We offered a new approach for constructing individual-based mortality models based on a multi-level, Gompit-exposure, and binary mixed-effects model using all possible combinations of the available increment data. This model provided us with a suitable, relatively consistent, and rather robust statistical framework for both prediction and hypotheses testing when using complex repeated observations with varying period lengths. Future analyses would likely benefit from using a similar modelling approach or at least evaluating alternative modelling strategies before selecting a final one. Overall, the study highlights the importance of crucial underlying assumptions for modelling dynamic ecological events such as individual-based mortality and suggests that there are a vital need and importance of evaluating these assumptions before determining the nature and cause of specific relationships.

CRediT authorship contribution statement

C. Salas-Eljatib: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Project administration, Software, Supervision, Writing - original draft, Writing - review & editing. **A.R. Weiskittel:** Methodology, Writing - review & editing, Project administration.

Declaration of Competing Interest

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

Acknowledgements

This study was supported by the Chilean research grants Fondo Nacional de Desarrollo Científico y Tecnológico (Fondecyt No. 1191816) and Fondo de Fomento al Desarrollo Científico y Técnológico (Fondef No. ID19|10421); National Science Foundation Center for Advanced Forestry Systems (Award No. 1915078), and National Science Foundation RII Track-2 FEC (Award No. 1920908). We would also like to thank all the researchers and field assistants involved on collecting the field data over the years.

Appendix A. On the logistic and the gompit regression models

In a generalized linear model (GLM), the quantity that is being fitted as a linear model is

$$\mu(\mathbf{X}_i) = \eta_i = g(\mathrm{E}[y_i]) = \mathbf{x}'\boldsymbol{\beta}, \tag{A.1}$$

where, $g(\cdot)$ is the link function, which transform the mean μ_i onto a scale where the covariate effects are additive (Schabenberger and Pierce, 2002). The mean of the outcome at any value of $\mathbf{X}$ is predicted as

$$\hat{\mu}_i = g^{-1}(\eta_i), \tag{A.2}$$

where $g^{-1}(\eta_i)$ is the inverse of the link function. Based on the above, a logistic regression model is a GLM where the random component is:

$$(Y|X = x_i) \sim \text{Bernoulli}(\eta_i), \tag{A.3}$$

the systematic component is the linear predictor $\mathbf{X}\boldsymbol{\beta}$, and the link function is

$$g\left(\mathrm{E}\left[Y_i \middle| X = x_i\right]\right) = \frac{1}{1 + \mathrm{e}^{-\mathbf{X}_i\boldsymbol{\beta}}} \tag{A.4}$$

which mimics the logistic function

$$f(z) = \frac{1}{1 + \mathrm{e}^{-z}}, \tag{A.5}$$

that is bounded by 0 and 1, for any possible value of the generic predictor variable z. Therefore (A.4) becomes a model for the probability of the event $Y = 1$, as follows

$$\pi_{y|x} = \frac{1}{1 + \mathrm{e}^{-\mathbf{X}\boldsymbol{\beta}}}. \tag{A.6}$$

From here, we solve $\pi_{y|x}$ as a function of $\mathbf{X}\boldsymbol{\beta}$, having

$$\ln\left[\frac{\pi_{y|x}}{1 - \pi_{y|x}}\right] = \mathbf{X}\boldsymbol{\beta} \longrightarrow \text{logit}\left[Y = 1\right] = \mathbf{X}\boldsymbol{\beta} = \eta, \tag{A.7}$$

where η is the link function. The left-hand side of (A.7) is know as the logit transformation or simply the *logit function*. Once the parameters are estimated ($\hat{\boldsymbol{\beta}}$), the predicted probability is obtained by

$$\hat{\pi}_{y|x} = \frac{1}{1 + \mathrm{e}^{-\mathbf{X}\hat{\boldsymbol{\beta}}}} = \frac{\mathrm{e}^{\mathbf{X}\hat{\boldsymbol{\beta}}}}{\mathrm{e}^{\mathbf{X}\hat{\boldsymbol{\beta}}} + 1} = [1 + \exp(-\mathbf{X}\hat{\boldsymbol{\beta}})]^{-1}. \tag{A.8}$$

Eq. (A.8), that resembles a logistic function (Ec. 1), is the inverse of the link function, therefore the model being fitted is know as "*logistic regression*".

Other functional form can be the Gompertz function (Gompertz, 1825) having the following formulation:

$$f(z) = 1 - \mathrm{e}^{(-\mathrm{e}^{z})} \tag{A.9}$$

being also bounded by 0 and 1, and therefore can be used as a potential link function of a binomial response in a GLM framework. The new link function will be:

$$g(\mathrm{E}[Y_i|X = x_i]) = 1 - \mathrm{e}^{(-\mathrm{e}^{\mathbf{X}\boldsymbol{\beta}})}. \tag{A.10}$$

Therefore (A.10) becomes a probability model for the random variable $Y = 1$ as follows:

$$\pi_{y|x} = 1 - \mathrm{e}^{(-\mathrm{e}^{\mathbf{X}\boldsymbol{\beta}})} \tag{A.11}$$

From here, we solve $\pi_{y|x}$ as a function of $\mathbf{X}\boldsymbol{\beta}$, having

$$\ln[-\ln(1 - \pi_{y|x})] = \mathbf{X}\boldsymbol{\beta} \quad \longrightarrow \text{loglog}[Y = 1] = \mathbf{X}\boldsymbol{\beta} = \eta, \tag{A.12}$$

where (A.12) is the link function, known as the log–log transformation or *log–log function*. After estimation, the mean of the outcome at any value of $\mathbf{X}$ is predicted as:

$$\hat{\pi}_{y|x} = 1 - \mathrm{e}^{\left(-\mathrm{e}^{\mathbf{X}\hat{\boldsymbol{\beta}}}\right)} = 1 - \exp[-\exp(\mathbf{X}_i\hat{\boldsymbol{\beta}})] \tag{A.13}$$

Eq. (A.13), which resembles a Gompertz function (Ec. 2), is the inverse of the link function, therefore the model being fitted here is known as "*Gompit regression*".

Appendix B. On the gompit model for unequal period lengths

By starting from the following annual mortality model

$$\ln[-\ln(1 - \pi_{y|x})] = \mathbf{X}\boldsymbol{\beta} \tag{B.1}$$

and re-arranged it to

$$\ln(1 - \pi_{y|x}) = -\mathrm{e}^{\mathbf{X}\boldsymbol{\beta}}. \tag{B.2}$$

From (B.2), we know that

$$1 - \pi_{y|x} = e^{-e^{\mathbf{X}\beta}} = Ps_1, \tag{B.3}$$

$$\pi_{y|x} = 1 - e^{-e^{\mathbf{X}\beta}} = Pm_1, \tag{B.4}$$

where Ps_1 and Pm_1 are the annual survival and mortality probability, respectively. As Flewelling and Monserud (2002) indicated, because of the Markov property, the probability of survival for a period of Δt years is:

$$Ps_{\Delta t} = Ps_1 Ps_1 \cdots Ps_{1(\Delta t)} = (Ps_1)^{\Delta t}, \tag{B.5}$$

and because of $Pm_1 = 1 - Ps_1$, this relationship holds in Δt years, as:

$$Pm_1 = 1 - (Ps_1)^{\Delta t}, \tag{B.6}$$

and we can replace (B.3) in (B.6), having

$$Pm_1 = 1 - e^{(-e^{\mathbf{X}\beta})\Delta t}. \tag{B.7}$$

Eq. (B.7) offers the ability to obtain the annual mortality probability from mortality being observed at a period length Δt. As we already defined our inverse function, we can now search for the link function. From (B.7) we have

$$\pi_{y|x} = 1 - e^{(-e^{\mathbf{X}\beta})\Delta t} \tag{B.8}$$

and the link function will be

$$\begin{aligned}
1 - \pi_{y|x} &= e^{(-e^{\mathbf{X}\beta})\Delta t} \\
\ln(1 - \pi_{y|x}) &= (-e^{\mathbf{X}\beta})\Delta t \\
-\ln(1 - \pi_{y|x}) &= (e^{\mathbf{X}\beta})\Delta t \\
\ln[-\ln(1 - \pi_{y|x})] &= \ln(e^{\mathbf{X}\beta}) + \ln(\Delta t) \\
\ln[-\ln(1 - \pi_{y|x})] &= \mathbf{X}\boldsymbol{\beta} + \ln(\Delta t).
\end{aligned} \tag{B.9}$$

Appendix C. Expected probabilities by period length adjustment method and data structure

See Figs. C.1 and C.2.

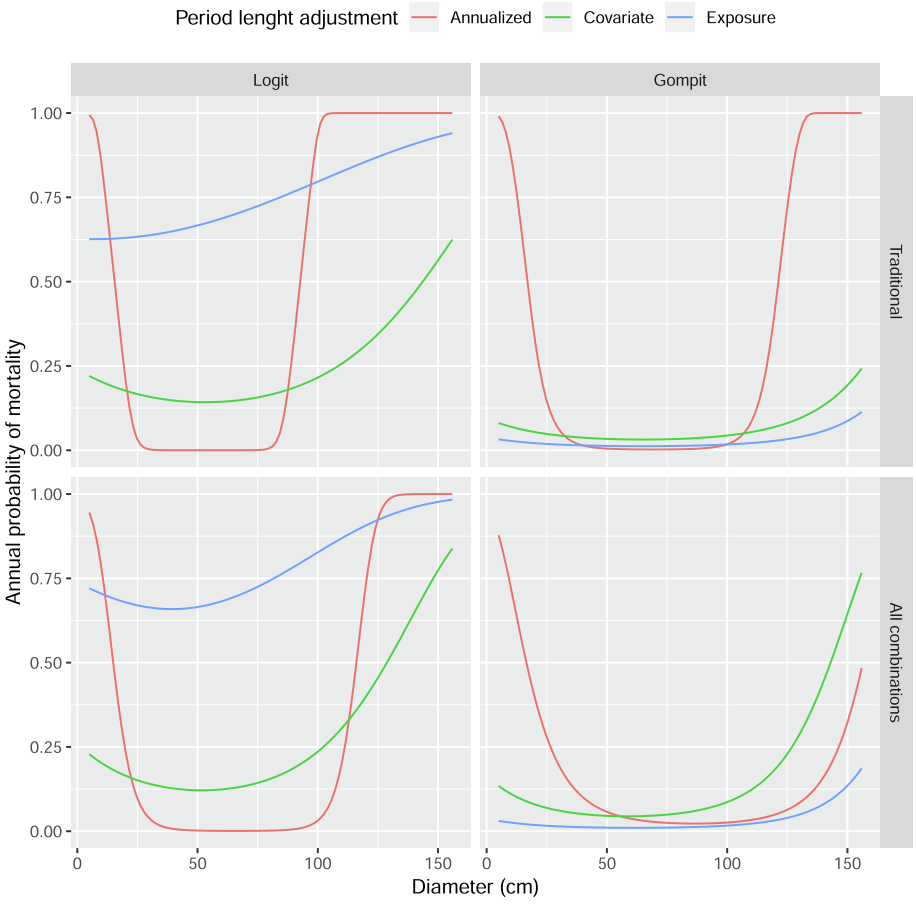


Fig. C.1. Average marginal predicted probability of annual individual tree-level mortality by period length adjustment method.

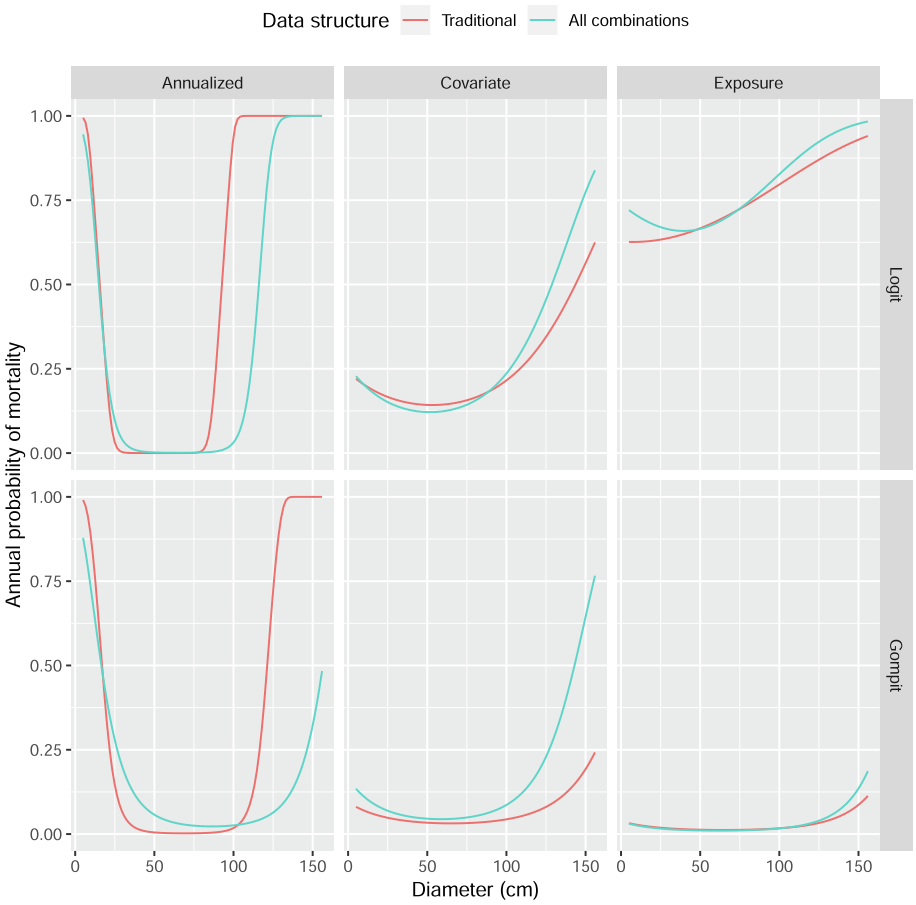


Fig. C.2. Average marginal predicted probability of annual individual tree-level mortality by data structure.

References

Anderegg, W.R.L., Flint, A., Huang, C.y., Flint, L., Berry, J.A., Davis, F., Sperry, J.S., Field, C.B., 2015. Tree mortality predicted from drought-induced vascular damage. Nat. Geosci. 8, 367–371.

Baltzer, J.L., Davies, S.J., Bunyavejchewin, S., Noor, N.S.M., 2008. The role of desiccation tolerance in determining tree species distributions along the Malay-Thai Peninsula. Funct. Ecol. 22, 221–231.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M., Rigling, A., 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems 9, 330–343.

Bircher, N., Cailleret, M., Bugmann, H., 2015. The agony of choice: different empirical mortality models lead to sharply different future forest dynamics. Ecol. Appl. 25, 1303–1318.

Bottero, A., D'Amato, A.W., Palik, B.J., Bradford, J.B., Fraver, S., Battaglia, M.A., Asherin, L.A., 2017. Density-dependent vulnerability of forest ecosystems to drought. J. Appl. Ecol. 54, 1605–1614.

Bravo, F., Hann, D.W., Maguire, D.A., 2001. Impact of competitor species composition on predicting diameter growth and survival rates of Douglas-fir trees in southwestern Oregon. Can. J. For. Res. 31, 2237–2247.

Cailleret, M., Bigler, C., Bugmann, H., Camarero, J.J., Cufar, K., Davi, H., Meszaros, I., Minunno, F., Peltoniemi, M., Robert, E.M.R., Suarez, M.L., Tognetti, R., Martinez-Vilalta, J., 2016. Towards a common methodology for developing logistic tree mortality models based on ring-width data. Ecol. Appl. 26, 1827–1841.

Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Čada, V., Camarero, J.J., Cherubini, P., Cochard, H., Coyea, M.R., Čufar, K., Das, A.J., Davi, H., Delzon, S., Dorman, M., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hartmann, H., Hereş, A.M., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Kramer, K., Lens, F., Levanic, T., Calderon, J.C.L., Lloret, F., Lobo-Do-Vale, R., Lombardi, F., Rodríguez, R.L., Mäkinen, H., Mayr, S., Mészáros, I., Metsaranta, J.M., Minunno, F., Oberhuber, W., Papadopoulos, A., Peltoniemi, M., Petritan, A.M., Rohner, B., Sangüesa-Barreda, G., Sarris, D., Smith, J.M., Stan, A.B., Sterck, F., Stojanović, D.B., Suarez, M.L., Svoboda, M., Tognetti, R., Torres-Ruiz, J.M., Trotsiuk, V., Villalba, R., Vodde, F., Westwood, A.R., Wyckoff, P.H., Zafirov, N., Martínez-Vilalta, J., 2017. A synthesis of radial growth patterns preceding tree mortality. Glob. Change Biol. 23, 1675–1690.

Cailleret, M., Nourtier, M., Amm, A., Durand-Gillmann, M., Davi, H., 2014. Drought-induced decline and mortality of silver fir differ among three sites in Southern France. Ann. For. Sci. 71, 643–657.

Crecente-Campo, F., Marshall, P., Rodríguez-Soalleiro, R., 2009. Modeling non-catastrophic individual-tree mortality for *Pinus radiata* plantations in northwestern Spain. For. Ecol. Manage. 257, 1542–1550.

Crowther, T.W., Glick, H.B., Covey, K.R., Bettigole, C., Maynard, D.S., Thomas, S.M., Smith, J.R., Hintler, G., Duguid, M.C., Amatulli, G., Tuanmu, M.N., Jetz, W., Salas, C., Stam, C., Piotto, D., Tavani, R., Green, S., Bruce, G., Williams, S.J., Wiser, S.K., Huber, M.O., Hengeveld, G.M., Nabuurs, G.J., Tikhonova, E., Borchardt, P., Li, C.F., Powrie, L.W., Fischer, M., Hemp, A., Homeier, J., Cho, P., Vibrans, A.C., Umunay, P.M., Piao, S.L., Rowe, C.W., Ashton, M.S., Crane, P.R., Bradford, M.A., 2015. Mapping tree density at a global scale. Nature 525, 201–205.

Damgaard, C., 2019. A critique of the space-for-time substitution practice in community ecology. Trends Ecol. Evol. 34, 416–421.

Das, A., Battles, J., Stephenson, N.L., van Mantgem, P.J., 2011. The contribution of competition to tree mortality in old-growth coniferous forests. For. Ecol. Manage. 261, 1203–1213.

Dennis, B., Brown, B.E., Stage, A.R., Burkhart, H.E., Clark, S., 1985. Problems of modeling growth and yield of renewable resources. Am. Stat. 39, 374–383.

Dennis, B., Ponciano, J.M., Lele, S.R., Taper, M.L., Staples, D., 2006. Estimating density dependence, process noise and observation error. Ecol. Monogr. 76, 323–341.

Dennis, B., Taper, M.L., 1994. Density dependence in time series observations of natural populations: Estimation and testing. Ecol. Monogr. 64, 205–224.

Donoso, C., 1995. Bosques templados de Chile y Argentina: Variación, estructura y dinámica, 3rd ed. Editorial Universitaria, Santiago, Chile, pp. 484.

Eid, T., Tuhus, E., 2001. Models for individual tree mortality in Norway. For. Ecol. Manage. 154, 69–84.

Fajardo, A., McIntire, E.J., Olson, M.E., 2019. When short stature is an asset in trees. Trends Ecol. Evol. 34, 193–199.

Flewelling, J.W., Monserud, R.A., 2002. Comparing methods for modelling tree mortality. In: Crookston, N.L., Havis, R.N. (Eds.), Proceeding of the 2nd Forest Vegetation Simulator Conference. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, pp. 168–177.

Fortin, M., Bédard, S., DeBlois, J., Meunier, S., 2008. Predicting individual tree mortality in northern hardwood stands under uneven-aged management in southern Québec. Canada. Ann. For. Sci. 65, 205.

Foster, J.R., D'Amato, A.W., Bradford, J.B., 2014. Looking for age-related growth decline in natural forests: unexpected biomass patterns from tree rings and simulated mortality. Oecologia 175, 363–374.
Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. Bioscience 37, 550–556.
Gelman, A., Hill, J., 2006. Data Analysis Using Regression and Multilevel/Hierarchical Models. Cambridge University Press, New York, NY, USA, pp. 625.
Gleason, K.E., Bradford, J.B., Bottero, A., D'Amato, A.W., Fraver, S., Palik, B.J., Battaglia, M.A., Iverson, L., Kenefic, L., Kern, C.C., 2017. Competition amplifies drought stress in forests across broad climatic and compositional gradients. Ecosphere 8, e01849.
Gompertz, B., 1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. Philos. Trans. R. Soc. Lond. 115, 513–583.
Gonzalez-Akre, E., Meakem, V., Eng, C.Y., Tepley, A.J., Bourg, N.A., McShea, W., Davies, S.J., Anderson-Teixeira, K., 2016. Patterns of tree mortality in a temperate deciduous forest derived from a large forest dynamics plot. Ecosphere 7, e01595.
Groom, J.D., Hann, D.W., Temesgen, H., 2012. Evaluation of mixed-effects models for predicting Douglas-fir mortality. For. Ecol. Manage. 276, 139–145.
Guo, G., Zhao, H., 2000. Multilevel modeling for binary data. Ann. Rev. Sociol. 26, 441–462.
Hamilton Jr., D.A., 1986. A logistic model of mortality in thinned and unthinned mixed conifer stands of northern Idaho. Forest Sci. 32, 989–1000.
Hartmann, H., Messier, C., Beaudet, M., 2007. Improving tree mortality models by accounting for environmental influences. Can. J. For. Res. 37, 2106–2114.
Hein, S., Weiskittel, A.R., 2010. Cutpoint analysis for models with binary outcomes: a case study on branch mortality. Eur. J. For. Res. 129, 585–590.
Herr, A., Dambacher, J.M., Pinkard, E., Glen, M., Mohammed, C., Wardlaw, T., 2016. The uncertain impact of climate change on forest ecosystems - How qualitative modelling can guide future research for quantitative model development. Environ. Modell. Softw. 76, 95–107.
Hülsmann, L., Bugmann, H., Brang, P., 2017. How to predict tree death from inventory data – lessons from a systematic assessment of European tree mortality models. Can. J. For. Res. 47, 890–900.
Hülsmann, L., Bugmann, H., Cailleret, M., Brang, P., 2018. How to kill a tree: empirical mortality models for 18 species and their performance in a dynamic forest model. Ecol. Appl. 28, 522–540.
Johnson, E.A., Miyanishi, K., 2008. Testing the assumptions of chronosequences in succession. Ecol. Lett. 11, 419–431.
Leites, L., Robinson, A.P., 2004. Improving taper equations with crown dimensions in a mixed-effects modeling framework. Forest Sci. 50, 204–212.
Li, J., Hong, Y., Thapa, R., Burkhart, H., 2015. Survival analysis of loblolly pine trees with spatially correlated random effects. J. Am. Stat. Assoc. 110, 486–502.
Lorimer, C.G., Dahir, S.E., Nordheim, E.V., 2001. Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. J. Ecol. 89, 960–971.
Lutz, J.A., Halpern, C.B., 2006. Tree mortality during early forest development: a long-term study of rates, causes, and consequences. Ecol. Monogr. 76, 257–275.
van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. Science 323, 521–524.
Martínez-Pastur, G., Lencinas, M.V., Cellini, J.M., Mundo, I., 2007. Diameter growth: can live trees decrease? Forestry 80, 83–88.
Monserud, R.A., 1976. Simulation of forest tree mortality. Forest Sci. 22, 438–444.
Monserud, R.A., Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. For. Ecol. Manage. 113, 109–123.
Mugasha, W.A., Eid, T., Bollandsås, O.M., Mbwambo, L., 2017. Modelling diameter growth, mortality and recruitment of trees in miombo woodlands of Tanzania. Southern Forests: J. For. Sci. 79, 51–64.
Norden, N., Angarita, H.A., Bongers, F., Martínez-Ramos, M., Granzow-de la Cerda, I.n., van Breugel, M., Lebrija-Trejos, E., Meave, J.A., Vandermeer, J., Williamson, G.B., Finegan, B., Mesquita, R., Chazdon, R.L., 2015. Successional dynamics in neotropical forests are as uncertain as they are predictable. PNAS 112, 8013–8018.
Nyland, R.D., 1996. Silviculture: Concepts and Applications. McGraw-Hill, USA, pp. 633.
O'Brien, M.J., Engelbrecht, B.M.J., Joswig, J., Pereyra, G., Schuldt, B., Jansen, S., Kattge, J., Landhäusser, S.M., Levick, S.R., Preisler, Y., Väänänen, P., Macinnis-Ng, C., 2017. A synthesis of tree functional traits related to drought-induced mortality in forests across climatic zones. J. Appl. Ecol. 54, 1669–1686.
Peet, R.K., Christensen, N.L., 1987. Competition and tree death. Bioscience 37, 586–595.
Pinheiro, J.C., Bates, D.M., 2000. Mixed-effects Models in S and Splus. Springer-Verlag, New York, USA, pp. 528.
Pogoda, P., Ochał, W., Orzeł, S., 2019. Modeling diameter distribution of black alder (*Alnus glutinosa* (L.) Gaertn.) stands in Poland. Forests 10, 412.
Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G., Harms, K.E., Licona, J.C., Martínez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Peña-Claros, M., Webb, C.O., Wright, I.J., 2008. Are functional traits good predictors of demographic rates? evidence from five neotropical forests. Ecology 89, 1908–1920.
Prabhakaran, S., 2016. InformationValue: Performance Analysis and Companion Functions for Binary Classification Models. R package version 1.2.3.
Pretzsch, H., 2009. Forest Dynamics, Growth and Yield. Springer-Verlag, Freising, Germany, pp. 664.
Pretzsch, H., Biber, P., Dursky, J., 2002. The single tree-based stand simulator SILVA: construction, application and evaluation. For. Ecol. Manage. 162, 3–21.
R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org.
Reynolds, M.R., Burk, T.E., Huang, W.C., 1988. Goodness-of-fit tests and model selection procedures for diameter distribution models. Forest Sci. 34, 373–399.
Rose Jr., C.E., Hall, D.B., Shiver, B.D., Clutter, M.L., Borders, B., 2006. A multilevel approach to individual tree survival prediction. Forest Sci. 52, 31–43.
Rossberg, A.G., Barabás, G., Possingham, H.P., Pascual, M., Marquet, P.A., Hui, C., Evans, M.R., Meszéna, G., 2019. Let's train more theoretical ecologists – here is why. Trends Ecol. Evol. 34, 759–762.
Salas, C., 2011. Modelling tree height growth of Nothofagus forests in south-central Chile: Merging differential equations and mixed-effects models. Ph.D. Dissertation. Yale University, New Haven, CT, USA 158 p.
Salas, C., Donoso, P.J., Vargas, R., Arriagada, C.A., Pedraza, R., Soto, D.P., 2016. The forest sector in Chile: an overview and current challenges. J. Forest. 114, 562–571.
Salas, C., Stage, A.R., Robinson, A.P., 2008. Modeling effects of overstory density and competing vegetation on tree height growth. Forest Sci. 54, 107–122.
Salas-Eljatib, C., Weiskittel, A.R., 2018. Evaluation of modeling strategies for assessing self-thinning behavior and carrying capacity. Ecol. Evol. 8, 10768–10779.
Schabenberger, O., Pierce, F.J., 2002. Contemporary Statistical Models for the Plant and Soil Sciences. CRC Press, Boca Raton, FL, USA, pp. 738.
Shaffer, T.L., 2004. A unified approach to analyzing nest success. Auk 121, 526–540.
Sheil, D., Burslem, D.F.R.P., Alder, D., 1995. The interpretation and misinterpretation of mortality rate measures. J. Ecol. 83, 331–333.
Suarez, M.L., Ghermandi, L., Kitzberger, T., 2004. Factors predisposing episodic drought-induced tree mortality in Nothofagus-site, climatic sensitivity and growth trends. J. Ecol. 92, 954–966.
Temesgen, H., Mitchell, S.J., 2005. An individual-tree mortality model for complex stands of southeastern British Columbia. West. J. Appl. For. 20, 101–109.
Temesgen, H., von Gadow, K., 2004. Generalized height–diameter models—an application for major tree species in complex stands of interior British Columbia. Eur. J. Forest Res. 123, 45–51.
Thapa, R., Burkhart, H.E., 2015. Modeling stand-level mortality of loblolly pine (*Pinus taeda* L.) using stand, climate, and soil variables. Forest Sci. 61, 834–846.
Veblen, T.T., Hill, R.S., Read, J. (Eds.), 1996. The Ecology and Biogeography of Nothofagus Forests. Yale University Press, New Haven, CT, pp. 428.
Wang, M., Borders, B., Zhao, D., 2007. Parameter estimation of base–age invariant site index models: Which data structure to use? Forest Sci. 53, 541–551.
Weiskittel, A.R., Hann, D.W., Kershaw Jr., J.A., Vanclay, J.K., 2011. Forest Growth and Yield Modeling. John Wiley & Sons.
Wilson, D., Monleon, V., Weiskittel, A, 2019. Quantification and incorporation of uncertainty in forest growth and yield projections using a Bayesian probabilistic framework: A demonstration for plantation coastal Douglas-fir in the Pacific Northwest, USA. Math. Comput. Fore. Natural-Resource Sci. 11, 264–285.
Wong, G.Y., Mason, W.M., 1985. The hierarchical logistic regression model for multilevel analysis. J. Am. Stat. Assoc. 80, 513–524.
Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R., Dalling, J.W., Davies, S.J., Díaz, S., Engelbrecht, B.M.J., Harms, K.E., Hubbell, S.P., Marks, C.O., Ruiz-Jaen, M.C., Salvador, C.M., Zanne, A.E., 2010. Functional traits and the growth-mortality trade-off in tropical trees. Ecology 91, 3664–3674.
Wunder, J., Reineking, B., Bigler, C., Bugmann, H., 2008. Predicting tree mortality from growth data: how virtual ecologists can help real ecologists. J. Ecol. 96, 174–187.
Wykoff, W.R., Crookston, N.L., Stage, A.R., 1982. User's guide to the Stand Prognosis Model. USDA For. Serv. Gen. Tech. Rep. INT-133. USA. 112 p.
Yang, Y., Huang, S., 2013. A generalized mixed logistic model for predicting individual tree survival probability with unequal measurement intervals. Forest Sci. 59, 177–187.
Yang, Y., Titus, S.J., Huang, S., 2003. Modeling individual tree mortality for white spruce in Alberta. Ecol. Model. 163, 209–222.
Yao, X., J, S.T., MacDonald, S.E., 2001. A generalized logistic model of individual tree mortality for aspen, white spruce, and lodgepole pine in Alberta mixedwood forests. Can. J. For. Res. 31, 283–291.
Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., Latimer, A.M., 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. Ecol. Lett. 20, 78–86.
Zens, M.S., Peart, D.R., 2003. Dealing with death data: individual hazards, mortality and bias. Trends Ecol. Evol. 18, 366–373.
Zhang, X., Cao, Q.V., Duan, A., Zhang, J., 2017. Modeling tree mortality in relation to climate, initial planting density, and competition in Chinese fir plantations using a Bayesian logistic multilevel method. Can. J. For. Res. 47, 1278–1285.
Zuleta, D., Benavides, A.M., López-Ríos, V., Duque, A., 2016. Local and regional determinants of vascular epiphyte mortality in the Andean mountains of Colombia. J. Ecol. 104, 841–849.