Tree mortality in Central Europe: Empirically-based modeling using long-term datasets

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Lisa Hülsmann
Universität Regensburg

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Empirically-based modeling using long-term datasets

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presented by
LISA HÜLSMANN

M.Sc. in Hydrogeology and Environmental Geoscience,
University of Göttingen

born on 31.05.1985
citizen of Germany

accepted on the recommendation of

Prof. Dr. Harald Bugmann, examiner
Dr. Peter Brang, co-examiner
Prof. Dr. Jürgen Bauhus, co-examiner

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We are only beginning to appreciate
the complexity of patterns of tree death.
(Franklin *et al.*, 1987)

Content

Summary

Tree mortality – one of the key processes of population dynamics – is increasingly studied against the backdrop of future climate change. Nevertheless, mortality studies are complicated by the high temporal and spatial variability and the complex and interacting factors contributing to tree death. Empirical models are particularly valuable to investigate tree mortality since they enable the identification of patterns and drivers of tree death, assist in management decisions and are key to reliably simulate future forest dynamics. In this thesis, I systematically assessed the state of the art in empirical tree mortality modeling, analyzed patterns of tree death and developed and evaluated robust mortality formulations based on extensive long-term datasets for incorporation in Dynamic Vegetation Models (DVMs).

Chapter 1. The aim of this chapter was to analyze the suitability of empirical mortality algorithms for extrapolation in space or time. To this end, 46 inventory-based models were systematically validated using nearly 80 000 independent records covering 11 species from unmanaged forests in Germany and Switzerland. Mortality models achieved higher accuracy if covariates for tree growth and/or competition at the individual tree level were included and if models were applied within the same ecological zone. The size of the calibration dataset did not influence model performance. Consequently, mortality algorithms for applications over a restricted spatial extent should be calibrated based on datasets from the same region, even if they include a few hundred observations only. However, the high variability of mortality patterns suggests that environmental influences should be considered explicitly in mortality models to obtain wide applicability.

Chapter 2. In this chapter, I explicitly addressed the differences among mortality models that had been identified in Chapter 1. The predicted mortality probabilities of a large set of inventory- and tree-ring-based mortality models were analyzed using hierarchical cluster analysis. The resulting dendrograms reflected the diversity of approaches in mortality modeling, i.e., the field design as well as the approach for statistical modeling (in particular the sampling scheme of tree-ring data). However, these differences did not modify mortality predictions in a systematic way. Because of the large variety of approaches, it was not possible to evaluate the need for species-specific models, nor to identify a reasonable

grouping of species with similar mortality patterns. The results emphasize – once more – that tree mortality is highly variable in space and time, and that our knowledge on the mechanisms behind this variability is limited.

Chapter 3. Using *Fagus sylvatica* L. as an example, I developed a calibration and evaluation approach for robust mortality models that allows one to consider additional environmental covariates. Tree death was modelled as a function of size and growth using generalized logistic regression accounting for unequal re-measurement intervals based on inventory data from nearly 19 000 trees from unmanaged European forests. Mortality patterns in Swiss and German strict forest reserves were dominated by competition processes, whereas a Ukrainian primeval beech forest was also characterized by disturbance-related mortality of large trees. The models revealed strong spatial and temporal variability in mortality that was independent of environmental and stand characteristics. Nevertheless, the Swiss and German models achieved good performance when validated against each other.

Chapter 4. Here, the approach of Chapter 3 that revealed robust mortality models with a high potential for incorporation in DVMs was applied to calibrate species-specific mortality models for 18 European tree species. I used more than 90 000 records from inventories in Swiss and German strict forest reserves along a wide environmental gradient. Mortality of almost all species was successfully predicted by tree size and growth, reflecting the indirect influences of resource availability and vitality on mortality. These relationships were further shaped by species-specific attributes, in particular lifespan, shade and drought tolerance. Only few species required additional covariates in their final model to capture key differences in stand structure or climate. Incorporated in the DVM ForClim, the new mortality functions revealed simulations of stand basal area and species composition that were generally close to historical observations. However, their performance was lower than simulated with the original ForClim version, resulting from feedbacks of simulated growth and mortality as well as from extrapolation to very small and very large trees.

Overall, the findings of this thesis suggest that tree mortality models based on size and growth alone are suited to reliably predict tree death. Their relationship is dominantly reverse J-shaped, suggesting competition as the most dominant mortality agent in Central European forests, whereas processes that amplify the mortality of large trees are only common in true old-growth forests. The results further emphasize the substantial value of inventory data for the calibration of mortality models since, in contrast to dendrochronological data, they provide stand-scale mortality rates. Additional climate and stand characteristics improved the accuracy of mortality models only weakly and were included for a few species only. I conclude that their predictions respond to water availability and stand density via the integrating vitality indicator tree growth. The climatic sensitivity of mortality models should be further investigated using data with annual resolution along wide and well-replicated environmental gradients. Empirical mortality models were found to be structurally suitable for incorporation in DVMs. To improve their performance, growth and mortality processes and their species-specific differences should be revisited jointly, with a particular focus on small trees and shade-tolerant species.

I propose the following strategies to further advance empirical mortality models: (1) develop models for sapling mortality, (2) intensify the efforts to address disturbance-related mortality, (3) continue the implementation of empirical mortality formulations in DVMs and account for the involved uncertainties, and (4) more effectively explore available and future datasets for the calibration of tree mortality models.

This thesis provides a systematical assessment of previous approaches for tree mortality modeling and suggests a strategy towards robust mortality models for a wide range of tree species. Their mortality patterns could be related to species-specific life history strategies. Finally, the analyses indicated the most important mortality factors and their importance in managed and unmanaged forests in Europe. Due to the unique spatial extent and the extensive database in combination with cautious, systematic analyses and modelling, the conclusions can be transferred to a wider European context.

Zusammenfassung

Baummortalität ist einer der Schlüsselprozesse der Walddynamik. In Zeiten eines sich wandelnden Klimas ist Mortalität vermehrt in den Fokus der Forschung gerückt. Die Untersuchung der Baummortalität wird allerdings durch ihre ausgeprägte Variabilität sowie die komplexen Faktoren, die dem Absterben von Bäumen zugrunde liegen, erschwert. Empirische Mortalitätsmodelle sind von besonderer Bedeutung, da sie helfen, Absterbeprozesse besser zu verstehen, als Hilfestellung für die Wald-Bewirtschaftung dienen und eine wichtige Grundlage für die Modellierung der Entwicklung von Wäldern darstellen. In dieser Dissertation wurden eine systematische Bestandsaufnahme und Evaluation der heute verfügbaren Mortalitätsmodelle durchgeführt und robuste Mortalitätsmodelle mithilfe von umfangreichen Langzeit-Datensätzen kalibriert und in dynamischen Vegetationsmodellen (DVMs) getestet.

Kapitel 1. Zunächst wurde die räumliche und zeitliche Übertragbarkeit von empirischen Mortalitätsmodellen untersucht. Zu diesem Zweck wurden 46 inventurbasierte Modelle mit fast 80 000 Datensätzen von 11 Baumarten aus unbewirtschafteten Wäldern in der Schweiz und in Deutschland validiert. Dabei erzielten jene Modelle die besten Ergebnisse, welche die Mortalitätswahrscheinlichkeit anhand des Zuwachses und/oder der Konkurrenzsituation des Einzelbaums vorhersagten und innerhalb der gleichen ökologischen Grossregion angewandt wurden. Umfangreichere Kalibrationsdatensätze führten hingegen nicht zu einer höheren Genauigkeit. Folglich sollten Mortalitätsmodelle für den räumlich begrenzten Einsatz mit Datensätzen aus der gleichen Region kalibriert werden, auch wenn diese nur wenige hundert Beobachtungen umfassen. Da die Mortalitätsmuster zwischen den untersuchten Modellen eine grosse Variabilität zeigten, ist es wichtig, die jeweiligen Standortverhältnisse explizit in Mortalitätsmodellen zu berücksichtigen, um ihre allgemeine Gültigkeit zu verbessern.

Kapitel 2. Die grosse Variabilität der Vorhersagen von Mortalitätsmodellen, die sich im ersten Kapitel abzeichnete, wurde im Folgenden näher analysiert. Dazu wurden inventur- und jahrringbasierte Modelle anhand ihrer prognostizierten Mortalitätswahrscheinlichkeit verglichen und in einer hierarchischen Clusteranalyse untersucht. Die resultierenden Dendrogramme ergeben sich aus einer Vielzahl von Modellierungsansätzen, z.B. der

statistischen Vorgehensweise sowie insbesondere dem Schema zur Aggregation von dendrochronologischen Daten. Die verschiedenen Methoden beeinflussten die Vorhersagen allerdings nicht auf systematische Weise. Aufgrund der grossen Unterschiede war es nicht möglich, die Notwendigkeit von artspezifischen Mortalitätsmodellen zu bestätigen oder Artgruppen mit ähnlichen Mustern zu identifizieren. Einmal mehr unterstreicht dies die grosse Variabilität der Baummortalität und das begrenzte Verständnis des Absterbeprozesses.

Kapitel 3. Am Beispiel von *Fagus sylvatica* L. und einem Datensatz von fast 19 000 Bäumen aus unbewirtschafteten europäischen Wäldern wurde eine Methode zur Kalibration und Evaluation von robusten Mortalitätsmodellen entwickelt, welche Klima- und Bestandsfaktoren berücksichtigt. Basierend auf einer generalisierten logistischen Regression, welche die Verwendung von Inventurdaten mit unterschiedlich langen Messintervallen ermöglicht, wurde die Mortalitätswahrscheinlichkeit anhand des Stammdurchmessers und des Grundflächenzuwachses vorhergesagt. Die Mortalitätsmuster weisen auf Konkurrenz als Hauptmortalitätsursache in Schweizer und deutschen Waldreservaten hin, wogegen in einem ukrainischen Urwald störungsbedingte Mortalität zu einer erhöhten Sterblichkeit von grossen Bäumen führte. Die Modelle zeigten eine grosse räumliche und zeitliche Variabilität der Mortalität, die durch Umweltvariablen nicht verringert werden konnte. Dennoch erzielten das Schweizer und das deutsche Modell auch im jeweils anderen Land eine hohe Genauigkeit.

Kapitel 4. Da mit dem zuvor entwickelten Vorgehen robuste und für die Implementierung in DVMs geeignete Mortalitätsmodelle kalibriert werden konnten, wurden auf gleiche Weise artspezifische Modelle für 18 Arten erstellt. Zu diesem Zweck verwendete ich mehr als 90 000 Inventurdatensätze aus Schweizer und deutschen Naturwaldreservaten entlang von nennenswerten Umweltgradienten. Durchmesser und Grundflächenzuwachs waren für fast alle Baumarten erfolgreiche Prädiktoren der Mortalität und spiegelten den indirekten Einfluss von Ressourcenverfügbarkeit und Vitalität auf das Absterben der Bäume wieder. Dieser Zusammenhang variierte je nach Baumart und korreliert mit dem Langlebigkeit sowie der Schatten- und Trockentoleranz. Nur wenige Mortalitätsmodelle benötigten zusätzliche Klima- oder Bestandsvariablen. Im DVM ForClim führten die neuen Mortalitätsmodelle zu einer ähnlichen Bestockung und Artenzusammensetzung wie im Beobachtungsdatensatz. Allerdings reichte ihre Genauigkeit nicht an die der ursprünglichen ForClim-Version heran, was auf Interaktionen zwischen der Wachstums- und Mortalitätssimulation in ForClim und die Extrapolation bei sehr kleinen und sehr grossen Bäumen zurückzuführen war.

Die Ergebnisse dieser Dissertation bestätigen, dass Modelle, die allein auf Durchmesser und Grundflächenzuwachs basieren, geeignet sind, um die Sterblichkeit von Bäumen vorherzusagen. Die zumeist abnehmende Mortalitätswahrscheinlichkeit mit zunehmender Grösse und schnellerem Wachstum weist auf Konkurrenz als wichtigste Mortalitätsursache in mitteleuropäischen Wäldern hin. Faktoren, die zum Tod von insbesondere grossen Bäumen führen, finden sich hingegen hauptsächlich in echten Urwäldern. Zudem zeigte sich, dass Inventurdaten unerlässlich für die Kalibration von Modellen zur Vorhersage von Mortalitätsraten auf Bestandsebene sind. Im Gegensatz dazu haben dendrochronologische Daten einen deutlichen Bias. Zusätzliche Klima- oder Bestandsvariablen verbesserten Mortalitätsmodelle nur geringfügig und nur für wenige Arten. Folglich wirken sich Umwelteinflüsse wie Trockenheit und Bestandsdichte in erster Linie indirekt, d.h. über die Wachstumsvariable, auf die Sterblichkeit aus. Es sollte daher im Detail untersucht werden, wie klimasensitiv die vorgeschlagenen Mortalitätsmodelle sind, z.B. anhand von jährlich-aufgelösten Daten mit einer guten Abdeckung von Umweltgradienten. Strukturell waren die empirischen Mortalitätsmodelle geeignet, um Mortalität in DVMs vorherzusagen. Die Vorhersagen sollten zusätzlich verbessert werden, indem die Abbildung von Wachstum und Mortalität gleichzeitig angepasst und dabei insbesondere auf die Vorhersage der Sterblichkeit von kleinen Bäumen und schattentoleranten Arten geachtet wird.

Ich schlage folgende Strategien zur Verbesserung empirischer Baummortalitätsmodelle vor: (1) das Entwickeln von Mortalitätsmodellen für sehr junge Bäume, (2) die verstärkte Berücksichtigung von störungsbedingter Mortalität, (3) die vermehrte Nutzung von empirischen Mortalitätsfunktionen in DVMs unter Beachtung der Modellunsicherheit, und (4) die intensivierte Erschliessung und Aggregation bereits vorliegender und zukünftiger Datensätze für die Kalibration von Mortalitätsmodellen.

Diese Dissertation ermöglicht eine systematische Einschätzung bisheriger Strategien in der Baummortalitätsmodellierung und stellt eine umfangreiche Palette von robusten Modellen zur Verfügung. Des Weiteren konnten die Mortalitätsmuster mit artspezifischen Überlebensstrategien in Verbindung gebracht und die wichtigsten Mortalitätsursachen und ihre Bedeutung in verschiedenen bewirtschafteten Wäldern Europas aufgezeigt werden. Aufgrund der umfangreichen Datengrundlage und der systematischen Vorgehensweise lassen die Ergebnisse dieser Arbeit Rückschlüsse auch in einem grösseren europäischen Kontext zu.

General introduction

Facing a variety of unprecedented environmental changes that are anticipated to unfold by the end of this century, scientists are confronted with the urgent need to quantify future responses of ecosystems to new climates and anthropogenic impacts (Evans, 2012). This knowledge is indispensable for the timely initiation of measures that are necessary to maintain ecosystem goods and services (De Groot *et al.*, 2002; Temperli *et al.*, 2012). Ecological simulation models of various kinds therefore have received great attention (e.g., Guisan & Zimmermann, 2000; Sitch *et al.*, 2008), are continuously refined (Busing & Mailly, 2004; Yue *et al.*, 2011) and, in spite of the uncertainties involved, serve as tools to support decision-making (Seidl *et al.*, 2011; Lindner *et al.*, 2014; Bircher, 2015).

Forests are expected to be particularly vulnerable to future environmental change since trees have a lower potential to quickly adapt to new environmental conditions due to their long life cycle (Lindner *et al.*, 2010). Consequently, tree mortality rates may increase and catastrophic mortality events may become more frequent and severe, resulting from higher temperature and reduced water availability (Allen *et al.*, 2010; Steinkamp *et al.*, 2015). Studies that aim at elucidating the drivers of tree death and that assist in quantifying mortality are thus highly needed (Bircher *et al.*, 2015), e.g., by using empirical methods to relate tree and environmental characteristics to mortality patterns (Weiskittel *et al.*, 2011).

Empirical tree mortality models are particularly valuable since they address three essential concerns: they (1) enable the identification of patterns and drivers of tree death, (2) assist in management decisions, and (3) are key for the reliable simulation of future forest dynamics (Cailleret *et al.*, 2016). Until now, the process descriptions in many dynamic vegetation models (DVMs), in particular the representation of tree survival, lack empirical justification (Loehle & LeBlanc, 1996; Keane *et al.*, 2001). Since tree death can be described quite precisely as ‘stochastic, rare and irregular’ (Eid & Tuhus, 2001), its investigation is hampered by limited data and high variability (Bugmann, 1996). Tree mortality thus remains one of the least understood processes in the simulation of stand dynamics (Hawkes, 2000; Adame *et al.*, 2010). This is particularly problematic since projections of future forest dynamics are highly sensitive to mortality formulations (Friend *et al.*, 2014; Bircher *et al.*, 2015). Consequently, improved concepts for the modeling of tree mortality are urgently needed (Liang & Picard, 2013).

Tree mortality as a key process of forest dynamics

Population dynamics are shaped by three key processes or vital rates: survival, growth and recruitment (Ruiz-Benito *et al.*, 2013; Merow *et al.*, 2014). While tree growth affects forests gradually, the influences of tree mortality are more abrupt. Additionally, the death of trees alters forests from the stand scale (e.g., forest structure and species composition; cf. Harper, 1977) to the regional scale (e.g., species range shifts; cf. Monleon & Lintz, 2015) and up to the global scale (e.g., carbon cycle; cf. Pan *et al.*, 2011).

Complex interactions of multiple factors control when, which and how many trees die (Franklin *et al.*, 1987). The factors that induce lethal stress can be abiotic, e.g., drought, heat, wind or rock fall, or biotic, e.g., inter- and intra-specific competition, insects, fungi or browsing. Mortality agents and rates strongly depend on tree age and the successional stage of forest stands (Holzwarth *et al.*, 2013). Higher mortality rates are typically found in younger trees, where competition is the main driver of death, but were also suggested for old trees as a result of a larger number of mortality agents or senescense (Buchman *et al.*, 1983). Because of these age and size effects, mortality over diameter is often considered to be reverse J- or U-shaped (Harcombe, 1987; Ruiz-Benito *et al.*, 2013).

Tree mortality is characterized by high temporal and spatial variability (Hawkes, 2000; Wunder, 2007), which is enhanced by catastrophic mortality events arising from wind, forest fires, insect attacks, disease or drought (Franklin *et al.*, 1987). In addition, mortality processes may vary due to site conditions with respect to soil, climate or pollutants (cf. Lines *et al.*, 2010; Dietze & Moorcroft, 2011; Uzoh & Mori, 2012). Since tree species have diverse life history strategies, among others lifespan and competitiveness, they vary in their reaction to stress (Franklin *et al.*, 1987). Stress-intolerant and short-lived species are assumed to have higher death rates (Harcombe, 1987).

Mortality formulations in DVMs

In forest simulation models, tree death is typically separated into ‘regular’ and ‘irregular’ mortality (Lee, 1971; Monserud, 1976; Kiernan *et al.*, 2009), although this differentiation is blurred (Weiskittel *et al.*, 2011). ‘Regular’ or ‘growth-dependent’ mortality is usually considered to be the result of competition and other non-extreme stress (Csilléry *et al.*, 2013) and affects individual trees. As it is determined by within-stand processes, regular mortality is assumed to be predictable using a set of tree and stand covariates that characterize vigor, competition or the lack of resources (Hawkes, 2000; Keane *et al.*, 2001). In contrast, ‘irregular’ or ‘disturbance-dependent’ mortality is ‘catastrophic’, resulting from larger-scale agents such as wind, disease and fire, and typically affects many trees simultaneously (Weiskittel *et al.*, 2011). It can be regarded as being unpredictable based on within-stand properties alone (Alenius *et al.*, 2003).

Early concepts of mortality in forest simulation models were developed based on theoretical assumptions, e.g., controlled by a threshold for tree growth (Botkin *et al.*, 1972; Bugmann, 2001), and remained the most common approach due to their simplicity and a lack of more sophisticated solutions (Monserud, 2003). However, the resulting projections of tree mortality were unsatisfactory since theoretical formulations are based on conceptual ideas of the mortality process that may contradict empirical relationships and thus are structurally questionable (Bigler & Bugmann, 2004; Wunder *et al.*, 2006).

In contrast, truly mechanistic approaches to capture tree mortality rely on physiological indicators of stress, e.g., based on water transport in the xylem or the whole-tree carbon budget, and aim at accounting for the underlying processes that ultimately result in mortality (Tague *et al.*, 2013; Anderegg *et al.*, 2015). In spite of the appeal of an explicit process representation, these models typically focus on one or few mortality factors only, i.e., they do not account for the full suite of stand-scale mortality agents and their potential interactions (McDowell *et al.*, 2013). In addition, the varying and interacting mortality factors and the underlying processes are not yet sufficiently understood. Advances in the development of truly mechanistic models thus may provide important insights on the involved processes, but to date only little progress has been made in applying fully mechanistic tree mortality models in DVMs (Weiskittel *et al.*, 2011; Adams *et al.*, 2013).

Recently, considerable efforts have been made to incorporate empirical mortality models into DVMs (e.g., Wernsdörfer *et al.*, 2008). Data-based approaches are common in growth and yield models, which simulate the short-term (i.e., decadal-scale) development of managed stands (cf. Hasenauer, 2006). Although the accuracy of yield predictions was improved by empirical mortality functions (cf. Radtke *et al.*, 2012), growth and yield models are only weakly sensitive to mortality formulations and thus do not provide a testbed for the thorough examination of the reliability of empirical mortality models (Bircher *et al.*, 2015). When implemented in DVMs, data-driven formulations partly improved the projections but also revealed inconsistencies in the interaction of growth and mortality (Bircher, 2015). Nevertheless, empirical models constitute a promising replacement of theoretical approaches, and their further development and incorporation in DVMs are thus highly recommended (Larocque *et al.*, 2011).

Empirical tree mortality models: Approaches and challenges

Going back to Keister (1972), Monserud (1976) and Hamilton *et al.* (1976), a considerable number of empirical mortality models for individual trees have been developed for several regions and species. These models use different data sources to elucidate the relation of tree death to various independent variables (Weiskittel *et al.*, 2011). Predictors of tree death were classified following different concepts (e.g., Hamilton, 1986; Hawkes, 2000; Fridman & Ståhl, 2001), but in general four main categories can be distinguished. First, tree size is used as a predictor of mortality based on variables such as diameter or height to reflect the tree's access to resources such as light and nutrients (Harcombe, 1987). Second, tree vigor is considered by using variables of stem growth or crown condition (e.g., Monserud, 1976; Cailleret *et al.*, 2016). Third, some mortality models account for competition based on stand structure and density or one-sided competition calculated at the tree level (e.g., Bravo-Oviedo *et al.*, 2006). Finally, spatial and temporal differences in mortality are addressed in some approaches using site characteristics such as climate, soil or productivity (e.g., Dietze & Moorcroft, 2011). With a few exceptions (e.g., Eid & Tuhus, 2001), such mortality models were calibrated at the species level to account for species-specific differences in the reaction to stress (Ireland *et al.*, 2014).

Methodologically, the death of individual trees is typically modeled using logistic regression, since the response variable (live or dead) is binary (Woolley *et al.*, 2012). However, the studies differ considerably with respect to the covariates considered and the strategy of model selection. Less common modeling techniques are artificial neural networks (Guan & Gertner, 1991), support vector methods (King *et al.*, 2000), classification and regression trees (Dobbertin & Biging, 1998), generalized estimating equations (Kiernan *et al.*, 2009), capturerecapture approaches (Moustakas & Evans, 2015) and semiparametric regression (Vieilledent *et al.*, 2009). In addition, increasing attention has been paid to non-parametric Bayesian inference (Wyckoff & Clark, 2000; Metcalf *et al.*, 2009).

Data for the development of mortality models can be derived from long-term re-measurements of permanent plots (e.g., Boeck *et al.*, 2014) or from increment cores (e.g., Macalady & Bugmann, 2014). Both data sources require intensive field campaigns and measurement effort (Wyckoff & Clark, 2000) and feature different assets and drawbacks. Inventory data allow for the derivation of the multi-annual mortality probability of individual trees as well as of population-based mortality rates and include a wide range of species and site conditions (Weiskittel *et al.*, 2011). In contrast, dendrochronological data provide a much higher temporal resolution and thus are likely to have higher potential for contributing to the understanding of the interactions between environment, growth and tree mortality (e.g., Bigler *et al.*, 2004; Gillner *et al.*, 2013). Tree-ring-based models rely nearly exclusively on tree growth as a predictor of tree death but analyze the influence of growth level, trend and variability on mortality in great detail (e.g., Carus, 2010; but cf. Gea-Izquierdo *et al.*, 2014). However, tree-ring datasets typically cover only few species and sites (Cailleret *et al.*, 2016). Additionally, they suffer from difficulties concerning the derivation of population-based mortality rates (Weiskittel *et al.*, 2011) and the accuracy of death dates (Jones & Daniels, 2012; Bigler & Rigling, 2013).

Datasets for deriving the relationship between explanatory variables and mortality considering species and site differences are rare (Keane *et al.*, 2001; Wyckoff & Clark, 2002) since they need to be large to reliably inform on the mortality process (Metcalf *et al.*, 2009). The transfer of empirical models to new environmental conditions must necessarily be based on the assumption of a stable relationship between predictors and mortality (Keane *et al.*, 2001) and is hence restricted by the calibration domain of the models in terms of space, time and resolution (Woolley *et al.*, 2012). This may constrain the performance of the models that are currently available when incorporated in DVMs, because they have usually been developed based on small, spatially restricted datasets. Nevertheless, empirical mortality models are increasingly applied in models of forest dynamics (Wernsdörfer *et al.*, 2008; Larocque *et al.*, 2011; Bircher, 2015), although information on their applicability at larger temporal extent and under different site conditions is mostly missing, since they have only rarely been validated with independent data (Hawkes, 2000).

In several studies, climatic, soil or stand covariates have been included in mortality models, but the regional-scale variability in tree mortality remains poorly understood (Dietze & Moorcroft, 2011). Conversely, growth has often not been considered as a covariate in models that explicitly account for environmental influences (e.g., Lines *et al.*, 2010), although growth itself is responsive to the environment (Dobbertin, 2005). Consequently, the interdependencies between tree size, growth, environment and mortality remain unclear. This is particularly unfortunate since additional environmental covariates may explain spatial and temporal differences in the relationship of tree characteristics and mortality (Hasenauer *et al.*, 2001; Wunder, 2007) and thus could increase the applicability and generality of mortality functions.

In conclusion, difficulties in simulating tree mortality are related to the restricted knowledge on the applicability of available mortality formulations and the lack of robust models for a broad set of tree species and site conditions. In this thesis, I thus focus on advancing empirical mortality models with respect to their development, evaluation and incorporation in DVMs by making consistent use of a large database.

Data sources

This thesis is fundamentally based on data from two large networks of strict forest reserves in Switzerland and Germany / Lower Saxony (Fig. 1; cf. Meyer *et al.*, 2006; Heiri *et al.*, 2011). The first reserves were founded in the 1940s (Switzerland) and 1970s (Germany), and since then, permanent plots in the reserves have been periodically re-measured up to six times. Forest management had been given up much earlier in many cases, so that the reserves provide an exceptional opportunity to study forest dynamics in the absence of direct human disturbances (Heiri *et al.*, 2009) and thus to investigate natural tree mortality, which is higher than in managed forests (Bravo-Oviedo *et al.*, 2006). Some of the Swiss reserve data have already been used for the investigation of mortality patterns and the development of mortality models (e.g., Wunder *et al.*, 2008; Rohner *et al.*, 2012). The full Swiss dataset can now be used together with the German data, thus providing an exceptional amount of information on the life history of single trees. The networks comprise data of ca. 180 000 individual trees of ca. 60 species on > 400 permanent plots in ca. 100 reserves. Although the reserves do not represent a random sample of the forested area, they cover a large gradient of environmental conditions and the most important forests types of Central Europe (Brang *et al.*, 2011).

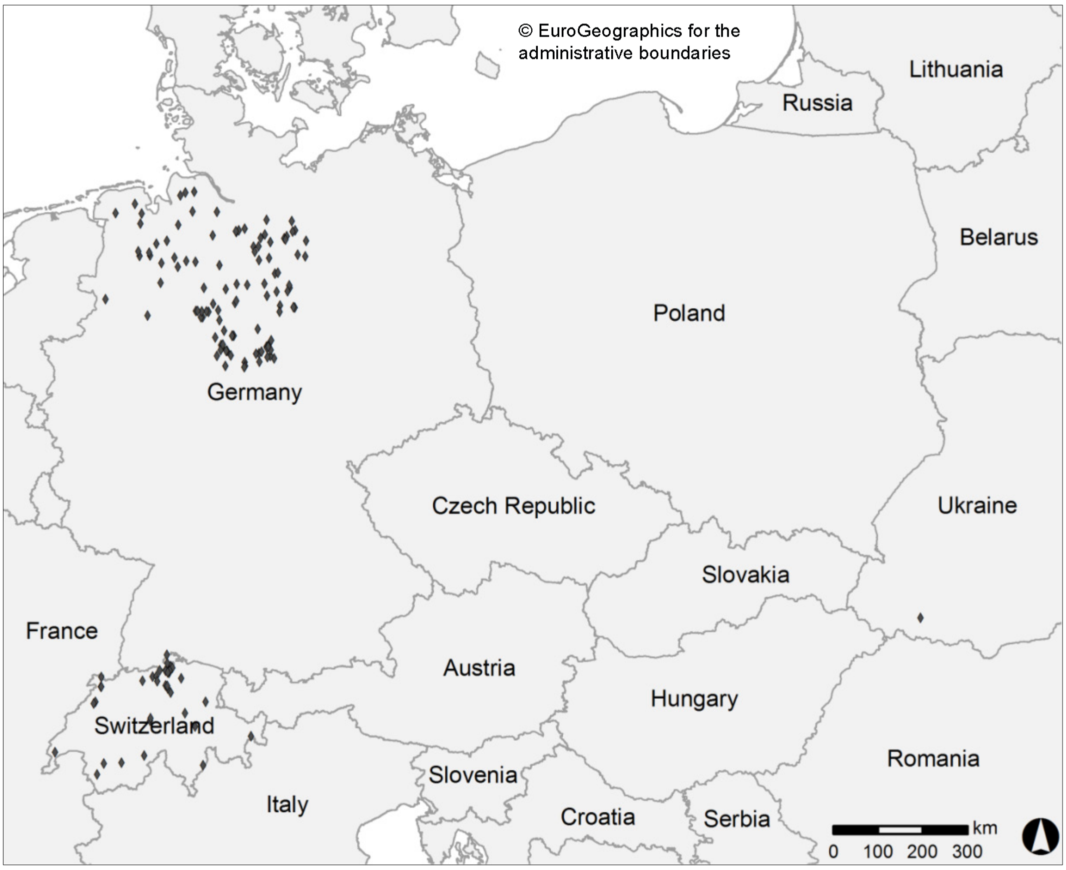

Fig. 1 Map of the strict forest reserves in Switzerland and Germany and the Ukrainian primeval forest used in this thesis.

In addition, a set of three inventories from a 10 ha plot in the primeval beech forest Uholka in Western Ukraine could be used as a reference for mortality patterns of *Fagus sylvatica* L. in truly unmanaged forests (Chapter 3; cf. Commarmot *et al.*, 2005; Peck *et al.*, 2015). Finally, the inventory data could be combined with an extensive dendrochronological dataset based on 1010 cored trees of eight species that were taken primarily from dead trees in the Swiss reserves (Chapter 2; cf. Vanoni *et al.*, 2016a; Vanoni *et al.*, 2016b; Vanoni *et al.*, in prep.). These were taken within an associated Ph.D. project. Both theses were carried out within the framework of the project ‘Predicting growth-dependent tree mortality: A key challenge for population ecology’ funded by the Swiss National Science Foundation (SNF). Particularly Chapters 2 and 4 of this thesis are the result of collaborations within this project.

Objectives and structure of the thesis

In order to analyze patterns of tree death and advance empirically-based mortality formulations, I (1) assessed the state of the art in tree mortality modeling based on long-term datasets and (2) developed and evaluated new mortality formulations for incorporation in DVMs. These two parts are structured as follows:

In Chapters 1 and 2, I assessed the transferability of European mortality models that have been published in the last decades to new environmental conditions and analyzed their predictive behavior. To this end,

- 46 inventory-based mortality models were validated with inventory data from Switzerland and Germany, and
- the predictive behavior of 46 inventory- and 52 tree-ring-based mortality models was analyzed using hierarchical clustering.

In Chapters 3 and 4, I addressed the need for robust mortality functions to be implemented in DVMs by making use of extensive inventory datasets and analyzed mortality patterns with respect to tree size and growth. For this purpose,

- a methodology for the calibration and evaluation of robust and parsimonious mortality models was developed and tested using the example species *Fagus sylvatica*,
- species-specific mortality models for 18 tree species were calibrated, and the potential of explaining the spatial and temporal variability of mortality was explored using environmental covariates, and
- these new mortality formulations were implemented in the DVM ForClim (Bugmann, 1996) to assess their suitability for the simulation of short- and long-term forest dynamics.

Chapter 1

In earlier studies, empirical mortality algorithms have been developed following contrasting strategies concerning the covariates considered, the types of forest stands used for calibration and the extent of the calibration data. To assess the suitability of these models for extrapolation in space or time, I rigorously validated 46 inventory-based mortality models using nearly 80 000 independent records from strict forest reserves in Switzerland and Germany and systematically analyzed model performance. In particular, I addressed the following questions: (1) Which predictors warrant high accuracy of simulated tree mortality? (2) Are 'regional models', i.e. functions that are calibrated and applied in similar environments, required to account for the variation in mortality? (3) Should model applications be restricted to the management intensity in the calibration data? (4) Does the size of the calibration and validation datasets influence the accuracy of mortality predictions? (5) Are predictions of individual tree mortality models sensitive to the length of census intervals?

Chapter 2

As found in Chapter 1, the mortality models differ considerably in the prediction of mortality patterns. To address these differences more explicitly, I analyzed the similarity of mortality predictions for a large set of inventory- and tree-ring-based models using hierarchical clustering. I hypothesized that (1) species or at least functional traits (e.g., deciduous vs. evergreen, shade tolerance), (2) predicted mortality type, i.e., 'regular' vs. 'irregular' mortality, (3) geographical origin of the calibration data, (4) management intensity and (5) the sampling scheme in tree-ring data should be influential model characteristics.

Chapter 3

Mortality models for the implementation in DVMs should be robust and thoroughly validated with good transferability to new environmental conditions. Taking these requirements into account, I developed parsimonious models for *Fagus sylvatica* based on inventory data from unmanaged forests in Switzerland, Germany and Ukraine, compared the mortality patterns between different European regions and comprehensively evaluated calibration and validation performance. Specifically, I aimed to answer three questions: (1) Does the growth-mortality relationship vary with site and stand characteristics, and particularly with water availability and competition? (2) How strongly does the prediction and classification accuracy of mortality models vary with tree size and between different sites? (3) How well do mortality models perform when applied outside their calibration range, i.e., in other forest reserves and in a primeval beech forest?

Chapter 4

Mortality models that consider species-specific traits are highly needed for the simulation of future forests under consideration of expected species range shifts and changes in species composition. To this end, I developed and validated mortality models for an extended set of 18 species using the approach presented in Chapter 3. In addition, the new mortality functions were incorporated in the DVM ForClim. I addressed three main questions: (1) Can life history strategies such as lifespan and stress tolerance be used to group tree species into reasonable PFTs that account for species differences in mortality? (2) How successful are mortality models that are based on size and growth *alone* compared to models that include further climate or stand characteristics in accurately predicting tree mortality? (3) How do the new mortality functions perform when embedded in a DVM?

In a related study that was carried out within the same SNF-project on growth-related tree mortality modeling, we combined annual growth data from increment cores with size-dependent mortality rates at the population level to develop mortality models for six tree species (cf. Vanoni *et al.*, in prep.). This has been proposed to provide high temporal resolution as well as accurate stand-scale mortality rates (Das *et al.*, 2007). The resulting tree-ring-based models were again incorporated and evaluated in ForClim based on short- and long-term simulations. In the synthesis, I refer to the findings of this study and discuss them jointly with the results of the four chapters in this thesis.

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How to predict tree death from inventory data – Lessons from a systematic assessment of European tree mortality models

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[1] Research Unit Forest Resources and Management, WSL Swiss Federal Institute of Forest, Snow and Landscape Research, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

[2] Forest Ecology, Institute of Terrestrial Ecosystems, ETH Zurich, Universitätstrasse 16, 8092 Zurich, Switzerland

Abstract

The future development of forest ecosystems depends critically on tree mortality. However, the suitability of empirical mortality algorithms for extrapolation in space or time remains untested. We systematically analyzed the performance of 46 inventory-based mortality models available from the literature using nearly 80000 independent records from 54 strict forest reserves in Germany and Switzerland covering 11 species. Mortality rates were predicted with higher accuracy if covariates for tree growth and/or competition at the individual level were included and if models were applied within the same ecological zone. In contrast, classification of dead vs. living trees was only improved by growth variables. Management intensity in the calibration stands as well as the census interval and size of the calibration datasets did not influence model performance. Consequently, future approaches should make use of tree growth and competition at the level of individual trees. Mortality algorithms for applications over a restricted spatial extent and under current climate should be calibrated based on datasets from the same region, even if they are small. To obtain models with wide applicability and enhanced climatic sensitivity, the spatial variability of mortality should be addressed explicitly by considering environmental influences using data of high temporal resolution covering large ecological gradients. Finally, such models need to be validated and documented thoroughly.

Key-words

Dynamic vegetation models; Empirical mortality models; Forest inventory data; Independent validation; Systematic review

Introduction

Tree death within a forest ecosystem initiates a wide range of responses (Franklin *et al.*, 1987; Gendreau-Berthiaume *et al.*, 2016) and is a key factor shaping forest structure in terms of diameter distribution, stand density and species diversity (Friend *et al.*, 2014). Typically, tree mortality is the result of several interacting factors such as competition, drought, pathogens, snow, fire or frost, all of which decrease tree vitality (Waring, 1987). Consequently, tree death can hardly be associated with a single cause, which greatly complicates the mechanistic understanding of mortality (Wang *et al.*, 2012). Robust tree mortality algorithms (Manusch *et al.*, 2012) are an important component of Dynamic Vegetation Models (DVMs), which have proven to be useful for simulating forest succession, species range dynamics and the provisioning of ecosystem services in response to environmental changes (Bugmann, 2014; Snell *et al.*, 2014) from the local (Bugmann, 2001) to the global scale (Bonan *et al.*, 2003).

Mechanistic tree mortality models typically emphasize a single mortality factor, e.g. drought (Anderegg *et al.*, 2015), and thus are not qualified to predict the multiple and interacting physiological processes of tree mortality beyond the scale of case studies (Adams *et al.*, 2013). In contrast, empirical mortality formulations are not process-oriented but consider the underlying mechanisms implicitly (Woolley *et al.*, 2012). They are expected to have a lower parameter uncertainty and require fewer data because of fewer model parameters. Therefore, they were suggested as a valid and rapid alternative to process-based models (Adams *et al.*, 2013).

Empirical mortality models for European tree species have been developed based on inventory and dendrochronological data. Although inventory data feature a lower temporal resolution, with plots being typically re-measured every 5-15 years only, inventory-based models are more frequent and cover more species and larger ecological gradients because more data are available compared to tree-ring records. Here, we focus on mortality models based on inventory data.

The available mortality algorithms were developed following contrasting strategies concerning the covariates considered, the types of forest stands used for calibration and the extent and temporal resolution of the calibration data, as reviewed below.

First, mortality predictions are typically based on tree size and a measure of competition or growth to consider resource availability and tree vitality (Waring, 1987). While nearly all models include a covariate of tree size – most commonly diameter at breast height (*DBH*) – competition and growth are typically used alternatively. It remains open which approach warrants higher model performance.

Second, climate, site conditions and development stage are influential in shaping forest dynamics including tree mortality (Aakala *et al.*, 2009). Thus, site-specific tree mortality models or the incorporation of additional covariates have been proposed (e.g. Monserud & Sterba, 1999). Yet, the superiority of 'regional models', i.e. mortality functions that are calibrated and applied under similar ecological conditions, has not been verified. Inventory data for the calibration of tree mortality models typically stem from three types of permanent plots: National Forest Inventories (NFI, e.g. Fridman & Ståhl, 2001), growth and yield research plots (e.g. Crecente-Campo *et al.*, 2010) and networks of strict forest reserves (e.g. Wunder *et al.*, 2008a). In contrast to NFI and growth and yield plots, no management is carried out in strict forest reserves. Since mortality rates in unmanaged forests are expected to be higher and thus tree death events more frequent, the use of such data has been favored for the derivation of mortality algorithms (e.g. Bravo-Oviedo *et al.*, 2006). Yet, it is not known whether model applications should be restricted to the management intensity in the calibration data.

Lastly, the number of records used for the calibration of mortality models differs strongly. Although the authors usually emphasize the need for large datasets for model development (e.g. Metcalf *et al.*, 2009), the influence of sample size on model robustness has not been assessed in a systematic way (but cf. Wunder *et al.*, 2008b). Additionally, inventories are carried out at different census intervals. However, mortality rates estimated for inhomogeneous populations decrease with increasing time between censuses since trees at high risk die on a short term, while trees with a lower mortality probability dominate estimates on the long term (Lewis *et al.*, 2004). Yet, the impact of different census intervals has not been examined in the context of mortality modeling of individual trees.

In spite of the many contrasting approaches that have been pursued in model development, their influence on the predictions and performance of mortality algorithms has not been investigated. Furthermore, the majority of the mortality models have not been validated with independent data. However, this is a prerequisite for assessing their transferability to other conditions as well as for selecting approaches for implementation in DVMs (Hawkes, 2000; Keane *et al.*, 2001). Yet, due to a lack of alternatives, empirical mortality models are increasingly applied in models of forest dynamics (e.g. Bircher *et al.*, 2015), although often no information on their temporal or spatial applicability is available.

We thus review mortality models based on European inventory data to assess their transferability and suitability for incorporation in DVMs. We rigorously validate the mortality models with extensive inventory data from unmanaged forests in Germany and Switzerland and systematically analyze model performance to address the following questions: (1) Which predictors warrant high accuracy of simulated tree mortality? (2) Are 'regional models', i.e. functions that are calibrated and applied in similar environments, required to account for the variation in mortality? (3) Should model applications be restricted to the management intensity in the calibration data? (4) Does the size of the calibration and validation datasets influence the accuracy of mortality predictions? (5) Are predictions of individual tree mortality models sensitive to the length of census intervals?

Material and methods

Study sites and validation data

Inventory data from 54 strict forest reserves in Switzerland and Germany that have been monitored repeatedly for up to 60 years were used to validate the mortality models (Fig. S1, see Appendix A for all additional Tables and Figures). Trees with a diameter at breast height (*DBH*) of > 4 and > 7 cm for Switzerland and Germany, respectively, have been measured on permanent plots ranging from 0.01 to 1.8 ha in size with census intervals of 4-27 years. We excluded permanent plots with considerable disturbances (wind: Josenwald, fire: Pfynwald; both Switzerland) or that are collapsing because of severe bark beetle infestation (Bruchberg, Germany). Data of 11 tree species or genera, i.e. *Abies alba* Mill., *Alnus glutinosa* Gaertn., *Betula* spp. (*B. pendula* Roth and *B. pubescens* Ehrh.), *Carpinus betulus* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Larix decidua* Mill., *Picea abies* (L.) Karst, *Pinus sylvestris* L., *Quercus* spp. (*Q. petraea* Liebl. and *Q. robur* L.) and *Tilia cordata* Mill. were selected (Table S1). Below, we refer to the species by their Latin genus name. Annual mortality rates were 1.7 % on average but differed between species (cf. Table 3).

A set of three consecutive inventories was used to generate records of trees that were alive in the first and second inventory, and either dead or alive in the third inventory. Since for 44.2 % of the permanent plots more than three inventories were available, individual trees can appear more than once in the dataset, as all possible sets of inventory data were used (29.6 % of the records are such ‘repeated measures’; for verification cf. Hülsmann *et al.*, 2016). The derivation of the tree, stand and site characteristics (cf. Table 1) that were used in the mortality models to explain tree status (dead or alive) in the third inventory is described in detail in Appendix B. Covariates for tree growth were derived for the interval between the first and the second inventory. All other tree and stand characteristics were calculated based on data from the second inventory.

Table 1 Tree, stand and site characteristics that were used as covariates in the mortality models. For each characteristic, the mean per tree species is given. Covariates that are considered to explain model performance are highlighted in grey, i.e. growth, competition at the level of single trees and competition at the stand level. Abbreviations: *DBH* = diameter at breast height, *DI* = annual diameter increment, *BAI* = annual basal area increment, *relBAI* = annual relative basal area increment, *h* = tree height, *CR* = crown ratio, *BAL* = basal area of larger trees, *relBAL* = share of *BAL* of stand basal area (*BA*), *mDBH* = arithmetic mean *DBH*, *qmDBH* = quadratic mean *DBH*, *CVd* = coefficient of variance of *DBH*, *hdom* = dominant height, *BA* = stand basal area, *N* = number of trees, *PBA* = percentage of basal area of the subject species, *LAT* = latitude, *ALT* = altitude, *GDD* = growing degree-days, *SI50* = site index expressed as the dominant height at the age of 50 years. For further information on the derivation of the covariates refer to Appendix B. For minimum and maximum values of the characteristics refer to Table S2.

		Abies	*Alnus*	*Betula*	*Carpinus*	*Fagus*	*Fraxinus*	*Larix*	*Picea*	*Pinus*	*Quercus*	*Tilia*
Tree	*DBH* (cm)	13.9	22.4	21.4	15.9	25.5	17.5	27.5	29.9	25.4	28.0	16.9
	DI (mm)	1.02	1.90	1.84	0.89	1.87	2.31	0.96	1.85	1.86	1.75	1.20
	BAI (cm^2)	3.47	7.34	6.94	2.93	9.85	7.71	4.95	10.75	7.78	8.67	4.12
	relBAI	0.017	0.018	0.021	0.011	0.015	0.030	0.007	0.015	0.020	0.014	0.016
	h (m)	9.9	19.4	18.1	14.4	20.6	17.9	17.8	17.9	15.0	19.4	14.1
	CR	0.35	0.29	0.34	0.41	0.43	0.26	0.39	0.49	0.31	0.35	0.40
	BAL (m^{2}ha^{-1})	44.1	23.3	20.9	34.1	29.8	24.9	27.2	34.1	18.0	24.7	31.9
	relBAL	0.91	0.63	0.71	0.90	0.74	0.75	0.65	0.75	0.56	0.64	0.80
Stand	*mDBH* (cm)	18.7	17.1	17.5	21.5	24.8	15.7	22.3	26.8	15.6	19.6	17.8
	qmDBH (cm)	24.0	19.7	20.5	25.4	28.1	18.6	25.3	31.6	18.4	23.1	20.7
	CVd	0.82	0.56	0.62	0.64	0.57	0.61	0.55	0.64	0.61	0.63	0.60
	hdom (m)	29.6	24.3	22.1	24.6	27.7	23.8	19.8	26.3	17.5	23.7	21.2
	BA (m^{2}ha^{-1})	48.5	37.6	29.7	37.7	40.1	33.3	42.1	45.8	33.3	38.2	39.9
	N (ha^{-1})	1147	1449	1064	971	851	1431	963	740	1401	1101	1408
	PBA			0.21					0.73	0.65		
Site	*LAT* (°)	47.2	47.1	48.5	49.2	48.5	47.5	46.6	47.1	47.6	47.9	47.3
	ALT (m)	830	471	439	350	527	531	1962	1336	551	478	601
	GDD	1597	1983	1936	1901	1802	1868	600	1093	1932	1909	1843
	SI50 (m)								14.7	17.0		

Mortality models

Literature databases and the reference lists of relevant papers were searched for publications that fulfill the following criteria: They (1) consider the mortality of individual trees, i.e. not of seedling populations or stand-level mortality rates, (2) predict mortality of native European tree species, (3) derive models that were calibrated with inventory data and (4) focus on ‘regular’, i.e. ‘background’ mortality (Keane *et al.*, 2001). Models restricted to ‘irregular’ mortality, e.g. after wind disturbance (e.g. Schmidt *et al.*, 2010) or at polluted sites (e.g. Juknys *et al.*, 2006) were discarded. From the resulting set of models we used only those that employed logistic regression (Table 2), by far the most common approach. We did not consider models that are based on survival analysis, neural networks or semiparametric approaches since these techniques either require annual inventory data or are based on entirely different statistics, thus making predictions less comparable. In addition, we excluded models requiring covariates that were unavailable from the inventories and could not reasonably be derived from existing data, e.g. tree and stand age, spatially explicit competition indices or information on soil fertility. Although mixed-effects approaches are increasingly applied in tree mortality models to account for the hierarchical structure of the data, only two such models could have been applied to our dataset; the others require covariates that were unavailable (e.g. Boeck *et al.*, 2014, cf. Table 2). Thus, we focused on fixed-effects models.

Overall, 13 publications provided suitable mortality models for varying sets of species and species groups, resulting in 46 model formulations that could be applied to one or more species (Table S3). Where a publication proposed more than one model per species, the models were distinguished using an index (cf. Table 2). From these mortality models, the coefficients and their units were extracted (Table S4). Subsequently, the parameterized mortality models were applied to our reserve dataset. To this end, mortality model j calibrated to data of species k was used to predict the mortality probability p of tree i of the same species following

$$p_{i,j,k} = logit^{-1}\left(X_i\beta_{j,k}\right) = \frac{\exp(X_i\beta_{j,k})}{1+\exp(X_i\beta_{j,k})} = \frac{1}{1+\exp(-X_i\beta_{j,k})} \qquad \text{eqn 1}$$

with X_i denoting the design matrix of the linear predictor and $\beta_{j,k}$ the respective parameter vector. Eqn 1 was modified if (1) models predicted survival rather than mortality and/or (2) the logistic model was formulated differently (cf. Appendix B). In addition, the mortality probability predicted for Δt_j was rescaled to the census interval (Δt) of the respective permanent plot (cf. Appendix B).

Table 2 List of the publications that fulfill the selection criteria: They (1) consider the mortality of individual trees, i.e. not of seedling populations or stand-level mortality rates, (2) predict mortality of native European tree species, (3) derive models that were calibrated with inventory data and (4) focus on 'regular' mortality. For models that were not applicable to the reserve data the exclusion criteria are given. Where more than one model was proposed within one publication, the models were distinguished using a numerical index.

Publication	**Exclusion criteria**
Adame *et al.* (2010)	calibrated for *Quercus pyrenaica* not present in Central Europe
Ahner and Schmidt (2011)	survival analysis
Alenius *et al.* (2003) 1 *	
Alenius *et al.* (2003) 2 *	mixed-effects approach
Boeck *et al.* (2014)	spatially explicit competition indices unavailable in reserve dataset, mixed-effects approach
Bravo-Oviedo *et al.* (2006)	
Castagneri *et al.* (2010)	spatially explicit competition indices and tree age unavailable in reserve dataset
Condés and Del Río (2015)	mixed-effects approach
Crecente-Campo *et al.* (2010)	
Diéguez-Aranda *et al.* (2005)	stand age unavailable in reserve dataset
Dobbertin and Brang (2001)	covariates (e.g., defoliation and crown form) unavailable in reserve dataset
Dursky (1997)	
Eid and Tuhus (2001)	
Fridman and Ståhl (2001)	
Hasenauer (1994)	spatially explicit competition indices unavailable in reserve dataset
Hasenauer *et al.* (2001)	neural networks
Hasenauer and Merkl (1997)	spatially explicit competition indices unavailable in reserve dataset
Holzwarth *et al.* (2013)	
Hynynen *et al.* (2002)	soil fertility classes unavailable in reserve dataset
Juknys *et al.* (2006)	stand age unavailable in reserve dataset
Jutras *et al.* (2003) 1	soil fertility classes unavailable in reserve dataset
Jutras *et al.* (2003) 2	soil fertility classes unavailable in reserve dataset, mixed-effects approach
Laarmann *et al.* (2009)	separates into different causes of death
Monserud and Sterba (1999)	
Neuner *et al.* (2015)	survival analysis
Nothdurft (2013)	survival analysis
Palahí *et al.* (2003) 1 †	stand age unavailable in reserve dataset
Palahí *et al.* (2003) 2 †	
Sims *et al.* (2009)	spatially explicit competition indices unavailable in reserve dataset, mixed-effects approach
Trasobares *et al.* (2004)	
Vieilledent *et al.* (2010)	semiparametric approach
Wunder *et al.* (2007) 1 ‡	
Wunder *et al.* (2007) 2 ‡	
Wunder *et al.* (2008a) 1 §	
Wunder *et al.* (2008a) 2 §	
Wunder *et al.* (in prep.)	

* Model 1 included only fixed-effects, model 2 included also random-effects.
† Model 1 is based on average growth, model 2 is based on growth during the past five years.
‡ Model 1 was calibrated with data from the Swiss reserve Tariche Bois Banal, model 2 with data from Tariche Haute Côte.
§ Model 1 was calibrated with data from Białowieża in Poland, model 2 with data from Swiss forest reserves.

Independent external validation of the mortality models was ensured by applying every model only to those reserves that had not been used for its calibration; i.e. models based on data from Swiss forest reserves were only applied to previously unused reserves (Wunder *et al.*, 2007; Wunder *et al.*, 2008a). Since we solely used measured crown ratios (*CR*, cf. Appendix B), models including *CR* were only applied to trees for which this variable had been assessed in the field. Consequently, some models were applied to partial datasets of a species (Table 3).

Model performance

Predicted mortality probabilities were compared with observed tree status by calculating two performance criteria. To quantify prediction accuracy (correct mortality rates), we defined prediction bias (p_{bias}) as the absolute difference of the mean predicted mortality probability ('simulated mortality') and the mean mortality rate ('observed mortality') both given in % over $\Delta t = 1$ year (cf. Appendix B). The Area Under the receiver operating characteristic Curve (*AUC*) quantifies classification accuracy (correct attribution of tree status dead/alive) (Fawcett, 2006). AUC values > 0.5 indicate an increasing ability to distinguish dead from living trees that is maximal for AUC = 1 (Hosmer & Lemeshow, 2000).

p_{bias} and *AUC* were calculated for the entire dataset of each species to assess the overall performance of each of the 58 possible model-species combinations (note that models calibrated for species groups were applied to several species). For both performance criteria, bootstrap confidence intervals (*CI*) were derived. Additionally, both performance criteria were derived at the level of each reserve, thus resulting in 857 'observations' of p_{bias} and *AUC* (note that not all species were present in every reserve). These 'observations' were used to assess the influence of model and dataset characteristics on model performance and to address the research questions (1-5).

We hypothesized that the performance of a mortality model in external validation depends on the explanatory variables included in the model (1), i.e. covariates that quantify growth (*DI* = annual diameter increment, *BAI* = annual basal area increment, *relBAI* = annual relative basal area increment) or competition at the individual level (*BAL* = basal area of larger trees, *relBAL* = share of *BAL* of stand basal area) or at the stand level (*BA* = stand basal area, *N* = number of trees, cf. Table S3). In addition, we tested if model performance is higher when a model is applied inside the same ecological zone (2). To this end, we assigned the models to ecological zones following Kuusela (1994), i.e. Alpine, Central, Eastern, Mediterranean, Northern and Sub-Atlantic, associating the German and Swiss reserves with the Central and Alpine zone, respectively. Furthermore, we expected management intensity (3), i.e. with the categories 'managed' and 'unmanaged' to affect model performance. Note that only models calibrated with data from strict forest reserves were considered as 'unmanaged'. To account for influences of dataset size (4), the number of records used to fit the mortality models (N_{cal}) and the number of records per species and reserve used for model validation (N_{val}) were considered as predictors of model performance. Finally, we investigated the effect of different census intervals (5) using the interval length in the calibration and validation data with the latter calculated as the median of all censuses in each forest reserve.

To test these hypotheses, we used linear mixed-effects models to explain model performance (p_{bias} and AUC) using the model and data characteristics as fixed effects (cf. Table 4). Since tree species are expected to differ considerably concerning the predictability of tree death, we included an additional fixed effect for 'species' and examined differences using multiple pairwise comparisons. To account for the hierarchical nature of the data and unexplained model differences, we included a random intercept for 'reserve' as well as for 'model'. AUC values were arcsine-transformed and $|p_{bias}|$ values square-root transformed to improve normality of the performance variables (Mosteller & Tukey, 1977; Breiner *et al.*, 2015). Since the level of mortality may influence the accuracy of model predictions, we additionally tested observed mortality rate as an explanatory variable in the models. However, the influences of the other covariates on *pbias* or AUC remained the same so that this covariate was dropped, particularly for not mixing explanatory variables and the performance to be modeled, i.e. p_{bias}.

All computations were performed within R (R Core Team 2015, R Foundation for Statistical Computing, Vienna, Austria). AUC was calculated using the function *auc*() from the package *SDMTools* (R package version 1.1-221, 2014). Since *auc*() prevents values below 0.5, which is not appropriate for AUC calculations for predefined models, the code was modified respectively. Linear mixed-effects models were calculated and evaluated with the packages *lme4* (Bates *et al.*, 2015) and *pbkrtest* (Halekoh & Højsgaard, 2014). R^2 of the models was determined based on the function *sem.model.fits*() from the package *piecewiseSEM*. Multiple pairwise comparisons were calculated using the package *lsmeans* (Lenth, 2016). Bootstrap confidence intervals were derived using the function *boot.ci*() from the package *boot*.

Results

Model characteristics

The mortality models differed strongly in terms of model formulation, covariates considered and datasets used. Out of the 46 model formulations, 16 predicted the probability of tree death while the remaining simulated survival, and predictions of tree status referred to intervals of 1 to 13 years (Table S3). Twenty-four mortality models included a covariate for tree growth. Competition was considered at the stand and tree level in six and eighteen models, respectively. Nearly half of the models were derived for the Alpine and ten for the Northern zone. For the Eastern, Central and Mediterranean zones, only few models were available. Twenty-six mortality models were calibrated using data from unmanaged forests while 20 were based on managed stands. The smallest calibration dataset included 216 observations, the largest 34 403 (median = 1922). The calibration datasets included between seven and 2382 dead trees (median = 143). Census intervals in the calibration data ranged between 5 and 13 years.

Mortality patterns

Observed mortality as a function of *DBH* was reverse J-shaped for nearly all species, i.e. mortality rates continuously decreased with increasing tree size (Fig. 1). In contrast, mortality risk of *Picea* was almost constant over the entire *DBH* range. Mortality rates of *Betula* revealed a maximum at a *DBH* of ca. 15 cm. For none of the species, the mortality pattern was clearly U-shaped. Only *Quercus* exhibited a slight increase of mortality for the largest trees. In contrast to the dominating J-shaped pattern, the magnitude of mortality differed considerably. Annual mortality rates for *Abies*, *Larix* and *Tilia* were rather low, while mortality was more pronounced for *Betula* and *Quercus*. Specifically, species differed in the mortality risk of small and/or large trees and in the *DBH* above which mortality rates remained constantly low.

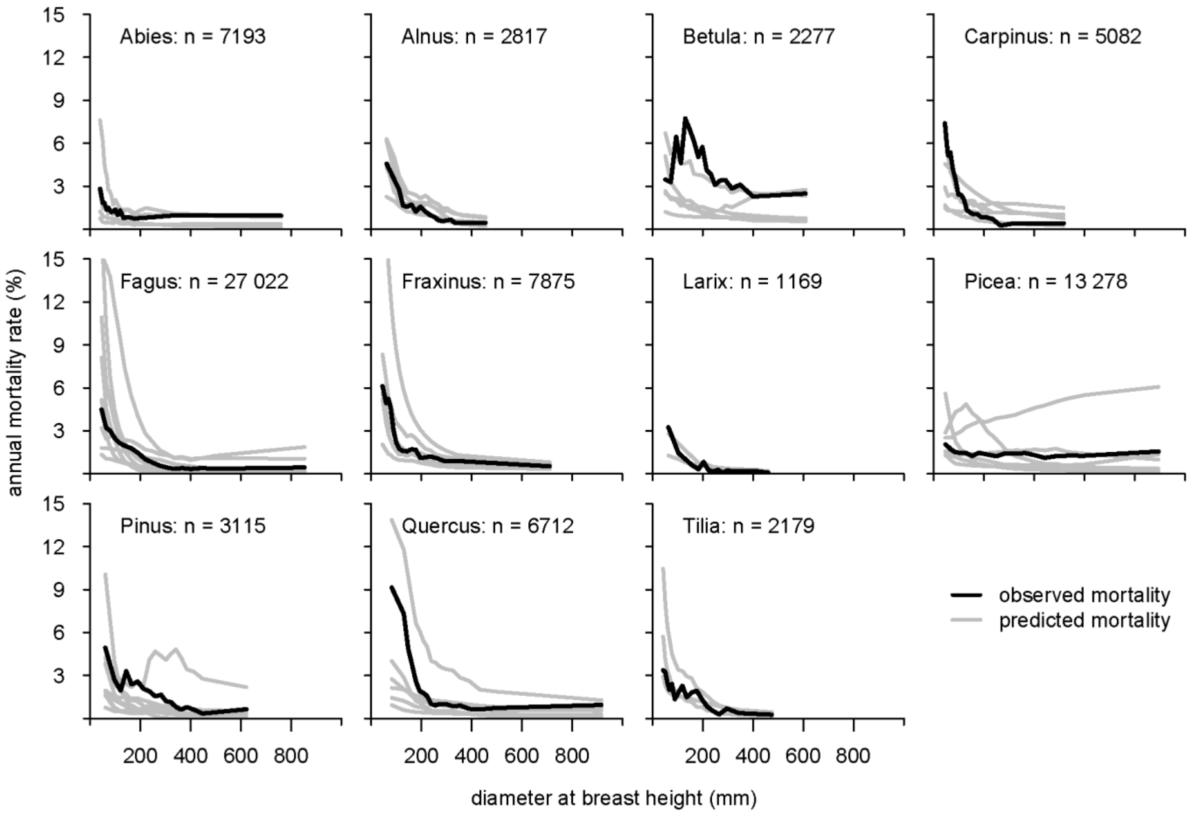

Fig. 1 Observed and predicted annual mortality rates as a function of *DBH* per tree species. Each grey line represents the predictions of one mortality model. For the sake of simplicity and to focus on overall patterns, we did not differentiate mortality models but show all model predictions in grey. Note that some models had to be validated with reduced datasets (cf. Table 3) and thus the black and grey lines do not always allow for a direct comparison of observed and predicted mortality rates. For a more precise evaluation of specific models, cf. Table 3 and Fig. S12.

Consistent with observed mortality patterns, predictions of almost all mortality models resulted in reverse J-shaped mortality rates as a function of *DBH* (Fig. 1). However, the predictions were characterized by strong variability in the magnitude of mortality. While for most species the models equally over- and underestimated mortality, simulated mortality rates of *Betula*, *Pinus* and *Quercus* were predominantly too low. The models that deviated from the J-shaped pattern either predicted a continuous increase of mortality with increasing *DBH* (*Picea*, Wunder *et al.*, 2008a 1, cf. Fig. S12), hump-shaped mortality (*Pinus*, Alenius *et al.*, 2003 1), U-shaped mortality (e.g. *Betula*, Fridman & Ståhl, 2001) or no trend of mortality with *DBH* (e.g. *Picea*, Fridman & Ståhl, 2001). In most of these cases, the models did not fit well the observed mortality pattern.

Table 3 Performance of each model-species combination in terms of p_{bias} and AUC. For each model application, the respective proportion of the data used and the annual mortality probability are indicated.

Publication	**Species**	**Proportion of data used**	**Observed annual mortality rate %)**	p_{bias} **(%)**	p_{bias} **(%)** ***CI***	***AUC***	***AUC CI***
Alenius *et al.* (2003) 1	*Pinus*	1.00	1.6	1.8	1.6 ... 2.0	0.56	0.53 ... 0.59
Bravo-Oviedo *et al.* (2006)	*Pinus*	1.00	1.6	-1.0	-1.1 ... -0.8	0.59	0.57 ... 0.62
Crecente-Campo *et al.* (2010)	*Pinus*	1.00	1.6	-0.8	-0.9 ... -0.7	0.72	0.70 ... 0.74
Dursky (1997)	*Fagus*	1.00	1.3	2.8	2.7 ... 2.8	0.78	0.78 ... 0.79
Dursky (1997)	*Picea*	0.99	1.4	0.7	0.7 ... 0.8	0.57	0.56 ... 0.58
Eid and Tuhus (2001)	*Betula*	1.00	4.1	-3.2	-3.5 ... -2.9	0.58	0.56 ... 0.60
Eid and Tuhus (2001)	*Picea*	0.99	1.4	-0.9	-0.9 ... -0.8	0.60	0.59 ... 0.61
Eid and Tuhus (2001)	*Pinus*	1.00	1.6	-1.2	-1.3 ... -1.0	0.62	0.59 ... 0.65
Eid and Tuhus (2001)	*Quercus*	1.00	2.0	-0.6	-0.7 ... -0.5	0.77	0.76 ... 0.79
Fridman and Ståhl (2001)	*Alnus*	1.00	1.4	0.4	0.3 ... 0.5	0.74	0.72 ... 0.77
Fridman and Ståhl (2001)	*Betula*	1.00	4.1	-2.4	-2.7 ... -2.1	0.50	0.47 ... 0.52
Fridman and Ståhl (2001)	*Fagus*	1.00	1.3	-0.2	-0.3 ... -0.2	0.70	0.69 ... 0.71
Fridman and Ståhl (2001)	*Picea*	1.00	1.4	0.1	0.0 ... 0.1	0.61	0.60 ... 0.62
Fridman and Ståhl (2001)	*Pinus*	1.00	1.6	-1.0	-1.2 ... -0.9	0.72	0.70 ... 0.75
Fridman and Ståhl (2001)	*Quercus*	1.00	2.0	-1.3	-1.4 ... -1.2	0.78	0.77 ... 0.80
Holzwarth *et al.* (2013)	*Carpinus*	1.00	2.0	0.8	0.7 ... 0.9	0.78	0.76 ... 0.79
Holzwarth *et al.* (2013)	*Fagus*	1.00	1.3	0.7	0.6 ... 0.7	0.76	0.75 ... 0.76
Holzwarth *et al.* (2013)	*Fraxinus*	1.00	2.1	3.4	3.2 ... 3.5	0.71	0.70 ... 0.73
Monserud and Sterba (1999)	*Abies*	0.13	1.0	1.4	1.2 ... 1.6	0.64	0.58 ... 0.69
Monserud and Sterba (1999)	*Alnus*	0.12	1.7	0.1	-0.4 ... 0.5	0.73	0.66 ... 0.81
Monserud and Sterba (1999)	*Betula*	0.20	3.6	-2.1	-2.7 ... -1.5	0.76	0.71 ... 0.80
Monserud and Sterba (1999)	*Carpinus*	0.08	2.0	0.6	0.1 ... 0.9	0.78	0.72 ... 0.83
Monserud and Sterba (1999)	*Fagus*	0.11	1.2	-0.3	-0.4 ... -0.2	0.76	0.73 ... 0.79
Monserud and Sterba (1999)	*Fraxinus*	0.22	2.6	-0.3	-0.5 ... -0.1	0.81	0.79 ... 0.83
Monserud and Sterba (1999)	*Larix*	0.11	0.4	0.3	0.0 ... 0.5	0.89	0.77 ... 0.98
Monserud and Sterba (1999)	*Picea*	0.12	1.1	0.2	0.0 ... 0.3	0.60	0.56 ... 0.64
Monserud and Sterba (1999)	*Pinus*	0.15	1.5	-0.8	-1.2 ... -0.5	0.68	0.61 ... 0.75
Monserud and Sterba (1999)	*Quercus*	1.00	2.0	-1.5	-1.7 ... -1.4	0.75	0.74 ... 0.77
Palahí *et al.* (2003) 2	*Pinus*	1.00	1.6	-1.2	-1.3 ... -1.1	0.80	0.77 ... 0.82
Trasobares *et al.* (2004)	*Pinus*	1.00	1.6	-0.7	-0.8 ... -0.5	0.70	0.68 ... 0.72
Wunder *et al.* (2007) 1	*Abies*	0.86	1.4	-0.9	-1.0 ... -0.8	0.71	0.69 ... 0.72
Wunder *et al.* (2007) 1	*Fagus*	0.92	1.3	0.1	0.1 ... 0.2	0.80	0.79 ... 0.81
Wunder *et al.* (2007) 2	*Abies*	0.46	1.2	0.1	0.0 ... 0.2	0.72	0.69 ... 0.74
Wunder *et al.* (2007) 2	*Fagus*	0.92	1.4	-0.3	-0.3 ... -0.2	0.80	0.79 ... 0.81
Wunder *et al.* (2008) 1+2	*Betula*	0.90	4.1	-0.2	-0.5 ... 0.1	0.74	0.72 ... 0.77
Wunder *et al.* (2008) 1	*Alnus*	1.00	1.4	0.9	0.8 ... 1.0	0.77	0.74 ... 0.79
Wunder *et al.* (2008) 1	*Carpinus*	1.00	2.0	-0.8	-0.9 ... -0.7	0.70	0.69 ... 0.72
Wunder *et al.* (2008) 1	*Fraxinus*	1.00	2.1	-0.5	-0.6 ... -0.4	0.80	0.78 ... 0.81
Wunder *et al.* (2008) 1	*Picea*	1.00	1.4	2.6	2.5 ... 2.6	0.59	0.57 ... 0.60
Wunder *et al.* (2008) 1	*Quercus*	1.00	2.0	2.8	2.7 ... 2.8	0.83	0.82 ... 0.84
Wunder *et al.* (2008) 1	*Tilia*	1.00	1.5	1.5	1.4 ... 1.7	0.78	0.76 ... 0.80
Wunder *et al.* (2008) 2	*Alnus*	0.68	1.3	-0.4	-0.5 ... -0.2	0.76	0.73 ... 0.79
Wunder *et al.* (2008) 2	*Carpinus*	0.89	2.0	0.0	-0.1 ... 0.1	0.71	0.70 ... 0.73
Wunder *et al.* (2008) 2	*Fagus*	0.79	1.3	0.5	0.4 ... 0.5	0.76	0.76 ... 0.77
Wunder *et al.* (2008) 2	*Fraxinus*	0.89	2.0	0.9	0.8 ... 1.0	0.82	0.81 ... 0.83
Wunder *et al.* (2008) 2	*Quercus*	0.69	2.2	-1.2	-1.3 ... -1.1	0.84	0.83 ... 0.86
Wunder *et al.* (2008) 2	*Tilia*	0.69	1.8	-0.2	-0.4 ... -0.1	0.79	0.76 ... 0.81
Wunder *et al.* (in prep.)	*Abies*	1.00	1.3	-0.6	-0.7 ... -0.5	0.68	0.66 ... 0.69
Wunder *et al.* (in prep.)	*Alnus*	1.00	1.4	-0.3	-0.5 ... -0.2	0.76	0.73 ... 0.78
Wunder *et al.* (in prep.)	*Betula*	1.00	4.1	-2.8	-3.1 ... -2.5	0.72	0.70 ... 0.74
Wunder *et al.* (in prep.)	*Carpinus*	1.00	2.0	-1.2	-1.3 ... -1.0	0.78	0.77 ... 0.80
Wunder *et al.* (in prep.)	*Fagus*	1.00	1.3	-0.8	-0.8 ... -0.8	0.80	0.79 ... 0.80
Wunder *et al.* (in prep.)	*Fraxinus*	1.00	2.1	-1.2	-1.3 ... -1.1	0.79	0.78 ... 0.80
Wunder *et al.* (in prep.)	*Larix*	1.00	0.4	0.1	0.0 ... 0.1	0.82	0.77 ... 0.87
Wunder *et al.* (in prep.)	*Picea*	1.00	1.4	-0.8	-0.8 ... -0.7	0.56	0.55 ... 0.57
Wunder *et al.* (in prep.)	*Pinus*	1.00	1.6	-0.5	-0.7 ... -0.4	0.78	0.76 ... 0.81
Wunder *et al.* (in prep.)	*Quercus*	1.00	2.0	-0.8	-0.9 ... -0.8	0.81	0.80 ... 0.82
Wunder *et al.* (in prep.)	*Tilia*	1.00	1.5	-0.1	-0.2 ... 0.0	0.78	0.75 ... 0.80

Prediction accuracy

On average, prediction accuracy was high, as indicated by the mean p_{bias} of 0.03 % at the reserve level. However, p_{bias} at the level of the full dataset of each species (Table 3; standard deviation = 1.3 %) and of single reserves (Fig. S2; standard deviation = 1.7 %) varied considerably. While some models overestimated the observed annual mortality rate by > 3 % (e.g. *Fraxinus*, Holzwarth *et al.*, 2013), others underestimated it by > 3 % (e.g. *Betula*, Eid & Tuhus, 2001). At the level of single reserves, p_{bias} varied even more, i.e. between -5.5 and 8.6 %. Nevertheless, p_{bias} between -1.6 and 2.1 % was achieved in 80 % of the applications.

Species identity significantly influenced the accuracy of mortality predictions as revealed by the linear mixed-effect model for the square-root of $|p_{bias}|$ (Table 4). While $|p_{bias}|$ was rather low for *Alnus*, *Fagus* and *Larix*, models for *Betula* simulated mortality less accurately (Fig. S3). Nevertheless, the results of multiple pairwise comparison between the species showed that $|p_{bias}|$ is quite similar for all species except for *Betula* (Fig. S4). As indicated by mostly negative p_{bias} values (Fig. S2), low prediction accuracy of *Betula* but also of *Pinus* and *Quercus* was caused by a pronounced underestimation of mortality.

$|p_{bias}|$ was reduced significantly when covariates for growth and/or competition at the tree level were used to predict tree mortality (Table 4 and Fig. S5). Moreover, mortality rates were predicted more accurately when the models were applied within the same ecological zone and using validation data with long census intervals (Fig. S6+7). However, the improvement of prediction accuracy was largest for covariates of growth (cf. Fig. S3). Stand-level competition, management intensity, the census interval in the calibration data as well as N_{cal} and N_{val} did not significantly affect $|p_{bias}|$.

Classification accuracy

Following the criteria of Hosmer and Lemeshow (2000), *AUC* values obtained at the level of full datasets (Table 3) indicated a range of classification accuracy between no discriminative power, e.g. for *Betula* (Fridman & Ståhl, 2001), *Picea* (Wunder *et al.*, in prep.) and *Pinus* (Alenius *et al.*, 2003 1), and excellent classification, e.g. for *Larix* (Monserud & Sterba, 1999) and *Quercus* (Wunder *et al.*, 2008a 2). Assuming $AUC > 0.7$ as acceptable, 43 of the 58 model applications were successful in killing the right trees. At the reserve level, the classification accuracy was still acceptable for 63.4 % of the reserves ($AUC > 0.7$).

Table 4. Estimates of the influence of model and data characteristics on p_{bias} and *AUC* with respective standard errors, P-values and significance levels (*** P ≤ 0.001, ** P ≤ 0.01, * P ≤ 0.05) estimated with linear mixed-effects models (t-tests use the Satterthwaite approximation). Model performance, evaluated by the square-root of $|p_{bias}|$ and arcsine-transformed *AUC*, was considered to be a function of species, use of covariates for growth (*DI*, *BAI*, *relBAI*) and competition at the tree (*BAL*, *relBAL*) and stand level (*BA*, *N*), application within the same ecological zone, management intensity, length of the census interval in calibration and validation and size of the calibration (N_{cal}) and validation datasets (N_{val}). Note that a 'good' model features low $|p_{bias}|$ and high *AUC*. Both performance measures show significant species differences. $|p_{bias}|$ was significantly reduced by covariates for growth and competition at the level of individual trees and when models are applied in the same ecological zone. Significantly larger *AUC* was achieved when growth was included. 'Reserve' and 'model' were used as random effects. Marginal and conditional R^2 of the models were 0.14 and 0.44 for p_{bias} and 0.19 and 0.52 for *AUC*.

p_{bias}	Estimate	Standard error	P-value		*AUC*	Estimate	Standard error	P-value	
(Intercept)	0.145	0.055	0.018	*	(Intercept)	0.763	0.108	<0.001	***
Species			<0.001	***	Species			<0.001	***
Alnus	-0.020	0.015			*Alnus*	0.263	0.038		
Betula	0.038	0.013			*Betula*	0.156	0.032		
Carpinus	-0.010	0.012			*Carpinus*	0.182	0.030		
Fagus	-0.015	0.011			*Fagus*	0.165	0.027		
Fraxinus	-0.007	0.012			*Fraxinus*	0.210	0.029		
Larix	-0.028	0.027			*Larix*	0.520	0.069		
Picea	-0.000	0.012			*Picea*	0.088	0.030		
Pinus	0.001	0.013			*Pinus*	0.141	0.032		
Quercus	0.004	0.011			*Quercus*	0.241	0.029		
Tilia	-0.001	0.014			*Tilia*	0.267	0.034		
Growth	-0.027	0.012	0.021	*	Growth	0.057	0.018	0.005	**
Competition stand	0.039	0.027	0.181		Competition stand	-0.023	0.022	0.343	
Competition tree	-0.019	0.009	0.037	*	Competition tree	0.002	0.021	0.930	
Same ecological zone	-0.014	0.004	0.002	**	Same ecological zone	0.017	0.010	0.085	
Managed	-0.014	0.020	0.491		Managed	0.017	0.024	0.474	
Census interval calibration (sqrt)	0.008	0.016	0.647		Census interval calibration (sqrt)	0.008	0.014	0.589	
Census interval validation (sqrt)	-0.011	0.005	0.033	*	Census interval validation (sqrt)	-0.004	0.026	0.872	
N_{cal} (sqrt)	-0.000	0.000	0.828		N_{cal} (sqrt)	0.000	0.000	0.631	
N_{val} (sqrt)	0.000	0.000	0.696		N_{val} (sqrt)	0.001	0.000	0.031	*

Classification accuracy was not significantly influenced by model and data characteristics except for 'species', 'growth' and N_{val} when analyzing *AUC* at the reserve level (Table 4 and Fig. S8). Living and dead trees were discriminated best for *Larix* and still well for *Alnus* and *Tilia*, while the models for *Abies* and *Picea* performed clearly worse (Fig. S9). *AUC* differed more clearly between species than $|p_{bias}|$, but the multiple pairwise comparison revealed no clearly distinguishable groups. Models that included covariates of tree growth had significantly higher classification accuracy (Fig. S10). Additionally, *AUC* increased with the size of the validation dataset (N_{val}, Fig. S11). In contrast to prediction accuracy, classification accuracy was not significantly affected by covariates for competition at the tree level, the application within the same ecological zone, nor by the census interval in the validation data.

Discussion

Documentation of mortality models

We evaluated 46 individual-tree mortality models that had been developed based on European inventory data. We found large differences concerning calibration data, methodology and the covariates considered. Bearing in mind that these characteristics influence the predicted mortality and thus the suitability of a model for being applied in a new context, a comprehensive documentation of the data and its processing, the model development and the covariate selection is pivotal, but was not consistently provided.

For example, this applies to the specification of the *DBH* range covered in the calibration data, which may severely limit the suitable application domain. Using a model in extrapolation mode (Adams *et al.*, 2013) increases the risk of erroneous mortality predictions, particularly for small trees (Bircher *et al.*, 2015). Documentation was also poor for disturbance-related mortality. Some authors explicitly defined the mortality type that they intended to simulate and the criteria applied for this purpose (e.g. exclusion of certain plots or trees, cf. Bravo-Oviedo *et al.*, 2006; Wunder *et al.*, 2007). However, often it was not documented whether a model was aimed at 'regular' or both 'regular' and 'irregular' mortality. More details are also needed concerning the covariates considered and their selection, which is not only an issue of statistical significance but often includes a pre-selection based on expert knowledge.

Although we assume that several mortality models were not published with the primary aim of allowing for their reconstruction, a comprehensive documentation of all steps that are part of model development would be very important. Much progress is still possible in mortality modeling and in the future, forest data that become increasingly available could and should be used for developing more robust models (Wunder *et al.*, 2008a), which would benefit strongly from good documentation and reporting guidelines, as suggested, e.g. for tree allometric equations (Cifuentes Jara *et al.*, 2014).

Implications of p_{bias} and AUC: How good is good enough?

Prior to discussing the performance of the mortality algorithms and the implications of particular p_{bias} and AUC values, we wish to emphasize that models that considerably over- or underestimated mortality or had a low discriminative ability when applied to the reserve data should not be considered as generally poor. Rather, our validation approach revealed that these models were less appropriate to predict mortality in unmanaged forests of Central Europe, e.g. because of a considerably different environment in the calibration data and because the authors may not have aimed to build models with high generality. Although the reserve data that we used for validating the mortality algorithms consist of an extensive assemblage of trees and site conditions and the size of the data exceeds the extent of the datasets used for calibrating the models for most tree species (cf. Tables S1+2), the reserve data, which we consider here as a reference, represent only one realization of possible mortality patterns. This uncertainty should be taken into account when evaluating model performance.

When implemented in DVMs, empirically based mortality algorithms that result in a consistent overestimation of mortality rates will cause an accelerated turnover of tree populations or a breakdown of the stand if mortality rates exceed the recruitment potential. In contrast, severely underestimated mortality can cause exceedingly high tree density and basal area. However, it is rather difficult to specify the level of p_{bias} above which seriously flawed stand dynamics are predicted, and the sensitivity of DVMs to p_{bias} has not been systematically assessed to date. Additionally, the consequences of p_{bias} differ depending on the *DBH* range affected. Over short periods, considerable p_{bias} for large trees affects both *N* and *BA*, while incorrect mortality rates for trees with $DBH < 10$ cm may dominantly influence *N*. For long-term simulations (> 100 years), the impact of considerable p_{bias} becomes more complex due to feedbacks between the number and size of stems, light availability and the rates of growth and regeneration.

Bearing these difficulties in mind, the criterion to select models according to p_{bias} should not be overly strict. Assuming that mortality models with $|p_{bias}| < 1.5$ % are promising enough to be considered for incorporation in DVMs, the benefit of more than 80 % of the models investigated here should be further evaluated in DVMs. Thus, only a few models need to be discarded from the set of possible mortality formulations. For the selection of new algorithms predicting 'background' mortality in DVMs, the systematic presentation of the expected mortality patterns for each algorithm (Fig. S12) and of p_{bias} resulting from external validation provide valuable assistance.

Low *AUC* should be considered as less critical than considerable p_{bias} since model formulations that are poor in classification, i.e. $AUC < 0.7$ (Hosmer & Lemeshow, 2000), may still result in correct mortality rates when implemented in DVMs, although they assign mortality to the wrong trees. However, problems may arise when applying a model with poor classification accuracy if low *AUC* values indicate that the pattern of mortality as a function of, e.g. tree size deviates from observations (e.g. *Betula*: Fridman & Ståhl, 2001; *Pinus*: Alenius *et al.*, 2003). Incorporated in DVMs, this would result in incorrect predictions of the diameter distribution, with cascading effects on recruitment and growth. Additionally, *AUC* maybe be consistently low for a specific dataset or species if none of the considered covariates has enough explanatory power to discriminate between dead and living trees. In our systematic model assessment, three out of four formulations achieved a classification accuracy that was at least acceptable. Hence, the majority of the algorithms investigated here capture the most relevant covariates for distinguishing living from dead trees. In addition, these covariates revealed sufficient predictive ability for a large fraction of the reserves.

Species-specific differences in mortality

The tree species analyzed here revealed distinct patterns and magnitudes of observed as well as predicted mortality. This justifies the development of species-specific models, which has been suggested to account for contrasting life history strategies, lifespan, competitiveness and varying reactions to abiotic factors (Franklin *et al.*, 1987; Harcombe, 1987). We cannot advocate the grouping of species into 'Plant Functional Types' (PFTs) for mortality modeling, unless simple distinctions such as shade tolerance classes have been proven to correctly classify the species-specific mortality behavior.

In addition, model performance was characterized by considerable species-specific differences in prediction and classification accuracy. Underestimation of mortality rates for *Betula*, *Pinus* and *Quercus* may be explained by their low shade tolerance (Ellenberg & Leuschner, 1996), which could have caused a higher mortality probability in unmanaged stands due to more competition for light. For *Pinus*, however, the validation dataset was rather small compared to the calibration datasets (cf. Tables S1+2), which may have induced low prediction accuracy because the reserve data may not be representative for *Pinus* mortality. In contrast, simulated mortality rates were fairly accurate for *Alnus* and *Larix*, presumably because most of the models for these species were derived for the Alpine zone and could be applied to Swiss reserve data only, as these species are largely missing in the German data.

For *Abies* and *Picea*, considerably lower classification accuracy was achieved, which may be due to the weak or missing trend of mortality over *DBH* for these species, hence reducing the predictive power of *DBH*, i.e. the most common predictor of tree death, and thus of the entire model. In addition, *AUC* may be low because agents causing 'irregular' mortality are relevant, including wind disturbance, snow damage and, in the case of *Picea*, also insect attacks. When being implemented in DVMs, the degree of uncertainty in terms of prediction and classification accuracy associated with a particular species should be taken into account.

Drivers of model performance

We propose that the following model and data characteristics promote high accuracy of mortality algorithms and discuss restrictions regarding our validation approach.

First, the advantage of tree-specific covariates, i.e. one-sided competition and tree growth, for accurately predicting mortality was clearly demonstrated by the linear mixed-effects models. Tree growth has often been suggested as a good mortality predictor because it dynamically reflects competition and tree vitality (Dobbertin, 2005). Its importance is supported by the high performance of tree-ring based mortality models (Cailleret *et al.*, 2016) and the fact that growth mostly remained in the models during variable selection. Our results suggest that although *BAL* and *relBAL* allow for a similarly good prediction of mortality rates, tree growth has significantly more power to differentiate between living and dead trees, i.e. to achieve high *AUC* values. This is because growth integrates the internal and external factors that influence tree vitality much better than, e.g. *BAL*, which is a measure of a tree's exposure to competition by larger trees on the entire plot but does not consider neighborhood effects. In contrast to covariates at the level of individual trees, covariates that quantify competition at the stand level, i.e. *BA*, did not enhance model accuracy. This clearly shows that competition calculated at the plot level has little explanatory power for the mortality probability of single trees, especially on large plots, whereas it allows for the prediction of population-level mortality rates (Rohner *et al.*, 2012).

Although we were able to show the superiority of tree growth and competition at the tree level, it must be kept in mind that the incorporation of mortality algorithms in DVMs includes the prediction of tree death based on simulated covariates. For example, simulated tree growth does not necessarily reflect the same magnitude and interannual variability as measured growth (cf. Rasche *et al.*, 2012). In addition, growth modules in DVMs do typically neither simulate biotic and mechanical damage nor reduce tree growth in response to such factors, which are of great importance for forest dynamics – albeit less than competition and environmental stress (Dobbertin, 2005). Therefore, growth rates simulated by a DVM are expected to have a lower skill than observed growth to accurately predict mortality using empirical mortality algorithms. In addition, tree-level competition, e.g. *BAL*, strongly relies on an adequate representation of the diameter distribution. Feedbacks between such variables and tree mortality in DVMs require further investigation (Wernsdörfer *et al.*, 2008; Larocque *et al.*, 2011; Radtke *et al.*, 2012; Bircher *et al.*, 2015).

Second, our results confirm the regional variation of mortality relationships proposed in other studies (e.g. Monserud & Sterba, 1999) since the application of models within the same ecological zone resulted in more accurate mortality rates. Consequently, mortality models derived from data with restricted ecological and/or environmental coverage should be considered as case studies with limited transferability. Yet, we were unable to evaluate whether additional environmental covariates may improve model performance (e.g. Hartmann *et al.*, 2007), as only few such covariates had been used in the mortality algorithms, e.g. elevation, growing degree-days, site index or soil moisture (but cf. Hülsmann *et al.*, 2016). In addition, the ecological zones considered here are rather coarse and thus do not allow to identify an efficient geographical stratification for the calibration of mortality models.

Third, we tested whether the management intensity of the calibration data influenced model performance, particularly prediction accuracy (Bravo-Oviedo *et al.*, 2006). However, there was no indication that models from managed stands were less able to predict mortality probabilities for the reserve data than those from unmanaged forests. This suggests that mortality patterns in forest reserves are similar to those in managed forests and that the reserves will require more time without management to develop truly natural dynamics. In addition, processes that may act to amplify the mortality of large trees such as stem rot or wind breakage can be found in old-growth forests only (cf. U-shaped mortality; Hülsmann *et al.*, 2016). For the application in DVMs however, a U-shaped form of mortality over tree size may be desirable since it confines tree age more strongly than a reverse J-shaped relationship and thus avoids the high persistence of large trees (Bircher, 2015). Nevertheless, the effect of management on mortality may have been attenuated by the large gradient of management intensities in the calibration data that we considered as ‘managed’.

Fourth, estimates of mortality rates may decrease with increasing census interval if the population is heterogeneous (Sheil & May, 1996). However, only the census interval of the validation data affected the prediction accuracy of the mortality models. This is because the variation in mortality rates and correspondingly also the deviation between observed and predicted mortality decreases for longer intervals (Lewis *et al.*, 2004). We conclude that different census intervals are negligible in the calibration of mortality models for individual trees since accounting for species, tree size and growth already captures large parts of the inhomogeneity in mortality risk that can be found at the population level.

Finally, mortality is a ‘noisy’ process, and therefore it is usually thought that signal detection is facilitated by extensive datasets and thus a robust empirical basis (Metcalf *et al.*, 2009; Lutz, 2015). To our surprise, the size of the calibration dataset did not significantly influence model performance, and even models calibrated using datasets with very few total/dead observations resulted in reliable mortality patterns and acceptable prediction and classification accuracy. Nevertheless, we found higher classification accuracy when models were applied to larger datasets, most likely due to an improved link between the predictors and mortality, i.e., trees at risk may not die in an interval of five years but quite likely die within 20 years (Dursky, 1997). We conclude that the success of a mortality model relies more on the degree of similarity of ecological processes between the forests used for calibration and validation, rather than on the amount of data used in model development, provided that the few death events support reliable mortality patterns and rates and no ‘irregular’ mortality occurred. Nevertheless, the risk that this condition is not fulfilled increases if models are calibrated using very small datasets.

In order to apply the mortality models to different datasets, we were forced to make several assumptions. Each mortality model was applied to all trees in the validation dataset, regardless of the *DBH* range covered by the calibration data. Thus we partly extrapolated the relationship of *DBH* and mortality probability. However, the exact degree of extrapolation remains unclear since the *DBH* range was not sufficiently documented for many calibration datasets. Where model covariates were not available for all records in the reserve data, e.g. tree height or site index, we used allometric or eco-topographic relationships to derive the required information. This surely influenced the accuracy and explanatory power of the covariates. In addition, we had to make somewhat arbitrary assumptions about the value to be used in the validation exercise for a few variables because they were not available in the calibration dataset (e.g. *CON* defined as distance to the Mediterranean Sea; Trasobares *et al.*, 2004). We further wish to point out that similar assumptions must be made if mortality algorithms are implemented in DVMs (e.g. *DBH* range; cf. Bircher *et al.*, 2015).

We would like to point out that species may differ with respect to model transferability and the suitability of mortality predictors. However, we were unable to test interaction terms between species and the characteristics examined since the different modeling approaches were not tested for every species thus resulting in rank deficiency. The same applies to species groups because it was not possible to clearly classify the species based on statistical significance. Non-parametric methods may provide further insights into the drivers of model performance but were not applied here since appropriate methods to account for the hierarchical data structure are missing. However, random effects explained a considerable proportion of the observed variation and should not be ignored (cf. Table 4). This is because tree mortality and thus model performance are highly variable, and it is not feasible to explicitly address this variability. Finally, the size of individual plots in the calibration data can influence the accuracy of mortality estimates but could not be tested since this information was not available for all mortality models. In spite of these assumptions, we argue that our validation of the mortality models still allows for highly valuable insights into model behavior and performance.

Conclusions

In this study, the characteristics, parameterization and expected predictions of relevant European tree mortality models were presented systematically for the first time. For modelers of forest dynamics, this offers a unique possibility to begin an evaluation of currently available mortality algorithms and to better understand their behavior based on simulated mortality patterns (cf. Fig. S12).

Validating mortality algorithms using independent datasets constitutes a rigorous examination of model transferability, which is a prerequisite for their implementation in DVMs. Our results indicate that many mortality models can be applied successfully outside their calibration domain. However, others failed to emulate the mortality pattern or achieved low prediction or classification accuracy. Consistently higher prediction accuracy was obtained by models that (1) included covariates for growth or competition at the level of individual trees and (2) were applied in a similar ecological context. Furthermore, our results emphasize the pivotal importance of tree growth to achieve a good discrimination between dead and living trees.

In conclusion, we suggest two strategies for further developing mortality models: (1) For incorporation in DVMs that are applied over a restricted spatial extent and under current climate, mortality algorithms should be calibrated based on datasets from the same region. Our results reveal that even if these datasets are small, they can still provide valid mortality estimates for the calibration domain. (2) In order to obtain mortality models with wider applicability and improved climatic sensitivity, the high spatial variability of mortality should be addressed explicitly. The systematic screening of available mortality models for European tree species uncovered that further efforts are needed in order to improve the climatic sensitivity of the mortality algorithms, e.g. using environmental variables or tree growth, which may implicitly integrate climatic influences into mortality models (Hülsmann *et al.*, 2016). Since data of high temporal resolution covering large ecological gradients are required to explore the influence of environmental variables on mortality (Lutz, 2015; Hülsmann *et al.*, 2016), forest inventory data and dendrochronological data should be combined, e.g. by applying the Bayesian framework suggested by Clark *et al.* (2007). Future efforts should also address an improved representation of disturbance-related mortality, both non-catastrophic, small-scale mortality and larger events of forest dieback, which are likely to gain in importance under future climates (Seidl *et al.*, 2011). Finally, future mortality models should be thoroughly validated to determine their transferability, and model development should be carefully documented, ideally based on standardized guidelines.

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Appendix A – Tables S1-4, Fig. S1-12

Table S1 Number of records per tree species and genus. Numbers are given for the total dataset, per country and for those that resulted in tree death. In addition, the number of permanent plots is given.

Genus	Species	total	Germany	Switzerland	dead	Permanent plots
Abies	*Abies alba*	7193	0	7193	1142	38
Alnus	*Alnus glutinosa*	2817	0	2817	380	11
Betula	spp.	2277	590	1687	852	26
	B. pendula	1987	300	1687	764	23
	B. pubescens	290	290	0	88	4
Carpinus	*Carpinus betulus*	5082	1637	3445	1137	41
Fagus	*Fagus sylvatica*	27 022	6869	20 153	4128	126
Fraxinus	*Fraxinus excelsior*	7875	159	7716	1757	80
Larix	*Larix decidua*	1169	0	1169	88	11
Picea	*Picea abies*	13 278	458	12 820	2242	82
Pinus	*Pinus sylvestris*	3115	317	2798	553	44
Quercus	spp.	6712	805	5907	1466	53
	Q. petraea	32	32	0	25	1
	Q. robur	6680	773	5907	1441	53
Tilia	*Tilia cordata*	2179	0	2179	396	42
All		78 719	10 835	67 884	14 141	197

Table S2 Minimum and maximum values of the tree, stand and site characteristics that were used as covariates in the mortality models. For abbreviations and further explanations refer to Table 1.

		Abies	***Alnus***	***Betula***	***Carpinus***	***Fagus***	***Fraxinus***	***Larix***	***Picea***	***Pinus***	***Quercus***	***Tilia***
Tree	*DBH* (cm)	3.2 - 110.5	3.9 - 53.0	3.9 - 78.5	3.7 - 68.9	3.5 - 117.2	3.6 - 104.5	3.8 - 78.9	3.2 - 114.7	3.8 - 77.5	4.3 - 129.5	3.7 - 57.5
	DI (mm)	0.0 - 10.4	0.0 - 13.2	0.0 - 13.7	0.0 - 17.1	0.0 - 43.0	0.0 - 28.4	0.0 - 10.5	0.0 - 29.6	0.0 - 14.7	0.0 - 15.6	0.0 - 11.3
	BAI (cm^2)	0.0 - 116.1	0.0 - 64.3	0.0 - 101.3	0.0 - 152.2	0.00 - 249.91	0.00 - 336.91	0.00 - 70.66	0.00 - 215.26	0.00 - 151.69	0.00 - 113.30	0.00 - 67.54
	relBAI	0.00 - 0.19	0.00 - 0.19	0.00 - 0.17	0.00 - 0.23	0.00 - 0.23	0.00 - 0.28	0.00 - 0.09	0.00 - 0.18	0.00 - 0.21	0.00 - 0.16	0.00 - 0.17
	h (m)	1.5 - 39.0	3.2 - 31.0	1.8 - 39.6	1.5 - 30.5	0.2 - 42.0	2.5 - 41.0	2.0 - 35.4	1.3 - 41.8	2.1 - 34.0	1.6 - 35.0	2.9 - 33.0
	CR	0.07 - 0.92	0.10 - 0.64	0.05 - 0.91	0.05 - 0.86	0.00 - 0.94	0.00 - 0.94	0.13 - 0.94	0.08 - 0.98	0.02 - 0.93	0.07 - 0.99	0.15 - 0.72
	BAL (m^2ha^{-1})	0.0 - 87.5	0.0 - 113.7	0.0 - 61.9	4.6 - 68.1	0.0 - 68.1	0.0 - 61.8	0.0 - 56.9	0.0 - 86.3	0.0 - 65.3	0.0 - 66.6	1.3 - 50.9
	relBAL	0.0 - 1.0	0.0 - 1.0	0.0 - 1.0	0.1 - 1.0	0.0 - 1.0	0.0 - 1.0	0.0 - 1.0	0.0 - 1.0	0.0 - 1.0	0.0 - 1.0	0.0 - 1.0
Stand	*mDBH* (cm)	10.0 - 38.9	10.6 - 31.4	7.1 - 37.3	10.6 - 39.4	10.0 - 53.0	8.7 - 37.4	12.8 - 31.5	10.0 - 45.2	7.1 - 28.8	12.3 - 39.4	8.7 - 34.5
	qmDBH (cm)	14.6 - 47.6	11.7 - 38.8	7.6 - 41.8	11.5 - 42.8	11.5 - 54.9	10.1 - 43.7	14.6 - 35.7	11.5 - 47.6	7.6 - 31.6	14.0 - 42.8	11.1 - 36.9
	CVd	0.33 - 1.21	0.21 - 1.14	0.38 - 0.99	0.34 - 0.99	0.16 - 1.21	0.33 - 1.14	0.38 - 0.73	0.27 - 1.21	0.31 - 0.87	0.39 - 0.99	0.38 - 0.99
	hdom (m)	12.5 - 37.0	18.3 - 28.5	7.2 - 31.7	18.5 - 30.8	13.4 - 37.0	9.9 - 33.7	12.5 - 29.9	11.2 - 37.0	7.3 - 31.1	12.3 - 35.0	10.9 - 33.7
	BA (m^2ha^{-1})	28.6 - 87.5	27.0 - 119.0	4.9 - 68.1	24.1 - 68.1	13.8 - 68.1	13.6 - 61.9	24.3 - 57.7	13.9 - 87.5	8.2 - 68.1	25.2 - 68.1	24.1 - 55.0
	N (ha^{-1})	367 - 2780	282 - 4000	258 - 2333	204 - 2333	78 - 2780	253 - 3281	482 - 1902	201 - 2780	312 - 2500	244 - 2595	367 - 3281
	PBA			0.00 - 0.86					0.00 - 1.00	0.01 - 1.00		
Site	*LAT* (°)	46.3 - 47.5	46.4 - 47.5	46.3 - 53.2	46.4 - 53.7	46.4 - 53.7	46.1 - 52.9	46.3 - 46.7	46.3 - 52.9	46.1 - 53.2	46.4 - 53.7	46.1 - 47.8
	ALT (m)	459 - 1560	334 - 564	24 - 599	4 - 632	4 - 1227	54 - 889	1441 - 2094	54 - 2034	83 - 1954	4 - 760	367 - 839
	GDD	903 - 2099	1822 - 2297	1654 - 2243	1443 - 2162	1169 - 2162	1552 - 2302	422 - 1019	465 - 2162	590 - 2243	1613 - 2162	1552 - 2162
	SI50 (m)								4.0 - 25.0	2.0 - 29.0		

Table S3 Mortality models, related species and the model characteristics used to explain achieved model performance. For each model, the calibration species or species group and the validation species are given. The information ‘predicted status’, ‘type’ of logistic regression and Δt are required to apply the mortality models (cf. Appendix B). The characteristics ‘growth’, ‘competition stand’, ‘competition tree’, ‘ecological zone’, ‘management intensity’, ‘census interval’ and N_{cal} were used in the linear mixed-effects models to explain differences in p_{bias} and AUC.

Publication	**Calibration species**	**Validation species**	**Predicted status**	**Type**	Δt	**Growth**	**Competition**		**Ecological zone**	**Management intensity**	**Census interval calibration**	N_{cal} (N_{dead})
							stand	**tree**				
Alenius *et al.* (2003)	*Pinus sylvestris*	*Pinus sylvestris*	mortality	II	5	no	yes	yes	Northern	managed	5	17 293 (372)
Bravo-Oviedo *et al.* (2006)	*Pinus sylvestris*	*Pinus sylvestris*	survival	II	5	no	no	yes	Mediterranean	unmanaged	5	14 197 (360)
Crecente-Campo *et al.* (2010)	*Pinus sylvestris*	*Pinus sylvestris*	survival	I	1	no	no	yes	Mediterranean	managed	7	5447 (475)
Dursky (1997)	*Fagus sylvatica*	*Fagus sylvatica*	survival	II	7	yes	no	no	Central	unmanaged	7.5	526 (263)
Dursky (1997)	*Picea abies*	*Picea abies*	survival	II	5	yes	no	no	Central	unmanaged	5.5	4764 (2382)
Eid and Tuhus (2001)	*Betula* spp.	*Betula* spp.	survival	II	1	no	no	no	Northern	managed	12	15 650 (706)
Eid and Tuhus (2001)	Broadleaf Other	*Quercus* spp.	survival	II	1	no	no	yes	Northern	managed	12	5405 (565)
Eid and Tuhus (2001)	*Picea abies*	*Picea abies*	survival	II	1	no	no	yes	Northern	managed	12	17 250 (461)
Eid and Tuhus (2001)	*Pinus sylvestris*	*Pinus sylvestris*	survival	II	1	no	no	yes	Northern	managed	12	7802 (179)
Fridman and Ståhl (2001)	*Betula* spp.	*Betula* spp.	mortality	II	5	no	yes	yes	Northern	managed	5	12 196 (935)
Fridman and Ståhl (2001)	Broadleaf Other	*Alnus glutinosa*	mortality	II	5	no	yes	yes	Northern	managed	5	4226 (464)
Fridman and Ståhl (2001)	Broadleaf Southern	*Fagus sylvatica*, *Quercus* spp.	mortality	II	5	no	yes	yes	Northern	managed	5	1183 (54)
Fridman and Ståhl (2001)	*Picea abies*	*Picea abies*	mortality	II	5	no	yes	yes	Northern	managed	5	34 403 (1565)
Fridman and Ståhl (2001)	*Pinus sylvestris*	*Pinus sylvestris*	mortality	II	5	no	yes	yes	Northern	managed	5	19 812 (1202)
Holzwarth *et al.* (2013)	*Carpinus betulus*	*Carpinus betulus*	mortality	II	1	no	no	no	Central	unmanaged	8	391 (30)
Holzwarth *et al.* (2013)	*Fagus sylvatica*	*Fagus sylvatica*	mortality	II	1	yes	no	no	Central	unmanaged	8	13 297 (1535)
Holzwarth *et al.* (2013)	*Fraxinus excelsior*	*Fraxinus excelsior*	mortality	II	1	no	no	no	Central	unmanaged	8	564 (39)
Monserud and Sterba (1999)	*Abies alba*	*Abies alba*	mortality	I	5	no	no	no	Alpine	managed	5	1878 (115)
Monserud and Sterba (1999)	Broadleaf Other	*Alnus glutinosa*, *Betula* spp., *Carpinus betulus*, *Fraxinus excelsior*	mortality	I	5	no	no	yes	Alpine	managed	5	2617 (209)
Monserud and Sterba (1999)	*Fagus sylvatica*	*Fagus sylvatica*	mortality	I	5	no	no	yes	Alpine	managed	5	4484 (193)
Monserud and Sterba (1999)	*Larix decidua*	*Larix decidua*	mortality	I	5	no	no	yes	Alpine	managed	5	3015 (87)
Monserud and Sterba (1999)	*Picea abies*	*Picea abies*	mortality	I	5	no	no	yes	Alpine	managed	5	26 699 (1175)
Monserud and Sterba (1999)	*Pinus sylvestris*	*Pinus sylvestris*	mortality	I	5	no	no	yes	Alpine	managed	5	4138 (178)
Monserud and Sterba (1999)	*Quercus* spp.	*Quercus* spp.	mortality	I	5	no	no	no	Alpine	managed	5	784 (25)
Palahí *et al.* (2003) 2	*Pinus sylvestris*	*Pinus sylvestris*	survival	II	5	yes	no	yes	Mediterranean	managed	5	11 110 (267)
Trasobares *et al.* (2004)	*Pinus sylvestris*	*Pinus sylvestris*	survival	II	10	no	no	yes	Mediterranean	managed	10	7823 (313)
Wunder *et al.* (2007) 1	*Abies alba*	*Abies alba*	survival	II	13	yes	no	no	Alpine	unmanaged	13	251 (14)
Wunder *et al.* (2007) 1	*Fagus sylvatica*	*Fagus sylvatica*	survival	II	13	yes	no	no	Alpine	unmanaged	13	634 (30)

Publication	Calibration species	Validation species	Predicted status	Type	Δt	Growth	Competition		Ecological zone	Management intensity	Census interval calibration	N_{cal} (N_{dead})
							stand	tree				
Wunder *et al.* (2007) 2	*Abies alba*	*Abies alba*	survival	II	12	yes	no	no	Alpine	unmanaged	12.5	527 (50)
Wunder *et al.* (2007) 2	*Fagus sylvatica*	*Fagus sylvatica*	survival	II	12	yes	no	no	Alpine	unmanaged	12.5	654 (7)
Wunder *et al.* (2008a) 1+2	*Betula* spp.	*Betula* spp.	survival	II	10	yes	no	no	Eastern	unmanaged	10	463 (145)
Wunder *et al.* (2008a) 1	*Alnus glutinosa*	*Alnus glutinosa*	survival	II	10	yes	no	no	Eastern	unmanaged	10	227 (26)
Wunder *et al.* (2008a) 1	*Carpinus betulus*	*Carpinus betulus*	survival	II	10	yes	no	no	Eastern	unmanaged	10	802 (74)
Wunder *et al.* (2008a) 1	*Fraxinus excelsior*	*Fraxinus excelsior*	survival	II	10	yes	no	no	Eastern	unmanaged	10	320 (23)
Wunder *et al.* (2008a) 1	*Picea abies*	*Picea abies*	survival	II	10	yes	no	no	Eastern	unmanaged	10	2253 (672)
Wunder *et al.* (2008a) 1	*Quercus robur*	*Quercus* spp.	survival	II	10	yes	no	no	Eastern	unmanaged	10	322 (52)
Wunder *et al.* (2008a) 1	*Tilia cordata*	*Tilia cordata*	survival	II	10	yes	no	no	Eastern	unmanaged	10	1024 (123)
Wunder *et al.* (2008a) 2	*Alnus glutinosa*	*Alnus glutinosa*	survival	II	10	yes	no	no	Alpine	unmanaged	10	278 (24)
Wunder *et al.* (2008a) 2	*Carpinus betulus*	*Carpinus betulus*	survival	II	10	yes	no	no	Alpine	unmanaged	10	219 (52)
Wunder *et al.* (2008a) 2	*Fagus sylvatica*	*Fagus sylvatica*	survival	II	10	yes	no	no	Alpine	unmanaged	10	1999 (243)
Wunder *et al.* (2008a) 2	*Fraxinus excelsior*	*Fraxinus excelsior*	survival	II	10	yes	no	no	Alpine	unmanaged	10	404 (83)
Wunder *et al.* (2008a) 2	*Quercus robur*	*Quercus* spp.	survival	II	10	yes	no	no	Alpine	unmanaged	10	1149 (141)
Wunder *et al.* (2008a) 2	*Tilia cordata*	*Tilia cordata*	survival	II	10	yes	no	no	Alpine	unmanaged	10	321 (24)
Wunder *et al.* (in prep.)	high shade tolerance	*Abies alba*, *Carpinus betulus*, *Fagus sylvatica*	survival	II	11	yes	no	no	Alpine	unmanaged	11	902 (33)
Wunder *et al.* (in prep.)	intermediate shade tolerance	*Alnus glutinosa*, *Fraxinus excelsior*, *Picea abies*, *Tilia cordata*	survival	II	11	yes	no	no	Alpine	unmanaged	11	1965 (93)
Wunder *et al.* (in prep.)	low shade tolerance	*Betula* spp., *Larix decidua*, *Pinus sylvestris*, *Quercus* spp.	survival	II	11	yes	no	no	Alpine	unmanaged	11	1448 (102)

Table S4 Table of coefficients for the validated mortality models. For an explanation of the covariates refer to Table 1 and Appendix B. Coefficients apply not only to individual tree, stand or site characteristics but also to their transformations or to interactions of two or more covariates (e.g., *relBAL***H00**sqrt*N*/100). Where necessary, annual growth was scaled to the interval that was used for model development using either linear or exponential scaling for absolute (*DI*, *BAI*) and relative growth increments (*relBAI*), respectively.

Publication	**Calibration species**	**Covariate**	**Coefficient**	**Unit**	**Remarks**
Alenius *et al.* (2003) 1	*Pinus sylvestris*	INTERCEPT	-5.719	-	*1-PBA* refers to the proportion of birch in mixed pine-birch forests, other than stated in the publication, the coefficient appears to be valid for the percentage between 0 and 1 not in %
Alenius *et al.* (2003) 1	*Pinus sylvestris*	relBAL	2.091	-	
Alenius *et al.* (2003) 1	*Pinus sylvestris*	1-PBA	2.133	-	
Alenius *et al.* (2003) 1	*Pinus sylvestris*	qmDBH	-0.128	cm	
Alenius *et al.* (2003) 1	*Pinus sylvestris*	BA	0.111	m^2/ha	
Alenius *et al.* (2003) 1	*Pinus sylvestris*	1/DBH	30.884	mm	
Bravo-Oviedo *et al.* (2006)	*Pinus sylvestris*	INTERCEPT	6.8548	-	*SI* refers to the dominant height at the age of 100 years
Bravo-Oviedo *et al.* (2006)	*Pinus sylvestris*	BAL*CVd	-0.121	m^2/ha	
Bravo-Oviedo *et al.* (2006)	*Pinus sylvestris*	SI	-0.037	m	
Bravo-Oviedo *et al.* (2006)	*Pinus sylvestris*	1/DBH	-9.792	cm	
Crecente-Campo *et al.* (2010)	*Pinus sylvestris*	INTERCEPT	-2.903	-	
Crecente-Campo *et al.* (2010)	*Pinus sylvestris*	relBAL*hdom*sqrtN/100	0.4687	m/ha	
Crecente-Campo *et al.* (2010)	*Pinus sylvestris*	relBAL	-3.214	-	
Crecente-Campo *et al.* (2010)	*Pinus sylvestris*	qmDBH	0.3007	cm	
Crecente-Campo *et al.* (2010)	*Pinus sylvestris*	DBH	-0.4087	cm	
Dursky (1997)	*Fagus sylvatica*	INTERCEPT	6.6686	-	*BAI* was defined as the basal area increment over 5 years
Dursky (1997)	*Fagus sylvatica*	h/DBH	-7.6495	m/cm	
Dursky (1997)	*Fagus sylvatica*	DBH	-0.261	cm	
Dursky (1997)	*Fagus sylvatica*	h	0.2695	m	
Dursky (1997)	*Fagus sylvatica*	BAI/DBH	3.0796	cm^2/a/cm	
Dursky (1997)	*Picea abies*	INTERCEPT	5.3908	-	*SI* refers to the dominant height at the age of 50 years *BAI* was defined as the basal area increment over 5 years
Dursky (1997)	*Picea abies*	h/DBH	-5.3998	m/cm	
Dursky (1997)	*Picea abies*	SI	-0.0406	m	
Dursky (1997)	*Picea abies*	DBH	-0.0089	cm	
Dursky (1997)	*Picea abies*	BAI/DBH	1.4802	cm^2/a/cm	
Eid and Tuhus (2001)	*Betula* spp.	INTERCEPT	4.8923	-	
Eid and Tuhus (2001)	*Betula* spp.	1/DBH	-2.528	cm	
Eid and Tuhus (2001)	Broadleaf Other	INTERCEPT	5.1575	-	
Eid and Tuhus (2001)	Broadleaf Other	BAL	-0.0199	m^2/ha	
Eid and Tuhus (2001)	Broadleaf Other	1/DBH	-7.3544	cm	
Eid and Tuhus (2001)	*Picea abies*	INTERCEPT	8.0599	-	*SI* refers to the dominant height at the age of 40 years
Eid and Tuhus (2001)	*Picea abies*	BAL	-0.0281	m^2/ha	
Eid and Tuhus (2001)	*Picea abies*	PBA	-0.0132	%	
Eid and Tuhus (2001)	*Picea abies*	SI	-0.0264	m	
Eid and Tuhus (2001)	*Picea abies*	1/DBH	-6.702	cm	
Eid and Tuhus (2001)	*Pinus sylvestris*	INTERCEPT	8.4904	-	*SI* refers to the dominant height at the age of 40 years
Eid and Tuhus (2001)	*Pinus sylvestris*	BAL	-0.0462	m^2/ha	
Eid and Tuhus (2001)	*Pinus sylvestris*	SI	-0.0761	m	
Eid and Tuhus (2001)	*Pinus sylvestris*	1/DBH	-14.266	cm	
Fridman and Ståhl (2001)	*Betula* spp.	INTERCEPT	-2.83	-	
Fridman and Ståhl (2001)	*Betula* spp.	BAL	0.0362	m^2/ha	
Fridman and Ståhl (2001)	*Betula* spp.	mDBH	15.7	m	
Fridman and Ståhl (2001)	*Betula* spp.	BA	-0.0665	m^2/ha	
Fridman and Ståhl (2001)	*Betula* spp.	ALT	0.0011	m	
Fridman and Ståhl (2001)	*Betula* spp.	DBH	-16.5	m	
Fridman and Ståhl (2001)	*Betula* spp.	DBH^2	27.7	m	
Fridman and Ståhl (2001)	Broadleaf Other	INTERCEPT	-5.4	-	the categorical variable '*≤20m clearcut*' was set to 0 for all observations since no management in the reserves was assumed
Fridman and Ståhl (2001)	Broadleaf Other	BAL	0.0693	m^2/ha	
Fridman and Ståhl (2001)	Broadleaf Other	BA	-0.0688	m^2/ha	
Fridman and Ståhl (2001)	Broadleaf Other	ALT	0.00212	m	
Fridman and Ståhl (2001)	Broadleaf Other	LAT	0.0498	degree	
Fridman and Ståhl (2001)	Broadleaf Other	<20m clearcut	-0.345	-	
Fridman and Ståhl (2001)	Broadleaf Other	1/DBH	0.0634	m	
Fridman and Ståhl (2001)	Broadleaf Southern	INTERCEPT	-3.67	-	
Fridman and Ståhl (2001)	Broadleaf Southern	BAL	0.168	m^2/ha	
Fridman and Ståhl (2001)	Broadleaf Southern	BA	-0.14	m^2/ha	
Fridman and Ståhl (2001)	Broadleaf Southern	DBH	3.34	m	
Fridman and Ståhl (2001)	*Picea abies*	INTERCEPT	-4.58	-	the categorical variable *PIDOM* quantifies the domination of *Pinus* with 1 indicating *PBA* of *Pinus* ≥ 0.7. the categorical variable '*≤20m clearcut*' was set to 0 for all observations since no management in the reserves was assumed
Fridman and Ståhl (2001)	*Picea abies*	BAL	0.0282	m^2/ha	
Fridman and Ståhl (2001)	*Picea abies*	PIDOM	-0.594	-	
Fridman and Ståhl (2001)	*Picea abies*	mDBH	11.2	m	
Fridman and Ståhl (2001)	*Picea abies*	BA	-0.0545	m^2/ha	
Fridman and Ståhl (2001)	*Picea abies*	<20m clearcut	0.577	-	
Fridman and Ståhl (2001)	*Picea abies*	management	0.323	-	
Fridman and Ståhl (2001)	*Picea abies*	1/DBH	0.042	m	

Publication	Calibration species	Covariate	Coefficient	Unit	Remarks
Fridman and Ståhl (2001)	*Pinus sylvestris*	INTERCEPT	-1.98	-	the categorical variable *PIDOM* quantifies the domination of *Pinus* with 1 indicating *PBA* of *Pinus* ≥ 0.7. the mean of the squared DBH (*mDBH^2*) is approximately equal to *(qmDBH)^2* the categorical variable *moist* quantifies soil water conditions with 1 indicating moist or wet
Fridman and Ståhl (2001)	*Pinus sylvestris*	BAL	0.028	m^2/ha	
Fridman and Ståhl (2001)	*Pinus sylvestris*	PIDOM	-0.456	-	
Fridman and Ståhl (2001)	*Pinus sylvestris*	mDBH	25.6	m	
Fridman and Ståhl (2001)	*Pinus sylvestris*	mDBH^2	-26.6	m	
Fridman and Ståhl (2001)	*Pinus sylvestris*	log(BA)	-0.739	m^2/ha	
Fridman and Ståhl (2001)	*Pinus sylvestris*	moist	0.327	-	
Fridman and Ståhl (2001)	*Pinus sylvestris*	DBH	-17.4	m	
Fridman and Ståhl (2001)	*Pinus sylvestris*	DBH^2	21.5	m	
Holzwarth *et al.* (2013)	*Carpinus betulus*	INTERCEPT	-2.8	-	in communication with the authors, both coefficients were corrected and thus are different from the original paper
Holzwarth *et al.* (2013)	*Carpinus betulus*	DBH	-0.051	cm	
Holzwarth *et al.* (2013)	*Fagus sylvatica*	INTERCEPT	1.8	-	two models for 'early' and 'late' mortality were fitted that add up to the total mortality for log-transformed *DBH*, an additive constant of 8 cm was used
Holzwarth *et al.* (2013)	*Fagus sylvatica*	log(DBH)	-2.1	cm	
Holzwarth *et al.* (2013)	*Fagus sylvatica*	DI	-1.4	cm/a	
Holzwarth *et al.* (2013)	*Fagus sylvatica*	INTERCEPT	-8.9	-	
Holzwarth *et al.* (2013)	*Fagus sylvatica*	DBH	0.052	cm	
Holzwarth *et al.* (2013)	*Fagus sylvatica*	log(DBH)	0	cm	
Holzwarth *et al.* (2013)	*Fagus sylvatica*	DI	0	cm/a	
Holzwarth *et al.* (2013)	*Fraxinus excelsior*	INTERCEPT	1.3	-	
Holzwarth *et al.* (2013)	*Fraxinus excelsior*	log(DBH)	-1.6	cm	
Monserud and Sterba (1999)	*Abies alba*	INTERCEPT	2.0985	-	
Monserud and Sterba (1999)	*Abies alba*	1/DBH	-10.9085	cm	
Monserud and Sterba (1999)	*Abies alba*	CR	3.9311	-	
Monserud and Sterba (1999)	Broadleaf Other	INTERCEPT	2.9223	-	
Monserud and Sterba (1999)	Broadleaf Other	BAL	-0.0228	m^2/ha	
Monserud and Sterba (1999)	Broadleaf Other	1/DBH	-8.4877	cm	
Monserud and Sterba (1999)	Broadleaf Other	CR	2.0609	-	
Monserud and Sterba (1999)	*Fagus sylvatica*	INTERCEPT	3.5734	-	
Monserud and Sterba (1999)	*Fagus sylvatica*	BAL	-0.0161	m^2/ha	
Monserud and Sterba (1999)	*Fagus sylvatica*	1/DBH	-13.9542	cm	
Monserud and Sterba (1999)	*Fagus sylvatica*	CR	3.1339	-	
Monserud and Sterba (1999)	*Larix decidua*	INTERCEPT	4.407	-	
Monserud and Sterba (1999)	*Larix decidua*	BAL	-0.0326	m^2/ha	
Monserud and Sterba (1999)	*Larix decidua*	1/DBH	-12.9395	cm	
Monserud and Sterba (1999)	*Larix decidua*	CR	2.2039	-	
Monserud and Sterba (1999)	*Picea abies*	INTERCEPT	2.1283	-	
Monserud and Sterba (1999)	*Picea abies*	BAL	-0.0186	m^2/ha	
Monserud and Sterba (1999)	*Picea abies*	1/DBH	-10.0745	cm	
Monserud and Sterba (1999)	*Picea abies*	DBH	0.0425	cm	
Monserud and Sterba (1999)	*Picea abies*	DBH^2	-0.00081	cm	
Monserud and Sterba (1999)	*Picea abies*	CR	3.8251	-	
Monserud and Sterba (1999)	*Pinus sylvestris*	INTERCEPT	4.1076	-	
Monserud and Sterba (1999)	*Pinus sylvestris*	BAL	-0.0234	m^2/ha	
Monserud and Sterba (1999)	*Pinus sylvestris*	1/DBH	-18.9714	cm	
Monserud and Sterba (1999)	*Pinus sylvestris*	CR	2.3267	-	
Monserud and Sterba (1999)	*Quercus* spp.	INTERCEPT	4.4508	-	
Monserud and Sterba (1999)	*Quercus* spp.	1/DBH	-12.0041	cm	
Palahí *et al.* (2003) 2	*Pinus sylvestris*	INTERCEPT	2.938	-	*DI* was defined as the diameter increment over 5 years
Palahí *et al.* (2003) 2	*Pinus sylvestris*	BAL	-0.02	m^2/ha	
Palahí *et al.* (2003) 2	*Pinus sylvestris*	DI	2.719	cm/a	
Trasobares *et al.* (2004)	*Pinus sylvestris*	INTERCEPT	2.728	-	for log-transformed *DBH*, an additive constant of 1 cm was used, the covariate *CON* that quantifies continentality was set to the maximum value within the calibration dataset = 186.6 km
Trasobares *et al.* (2004)	*Pinus sylvestris*	BAL/log(DBH)	-0.148	m^2/ha/cm	
Trasobares *et al.* (2004)	*Pinus sylvestris*	ALT	0.067	100m	
Trasobares *et al.* (2004)	*Pinus sylvestris*	CON	-0.006	km	
Trasobares *et al.* (2004)	*Pinus sylvestris*	h	0.107	m	
Wunder *et al.* (2007) 1	*Abies alba*	INTERCEPT	1.161	-	for coefficients and details on the construction of the restricted cubic splines of *relBAI* refer also to Wunder (2007) *relBAI1-4* refer to the coefficients, *KrelBAI1-4* mark the locations of the knots of the restricted cubic splines *relBAI* was defined as the relative basal area increment over 11 years
Wunder *et al.* (2007) 1	*Abies alba*	relBAI	29.17	1/a	
Wunder *et al.* (2007) 1	*Abies alba*	relBAI1	-518.37	1/a	
Wunder *et al.* (2007) 1	*Abies alba*	relBAI2	1038.53	1/a	
Wunder *et al.* (2007) 1	*Abies alba*	relBAI3	-505.01	1/a	
Wunder *et al.* (2007) 1	*Abies alba*	relBAI4	-15.15	1/a	
Wunder *et al.* (2007) 1	*Abies alba*	KrelBAI1	0.02	1/a	
Wunder *et al.* (2007) 1	*Abies alba*	KrelBAI2	0.104	1/a	
Wunder *et al.* (2007) 1	*Abies alba*	KrelBAI3	0.181	1/a	
Wunder *et al.* (2007) 1	*Abies alba*	KrelBAI4	0.395	1/a	
Wunder *et al.* (2007) 1	*Fagus sylvatica*	INTERCEPT	-17.63	-	for coefficients and details on the construction of the restricted cubic splines of *relBAI* refer also to Wunder (2007) *relBAI1-4* refer to the coefficients, *KrelBAI1-4* mark the locations of the knots of the restricted cubic splines *relBAI* was defined as the relative basal area increment over 11 years
Wunder *et al.* (2007) 1	*Fagus sylvatica*	log(DBH)	3.57	mm	
Wunder *et al.* (2007) 1	*Fagus sylvatica*	relBAI	29.17	1/a	
Wunder *et al.* (2007) 1	*Fagus sylvatica*	relBAI1	-518.37	1/a	
Wunder *et al.* (2007) 1	*Fagus sylvatica*	relBAI2	1038.53	1/a	
Wunder *et al.* (2007) 1	*Fagus sylvatica*	relBAI3	-505.01	1/a	
Wunder *et al.* (2007) 1	*Fagus sylvatica*	relBAI4	-15.15	1/a	
Wunder *et al.* (2007) 1	*Fagus sylvatica*	KrelBAI1	0.02	1/a	
Wunder *et al.* (2007) 1	*Fagus sylvatica*	KrelBAI2	0.104	1/a	
Wunder *et al.* (2007) 1	*Fagus sylvatica*	KrelBAI3	0.181	1/a	
Wunder *et al.* (2007) 1	*Fagus sylvatica*	KrelBAI4	0.395	1/a	

Publication	**Calibration species**	**Covariate**	**Coefficient**	**Unit**	**Remarks**
Wunder *et al.* (2007) 2	*Abies alba*	INTERCEPT	-0.4	-	for coefficients and details on the construction of the restricted cubic splines of *relBAI* refer also to Wunder (2007) *relBAI1-4* refer to the coefficients, *KrelBAI1-4* mark the locations of the knots of the restricted cubic splines *relBAI* was defined as the relative basal area increment over 12.5 years
Wunder *et al.* (2007) 2	*Abies alba*	relBAI	29.17	1/a	
Wunder *et al.* (2007) 2	*Abies alba*	relBAI1	-518.37	1/a	
Wunder *et al.* (2007) 2	*Abies alba*	relBAI2	1038.53	1/a	
Wunder *et al.* (2007) 2	*Abies alba*	relBAI3	-505.01	1/a	
Wunder *et al.* (2007) 2	*Abies alba*	relBAI4	-15.15	1/a	
Wunder *et al.* (2007) 2	*Abies alba*	KrelBAI1	0.02	1/a	
Wunder *et al.* (2007) 2	*Abies alba*	KrelBAI2	0.104	1/a	
Wunder *et al.* (2007) 2	*Abies alba*	KrelBAI3	0.181	1/a	
Wunder *et al.* (2007) 2	*Abies alba*	KrelBAI4	0.395	1/a	
Wunder *et al.* (2007) 2	*Fagus sylvatica*	INTERCEPT	-16.86	-	for coefficients and details on the construction of the restricted cubic splines of *relBAI* refer also to Wunder (2007) *relBAI1-4* refer to the coefficients, *KrelBAI1-4* mark the locations of the knots of the restricted cubic splines *relBAI* was defined as the relative basal area increment over 12.5 years
Wunder *et al.* (2007) 2	*Fagus sylvatica*	log(DBH)	3.57	mm	
Wunder *et al.* (2007) 2	*Fagus sylvatica*	relBAI	29.17	1/a	
Wunder *et al.* (2007) 2	*Fagus sylvatica*	relBAI1	-518.37	1/a	
Wunder *et al.* (2007) 2	*Fagus sylvatica*	relBAI2	1038.53	1/a	
Wunder *et al.* (2007) 2	*Fagus sylvatica*	relBAI3	-505.01	1/a	
Wunder *et al.* (2007) 2	*Fagus sylvatica*	relBAI4	-15.15	1/a	
Wunder *et al.* (2007) 2	*Fagus sylvatica*	KrelBAI1	0.02	1/a	
Wunder *et al.* (2007) 2	*Fagus sylvatica*	KrelBAI2	0.104	1/a	
Wunder *et al.* (2007) 2	*Fagus sylvatica*	KrelBAI3	0.181	1/a	
Wunder *et al.* (2007) 2	*Fagus sylvatica*	KrelBAI4	0.395	1/a	
Wunder *et al.* (2008) 1	*Alnus glutinosa*	INTERCEPT	0.958	-	for log-transformed *relBAI*, an additive constant of 0.002531 was used *log(relBAI)1-3* refer to the coefficients, *KrelBAI1-3* mark the locations of the knots of the restricted cubic splines in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder *et al.* (2008) 1	*Alnus glutinosa*	log(DBH)	1.105	cm	
Wunder *et al.* (2008) 1	*Alnus glutinosa*	log(relBAI)	1.217	1/a	
Wunder *et al.* (2008) 1	*Alnus glutinosa*	log(relBAI)1	-0.092	1/a	
Wunder *et al.* (2008) 1	*Alnus glutinosa*	log(relBAI)2	0.22	1/a	
Wunder *et al.* (2008) 1	*Alnus glutinosa*	log(relBAI)3	-0.128	1/a	
Wunder *et al.* (2008) 1	*Alnus glutinosa*	KrelBAI1	-4.8459	1/a	
Wunder *et al.* (2008) 1	*Alnus glutinosa*	KrelBAI2	-3.8672	1/a	
Wunder *et al.* (2008) 1	*Alnus glutinosa*	KrelBAI3	-3.16568	1/a	
Wunder *et al.* (2008) 1	*Carpinus betulus*	INTERCEPT	5.281	-	for log-transformed *relBAI*, an additive constant of 0.002531 was used *log(relBAI)1-3* refer to the coefficients, *KrelBAI1-3* mark the locations of the knots of the restricted cubic splines in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder *et al.* (2008) 1	*Carpinus betulus*	log(relBAI)	0.643	1/a	
Wunder *et al.* (2008) 1	*Carpinus betulus*	log(relBAI)1	-0.056	1/a	
Wunder *et al.* (2008) 1	*Carpinus betulus*	log(relBAI)2	0.123	1/a	
Wunder *et al.* (2008) 1	*Carpinus betulus*	log(relBAI)3	-0.067	1/a	
Wunder *et al.* (2008) 1	*Carpinus betulus*	KrelBAI1	-5.5368	1/a	
Wunder *et al.* (2008) 1	*Carpinus betulus*	KrelBAI2	-4.37017	1/a	
Wunder *et al.* (2008) 1	*Carpinus betulus*	KrelBAI3	-3.39317	1/a	
Wunder *et al.* (2008) 1	*Fraxinus excelsior*	INTERCEPT	-3.3	-	for log-transformed *relBAI*, an additive constant of 0.002531 was used *log(relBAI)1-3* refer to the coefficients, *KrelBAI1-3* mark the locations of the knots of the restricted cubic splines in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder *et al.* (2008) 1	*Fraxinus excelsior*	log(DBH)	1.171	cm	
Wunder *et al.* (2008) 1	*Fraxinus excelsior*	log(relBAI)	0.333	1/a	
Wunder *et al.* (2008) 1	*Fraxinus excelsior*	log(relBAI)1	0.71	1/a	
Wunder *et al.* (2008) 1	*Fraxinus excelsior*	log(relBAI)2	-1.305	1/a	
Wunder *et al.* (2008) 1	*Fraxinus excelsior*	log(relBAI)3	1.911	1/a	
Wunder *et al.* (2008) 1	*Fraxinus excelsior*	KrelBAI1	-4.65255	1/a	
Wunder *et al.* (2008) 1	*Fraxinus excelsior*	KrelBAI2	-3.91917	1/a	
Wunder *et al.* (2008) 1	*Fraxinus excelsior*	KrelBAI3	-3.04359	1/a	
Wunder *et al.* (2008) 1	*Picea abies*	INTERCEPT	4.647	-	for log-transformed *relBAI*, an additive constant of 0.002531 was used *log(relBAI)1-3* refer to the coefficients, *KrelBAI1-3* mark the locations of the knots of the restricted cubic splines in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder *et al.* (2008) 1	*Picea abies*	log(DBH)	-0.384	cm	
Wunder *et al.* (2008) 1	*Picea abies*	log(relBAI)	0.44	1/a	
Wunder *et al.* (2008) 1	*Picea abies*	log(relBAI)1	0.071	1/a	
Wunder *et al.* (2008) 1	*Picea abies*	log(relBAI)2	-0.196	1/a	
Wunder *et al.* (2008) 1	*Picea abies*	log(relBAI)3	0.125	1/a	
Wunder *et al.* (2008) 1	*Picea abies*	KrelBAI1	-5.08731	1/a	
Wunder *et al.* (2008) 1	*Picea abies*	KrelBAI2	-3.93875	1/a	
Wunder *et al.* (2008) 1	*Picea abies*	KrelBAI3	-3.29096	1/a	
Wunder *et al.* (2008) 1	*Quercus robur*	INTERCEPT	-2.785	-	for log-transformed *relBAI*, an additive constant of 0.002531 was used *log(relBAI)1-3* refer to the coefficients, *KrelBAI1-3* mark the locations of the knots of the restricted cubic splines in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder *et al.* (2008) 1	*Quercus robur*	log(DBH)	2.075	cm	
Wunder *et al.* (2008) 1	*Quercus robur*	log(relBAI)	1.801	1/a	
Wunder *et al.* (2008) 1	*Quercus robur*	log(relBAI)1	-0.157	1/a	
Wunder *et al.* (2008) 1	*Quercus robur*	log(relBAI)2	0.382	1/a	
Wunder *et al.* (2008) 1	*Quercus robur*	log(relBAI)3	-0.225	1/a	
Wunder *et al.* (2008) 1	*Quercus robur*	KrelBAI1	-5.38701	1/a	
Wunder *et al.* (2008) 1	*Quercus robur*	KrelBAI2	-4.41242	1/a	
Wunder *et al.* (2008) 1	*Quercus robur*	KrelBAI3	-3.73213	1/a	
Wunder *et al.* (2008) 1	*Tilia cordata*	INTERCEPT	-1.787	-	for log-transformed *relBAI*, an additive constant of 0.002531 was used *log(relBAI)1-3* refer to the coefficients, *KrelBAI1-3* mark the locations of the knots of the restricted cubic splines in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder *et al.* (2008) 1	*Tilia cordata*	log(DBH)	1.591	cm	
Wunder *et al.* (2008) 1	*Tilia cordata*	log(relBAI)	1.022	1/a	
Wunder *et al.* (2008) 1	*Tilia cordata*	log(relBAI)1	-0.095	1/a	
Wunder *et al.* (2008) 1	*Tilia cordata*	log(relBAI)2	0.289	1/a	
Wunder *et al.* (2008) 1	*Tilia cordata*	log(relBAI)3	-0.194	1/a	
Wunder *et al.* (2008) 1	*Tilia cordata*	KrelBAI1	-5.2202	1/a	
Wunder *et al.* (2008) 1	*Tilia cordata*	KrelBAI2	-3.64442	1/a	
Wunder *et al.* (2008) 1	*Tilia cordata*	KrelBAI3	-2.87098	1/a	

Publication	**Calibration species**	**Covariate**	**Coefficient**	**Unit**	**Remarks**
Wunder *et al.* (2008) 1+2	*Betula* spp.	INTERCEPT	1.073	-	for log-transformed *relBAI*, an additive constant of 0.002531 was used *log(relBAI)1-3* refer to the coefficients, *KrelBAI1-3* mark the locations of the knots of the restricted cubic splines in communication with the authors, the coefficients for *log(DBH)* and *site* (PL, CH) and the locations of the knots were corrected and thus are different from the original paper
Wunder *et al.* (2008) 1+2	*Betula* spp.	log(DBH)	0.623	cm	
Wunder *et al.* (2008) 1+2	*Betula* spp.	log(relBAI)	0.813	1/a	
Wunder *et al.* (2008) 1+2	*Betula* spp.	log(relBAI)1	-0.031	1/a	
Wunder *et al.* (2008) 1+2	*Betula* spp.	log(relBAI)2	0.073	1/a	
Wunder *et al.* (2008) 1+2	*Betula* spp.	log(relBAI)3	-0.042	1/a	
Wunder *et al.* (2008) 1+2	*Betula* spp.	KrelBAI1	-5.55349	1/a	
Wunder *et al.* (2008) 1+2	*Betula* spp.	KrelBAI2	-4.45592	1/a	
Wunder *et al.* (2008) 1+2	*Betula* spp.	KrelBAI3	-3.64797	1/a	
Wunder *et al.* (2008) 2	*Alnus glutinosa*	INTERCEPT	1.918	-	for log-transformed *relBAI*, an additive constant of 0.002531 was used *log(relBAI)1-3* refer to the coefficients, *KrelBAI1-3* mark the locations of the knots of the restricted cubic splines in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder *et al.* (2008) 2	*Alnus glutinosa*	log(DBH)	1.105	cm	
Wunder *et al.* (2008) 2	*Alnus glutinosa*	log(relBAI)	1.217	1/a	
Wunder *et al.* (2008) 2	*Alnus glutinosa*	log(relBAI)1	-0.092	1/a	
Wunder *et al.* (2008) 2	*Alnus glutinosa*	log(relBAI)2	0.22	1/a	
Wunder *et al.* (2008) 2	*Alnus glutinosa*	log(relBAI)3	-0.128	1/a	
Wunder *et al.* (2008) 2	*Alnus glutinosa*	KrelBAI1	-4.8459	1/a	
Wunder *et al.* (2008) 2	*Alnus glutinosa*	KrelBAI2	-3.8672	1/a	
Wunder *et al.* (2008) 2	*Alnus glutinosa*	KrelBAI3	-3.16568	1/a	
Wunder *et al.* (2008) 2	*Carpinus betulus*	INTERCEPT	1.827	-	for log-transformed *relBAI*, an additive constant of 0.002531 was used *log(relBAI)1-3* refer to the coefficients, *KrelBAI1-3* mark the locations of the knots of the restricted cubic splines in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder *et al.* (2008) 2	*Carpinus betulus*	log(relBAI)	0.207	1/a	
Wunder *et al.* (2008) 2	*Carpinus betulus*	log(relBAI)1	0.626	1/a	
Wunder *et al.* (2008) 2	*Carpinus betulus*	log(relBAI)2	-1.373	1/a	
Wunder *et al.* (2008) 2	*Carpinus betulus*	log(relBAI)3	0.747	1/a	
Wunder *et al.* (2008) 2	*Carpinus betulus*	KrelBAI1	-5.5368	1/a	
Wunder *et al.* (2008) 2	*Carpinus betulus*	KrelBAI2	-4.37017	1/a	
Wunder *et al.* (2008) 2	*Carpinus betulus*	KrelBAI3	-3.39317	1/a	
Wunder *et al.* (2008) 2	*Fagus sylvatica*	INTERCEPT	10.009	-	for log-transformed *relBAI*, an additive constant of 0.002531 was used *log(relBAI)1-3* refer to the coefficients, *KrelBAI1-3* mark the locations of the knots of the restricted cubic splines in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder *et al.* (2008) 2	*Fagus sylvatica*	log(relBAI)	1.743	1/a	
Wunder *et al.* (2008) 2	*Fagus sylvatica*	log(relBAI)1	-0.113	1/a	
Wunder *et al.* (2008) 2	*Fagus sylvatica*	log(relBAI)2	0.328	1/a	
Wunder *et al.* (2008) 2	*Fagus sylvatica*	log(relBAI)3	-0.215	1/a	
Wunder *et al.* (2008) 2	*Fagus sylvatica*	KrelBAI1	-5.32948	1/a	
Wunder *et al.* (2008) 2	*Fagus sylvatica*	KrelBAI2	-4.07211	1/a	
Wunder *et al.* (2008) 2	*Fagus sylvatica*	KrelBAI3	-3.40999	1/a	
Wunder *et al.* (2008) 2	*Fraxinus excelsior*	INTERCEPT	5.413	-	for log-transformed *relBAI*, an additive constant of 0.002531 was used *log(relBAI)1-3* refer to the coefficients, *KrelBAI1-3* mark the locations of the knots of the restricted cubic splines in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder *et al.* (2008) 2	*Fraxinus excelsior*	log(DBH)	1.171	cm	
Wunder *et al.* (2008) 2	*Fraxinus excelsior*	log(relBAI)	2.418	1/a	
Wunder *et al.* (2008) 2	*Fraxinus excelsior*	log(relBAI)1	-0.786	1/a	
Wunder *et al.* (2008) 2	*Fraxinus excelsior*	log(relBAI)2	1.444	1/a	
Wunder *et al.* (2008) 2	*Fraxinus excelsior*	log(relBAI)3	0.658	1/a	
Wunder *et al.* (2008) 2	*Fraxinus excelsior*	KrelBAI1	-4.65255	1/a	
Wunder *et al.* (2008) 2	*Fraxinus excelsior*	KrelBAI2	-3.91917	1/a	
Wunder *et al.* (2008) 2	*Fraxinus excelsior*	KrelBAI3	-3.04359	1/a	
Wunder *et al.* (2008) 2	*Quercus robur*	INTERCEPT	-0.465	-	for log-transformed *relBAI*, an additive constant of 0.002531 was used *log(relBAI)1-3* refer to the coefficients, *KrelBAI1-3* mark the locations of the knots of the restricted cubic splines in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder *et al.* (2008) 2	*Quercus robur*	log(DBH)	2.075	cm	
Wunder *et al.* (2008) 2	*Quercus robur*	log(relBAI)	1.801	1/a	
Wunder *et al.* (2008) 2	*Quercus robur*	log(relBAI)1	-0.157	1/a	
Wunder *et al.* (2008) 2	*Quercus robur*	log(relBAI)2	0.382	1/a	
Wunder *et al.* (2008) 2	*Quercus robur*	log(relBAI)3	-0.225	1/a	
Wunder *et al.* (2008) 2	*Quercus robur*	KrelBAI1	-5.38701	1/a	
Wunder *et al.* (2008) 2	*Quercus robur*	KrelBAI2	-4.41242	1/a	
Wunder *et al.* (2008) 2	*Quercus robur*	KrelBAI3	-3.73213	1/a	
Wunder *et al.* (2008) 2	*Tilia cordata*	INTERCEPT	-0.847	-	for log-transformed *relBAI*, an additive constant of 0.002531 was used *log(relBAI)1-3* refer to the coefficients, *KrelBAI1-3* mark the locations of the knots of the restricted cubic splines in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder *et al.* (2008) 2	*Tilia cordata*	log(DBH)	1.591	cm	
Wunder *et al.* (2008) 2	*Tilia cordata*	log(relBAI)	1.022	1/a	
Wunder *et al.* (2008) 2	*Tilia cordata*	log(relBAI)1	-0.095	1/a	
Wunder *et al.* (2008) 2	*Tilia cordata*	log(relBAI)2	0.289	1/a	
Wunder *et al.* (2008) 2	*Tilia cordata*	log(relBAI)3	-0.194	1/a	
Wunder *et al.* (2008) 2	*Tilia cordata*	KrelBAI1	-5.2202	1/a	
Wunder *et al.* (2008) 2	*Tilia cordata*	KrelBAI2	-3.64442	1/a	
Wunder *et al.* (2008) 2	*Tilia cordata*	KrelBAI3	-2.87098	1/a	
Wunder *et al.* (in prep.)	low shade tolerance	INTERCEPT	7.5825	-	the influence of relBAI was included via four growth categories: Very low growth: relBAI = 0 Low growth: relBAI 0…1.5% Fast growth: relBAI 1.5...3% Very fast growth: relBAI > 3%
Wunder *et al.* (in prep.)	low shade tolerance	DBH	0.0672	cm	
Wunder *et al.* (in prep.)	low shade tolerance	DBH^2	-0.0005	cm	
Wunder *et al.* (in prep.)	low shade tolerance	low relBAI	0.581	-	
Wunder *et al.* (in prep.)	low shade tolerance	fast relBAI	1.1968	-	
Wunder *et al.* (in prep.)	low shade tolerance	very fast relBAI	2.0417	-	
Wunder *et al.* (in prep.)	low shade tolerance	log(GDD)	-1.0107	-	
Wunder *et al.* (in prep.)	intermediate shade tolerance	INTERCEPT	7.7706	-	the influence of relBAI was included via four growth categories: Very low growth: relBAI = 0 Low growth: relBAI 0…1.5% Fast growth: relBAI 1.5...3% Very fast growth: relBAI > 3%
Wunder *et al.* (in prep.)	intermediate shade tolerance	DBH	0.0672	cm	
Wunder *et al.* (in prep.)	intermediate shade tolerance	DBH^2	-0.0005	cm	
Wunder *et al.* (in prep.)	intermediate shade tolerance	low relBAI	0.581	-	
Wunder *et al.* (in prep.)	intermediate shade tolerance	fast relBAI	1.1968	-	
Wunder *et al.* (in prep.)	intermediate shade tolerance	very fast relBAI	2.0417	-	
Wunder *et al.* (in prep.)	intermediate shade tolerance	log(GDD)	-1.0107	-	

Publication	**Calibration species**	**Covariate**	**Coefficient**	**Unit**	**Remarks**
Wunder *et al.* (in prep.)	high shade tolerance	INTERCEPT	8.59	-	the influence of relBAI was included via four growth categories: Very low growth: relBAI = 0 Low growth: relBAI 0…1.5% Fast growth: relBAI 1.5...3% Very fast growth: relBAI > 3%
Wunder *et al.* (in prep.)	high shade tolerance	DBH	0.0672	cm	
Wunder *et al.* (in prep.)	high shade tolerance	DBH^2	-0.0005	cm	
Wunder *et al.* (in prep.)	high shade tolerance	low relBAI	0.581	-	
Wunder *et al.* (in prep.)	high shade tolerance	fast relBAI	1.1968	-	
Wunder *et al.* (in prep.)	high shade tolerance	very fast relBAI	2.0417	-	
Wunder *et al.* (in prep.)	high shade tolerance	log(GDD)	-1.0107	-	

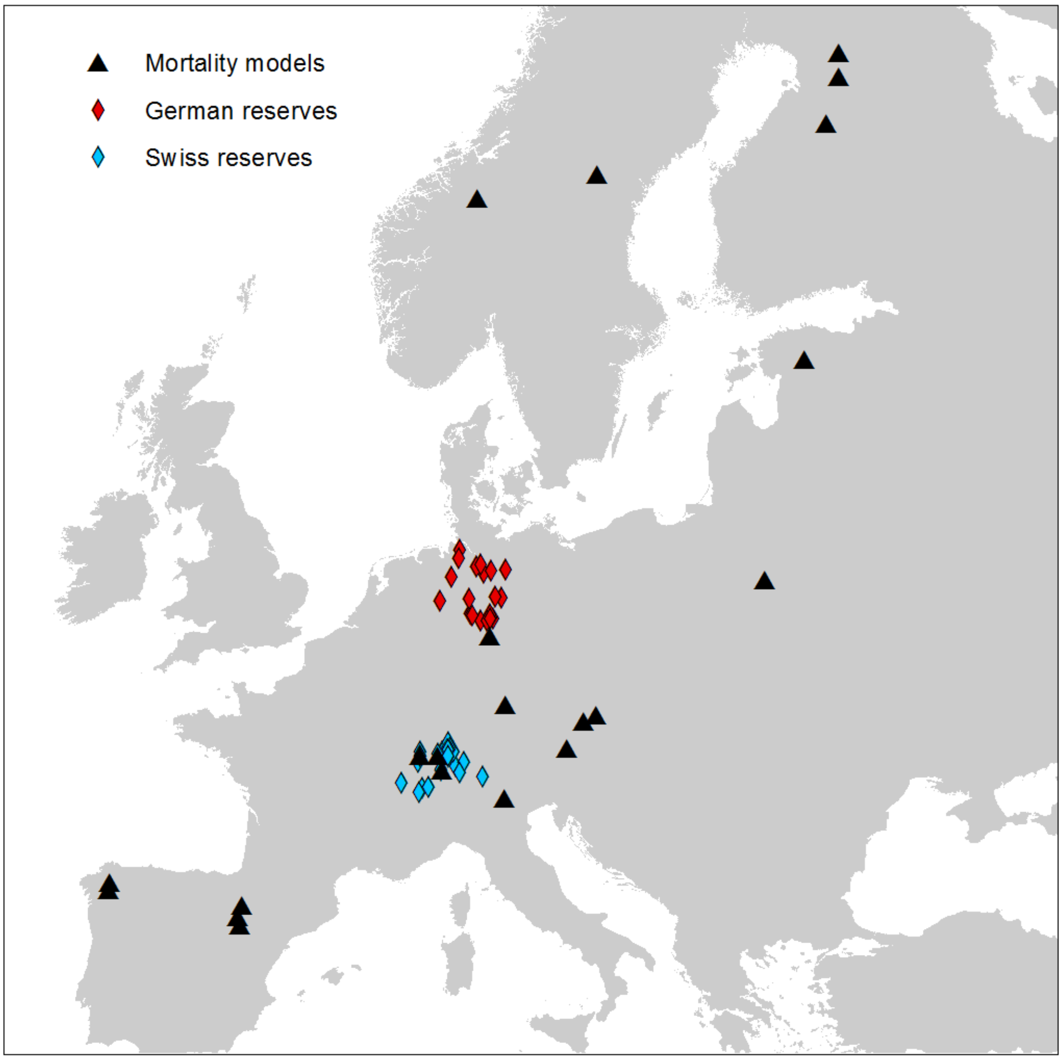

Fig. S1 Map of European tree mortality models and strict forest reserves in Germany and Switzerland. The location of the calibration dataset was estimated based on the information available from the publications. Number of reserves per respective validation dataset: Germany *n* = 22 and Switzerland *n* = 32.

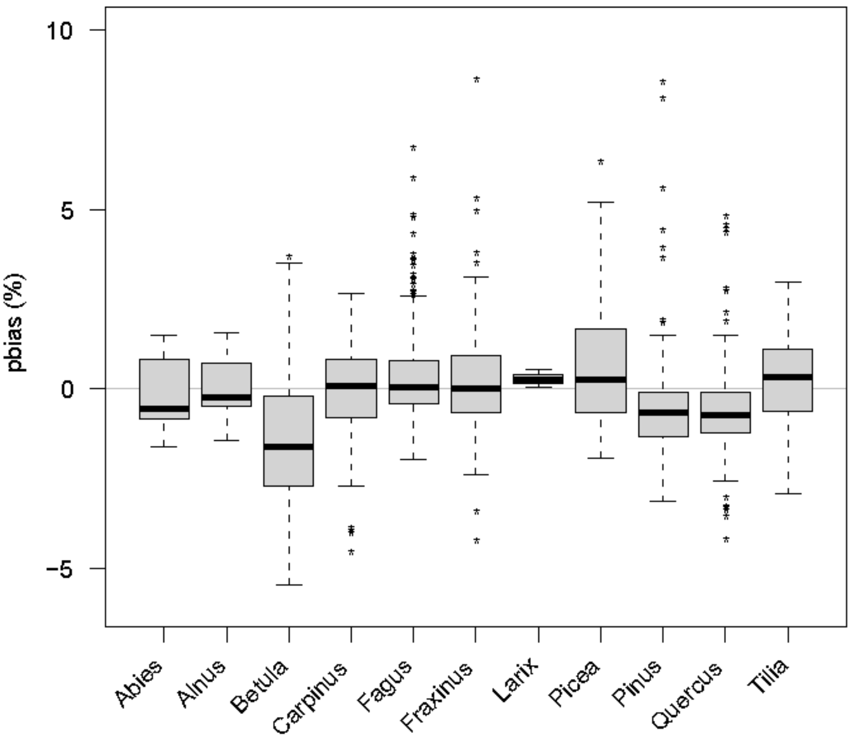

Fig. S2 Boxplot of p_{bias} at the reserve level for each tree species. Prevailing positive or negative p_{bias} values indicate that for the respective species the models used for prediction tend to over- or underestimate tree mortality, respectively.

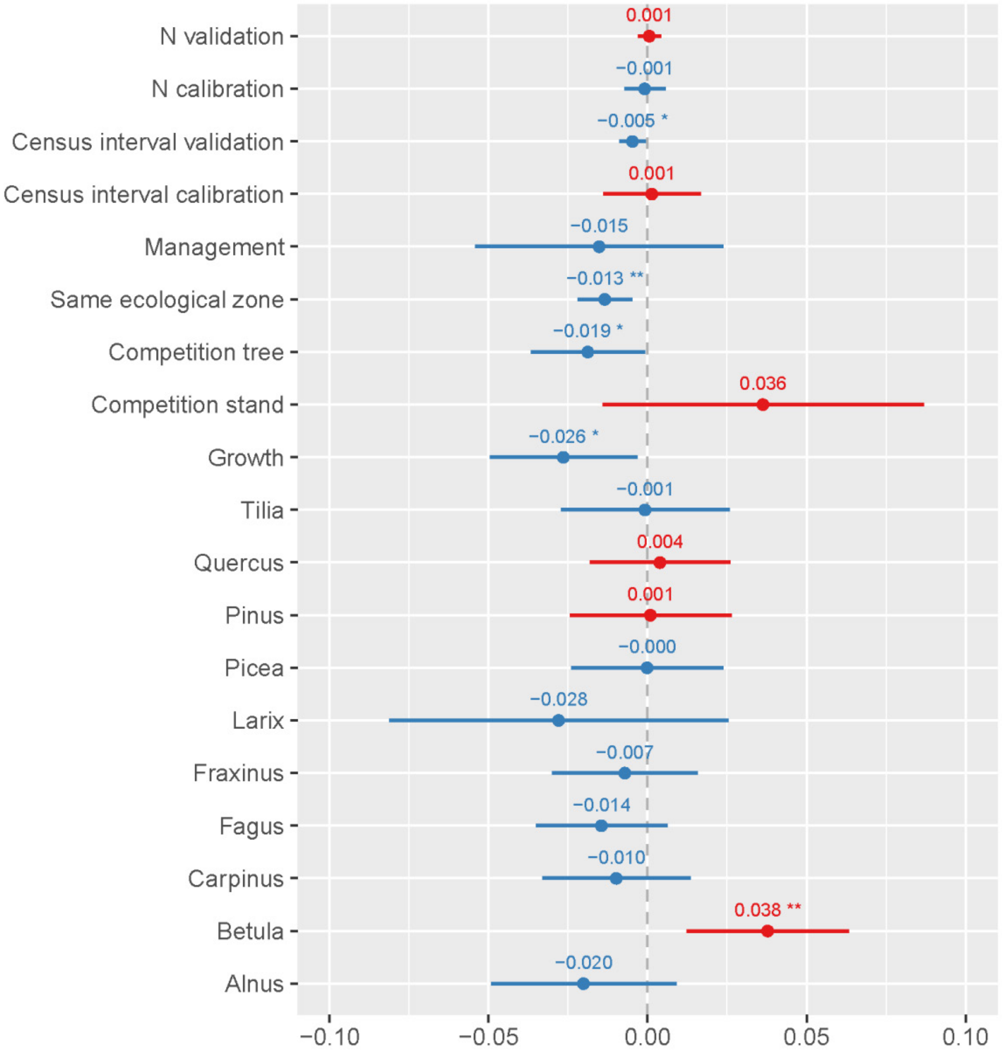

Fig. S3 Fixed effects of the influence of model and data characteristics on the square-root of $|p_{bias}|$. Note that a ‘good’ model features low $|p_{bias}|$. Positive and negative influences on performance are shown in blue and red, respectively. Note that the first level of all factors is the reference level, while the other levels are characterized by the shift relative to this reference level. The reference species is *Abies*.

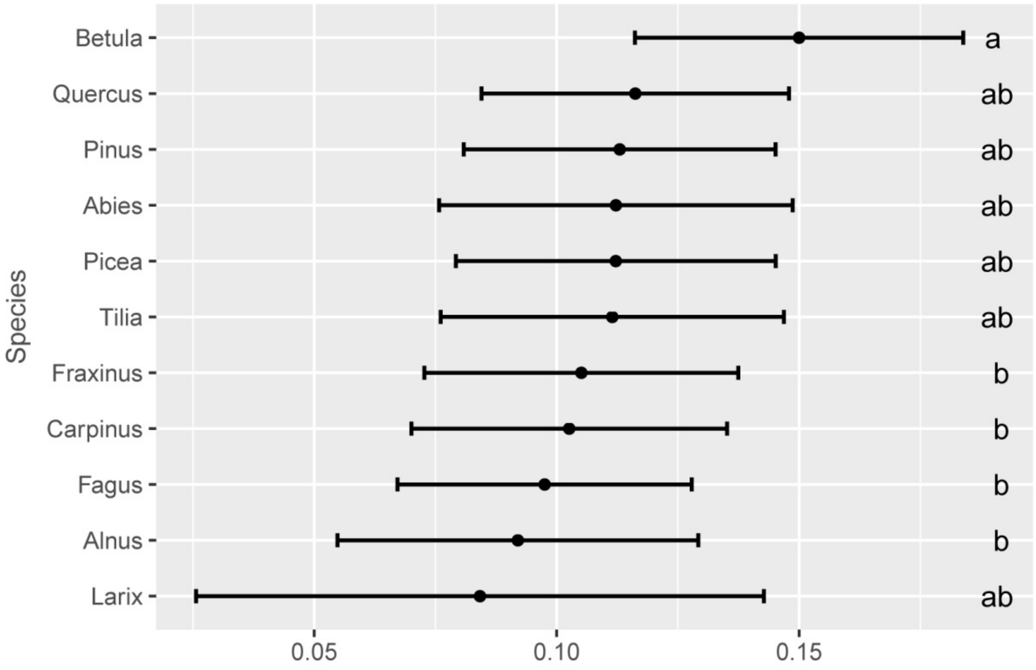

Fig. S4 Multiple pairwise comparison of least-squares means and confidence intervals for different species from the linear mixed-effect model of the square-root of $|p_{bias}|$. Different letters (a-e) indicate significant differences between species (p<0.05).

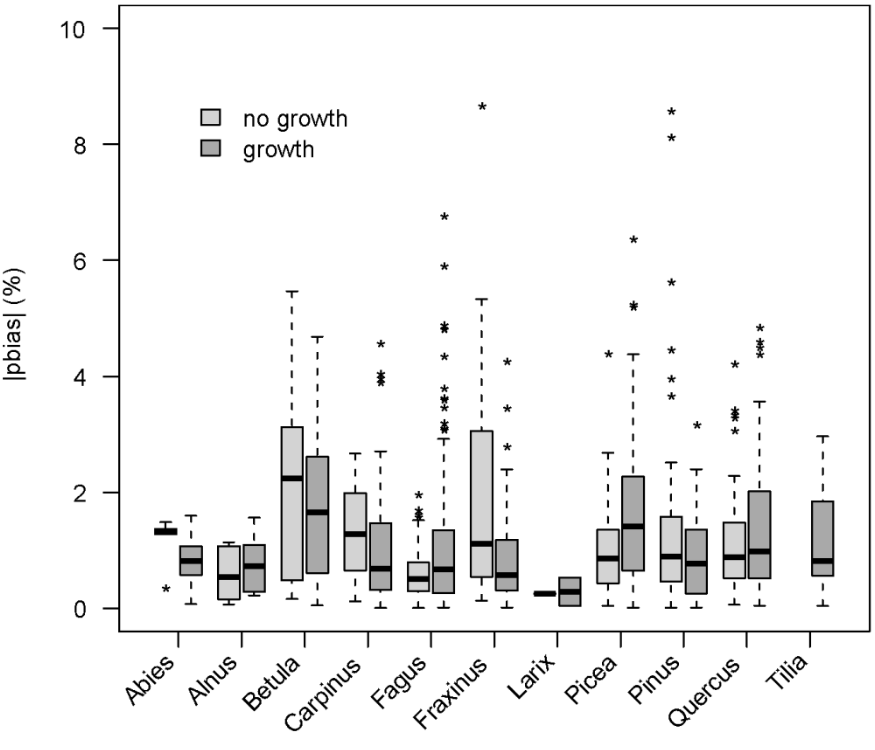

Fig. S5 Boxplot of $|p_{bias}|$ at the reserve level achieved by models with and without a covariate of growth for each tree species. Note that the design regarding the factors ‘species’ and ‘growth’ is not balanced.

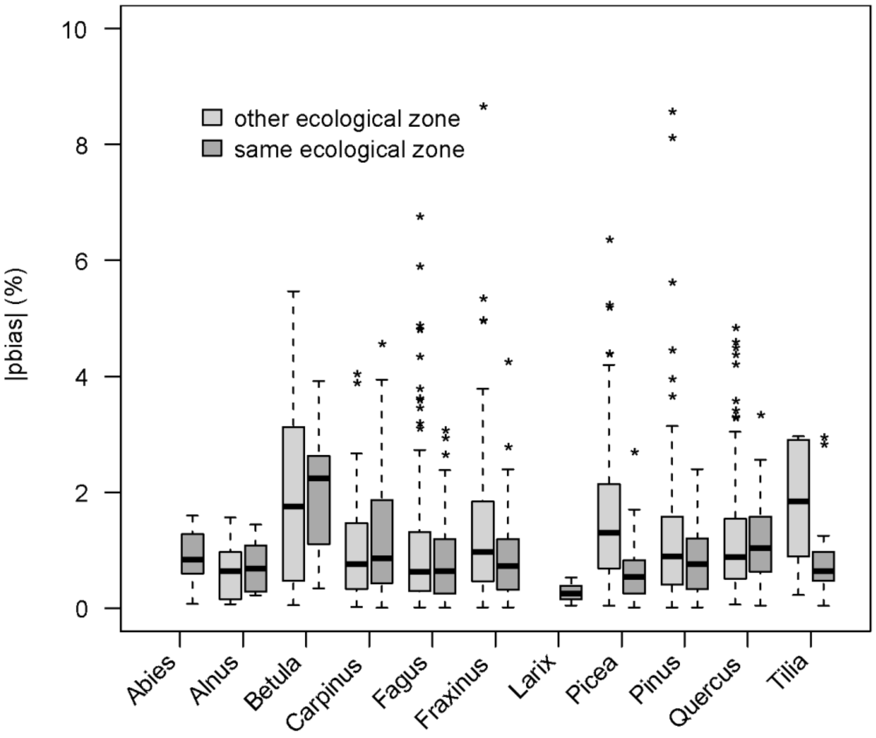

Fig. S6 Boxplot of $|p_{bias}|$ at the reserve level achieved by models that were applied inside or outside the ecological zone in which the models were calibrated for each tree species. Note that the design regarding the factors ‘species’ and ‘ecological zone’ is not balanced.

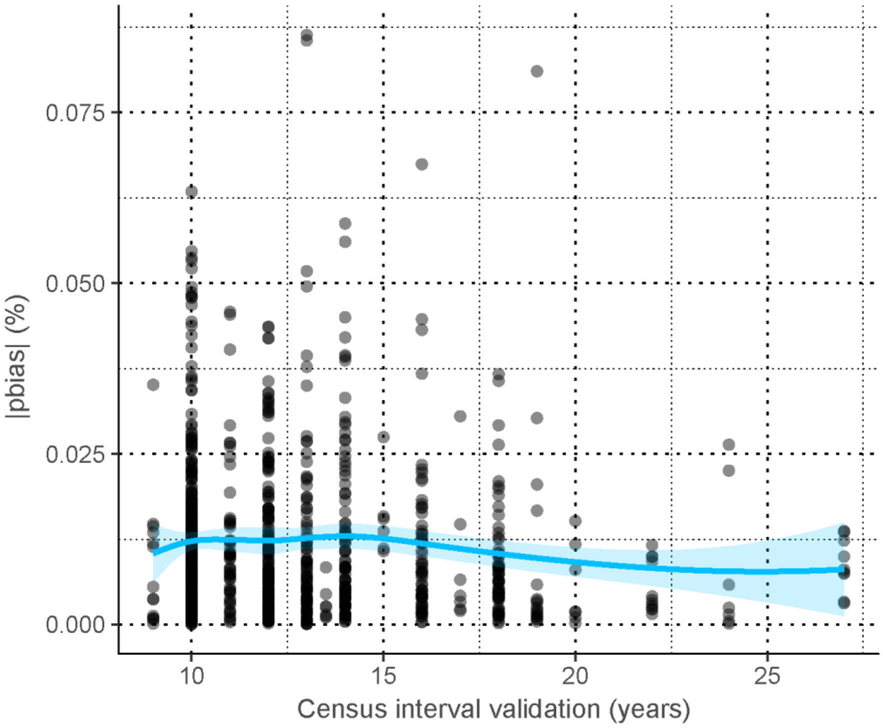

Fig. S7 $|p_{bias}|$ at the reserve level as a function of the census interval in the validation dataset including a loess smoothing (blue).

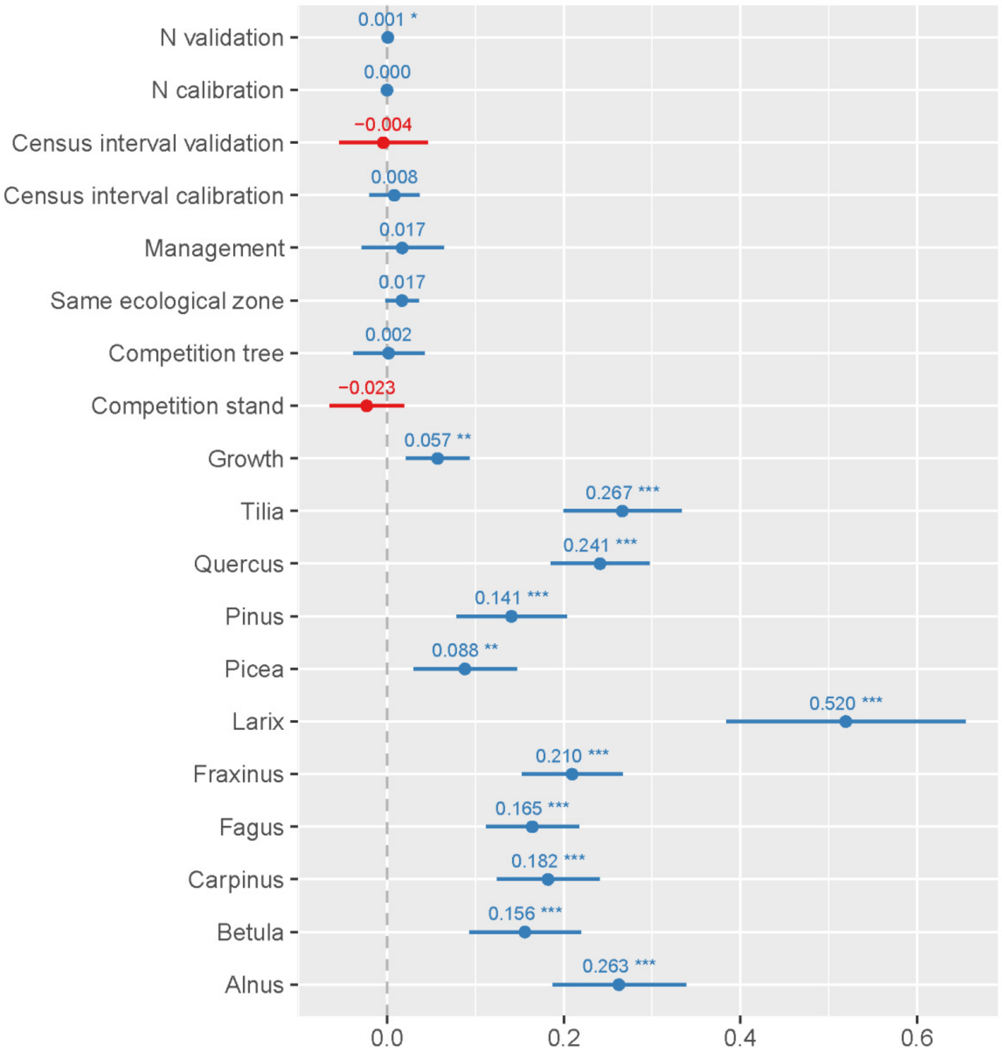

Fig. S8 Fixed effects of the influence of model and data characteristics on arcsine-transformed *AUC*. Note that a 'good' model features high *AUC*. Positive and negative influences on performance are shown in blue and red, respectively. Note that the first level of all factors is the reference level while the other levels are characterized by the shift relative to this reference leve8l. The reference species is *Abies*.

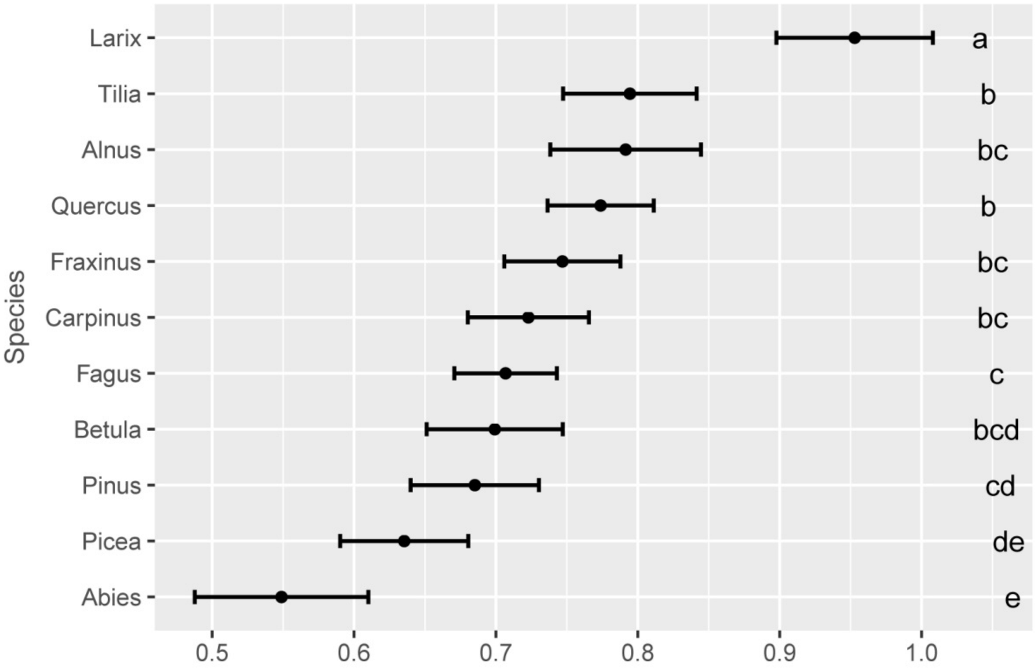

Fig. S9 Multiple pairwise comparison of least-squares means and confidence intervals for different species from the linear mixed-effect model of arcsine-transformed *AUC*. Different letters (a-e) indicate significant differences between species ($p<0.05$).

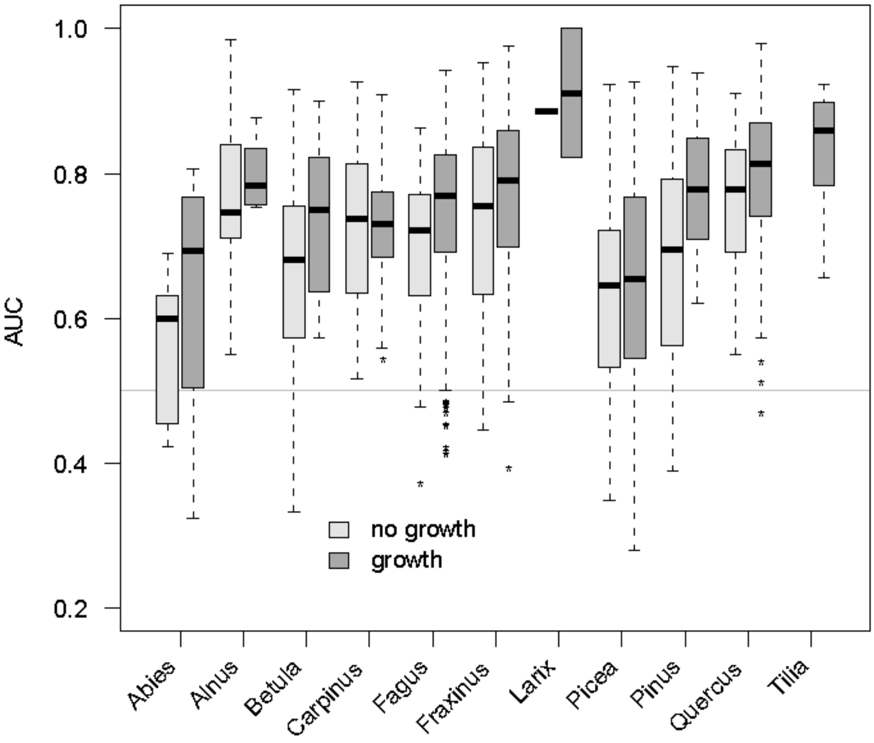

Fig. S10 Boxplot of *AUC* at the reserve level achieved by models with and without a covariate of growth for each tree species. Values larger than 0.5 (grey line) indicate an increasing ability to classify dead and living trees (Hosmer & Lemeshow, 2000). Note that the design regarding the factors ‘species’ and ‘growth’ is not balanced.

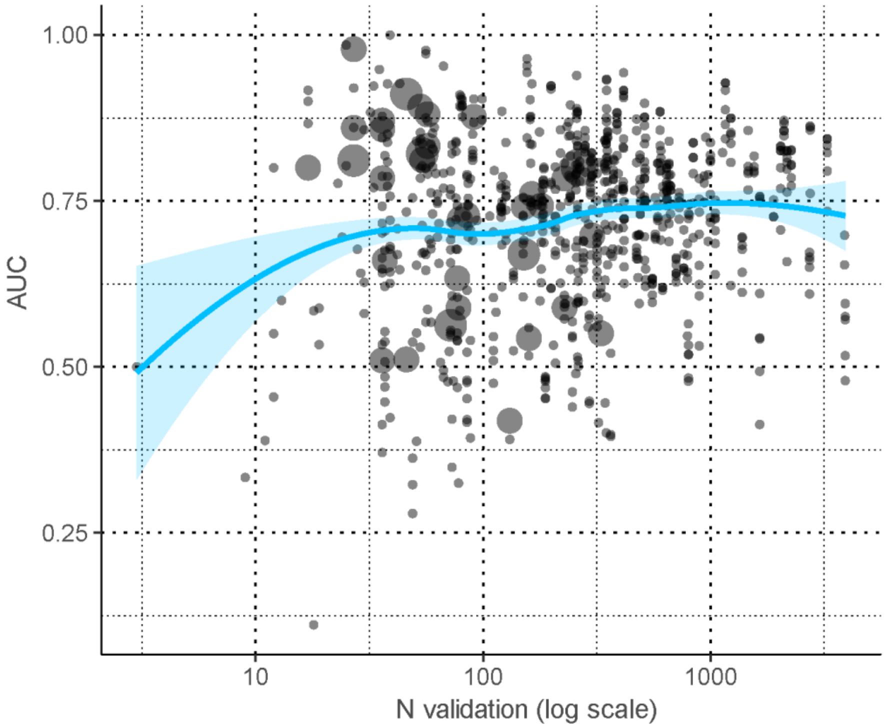

Fig. S11 *AUC* at the reserve level as a function of the number of records in the validation dataset (N_{val}) including a loess smoothing (blue). Note that the size of the points indicates the count of values at the respective location.

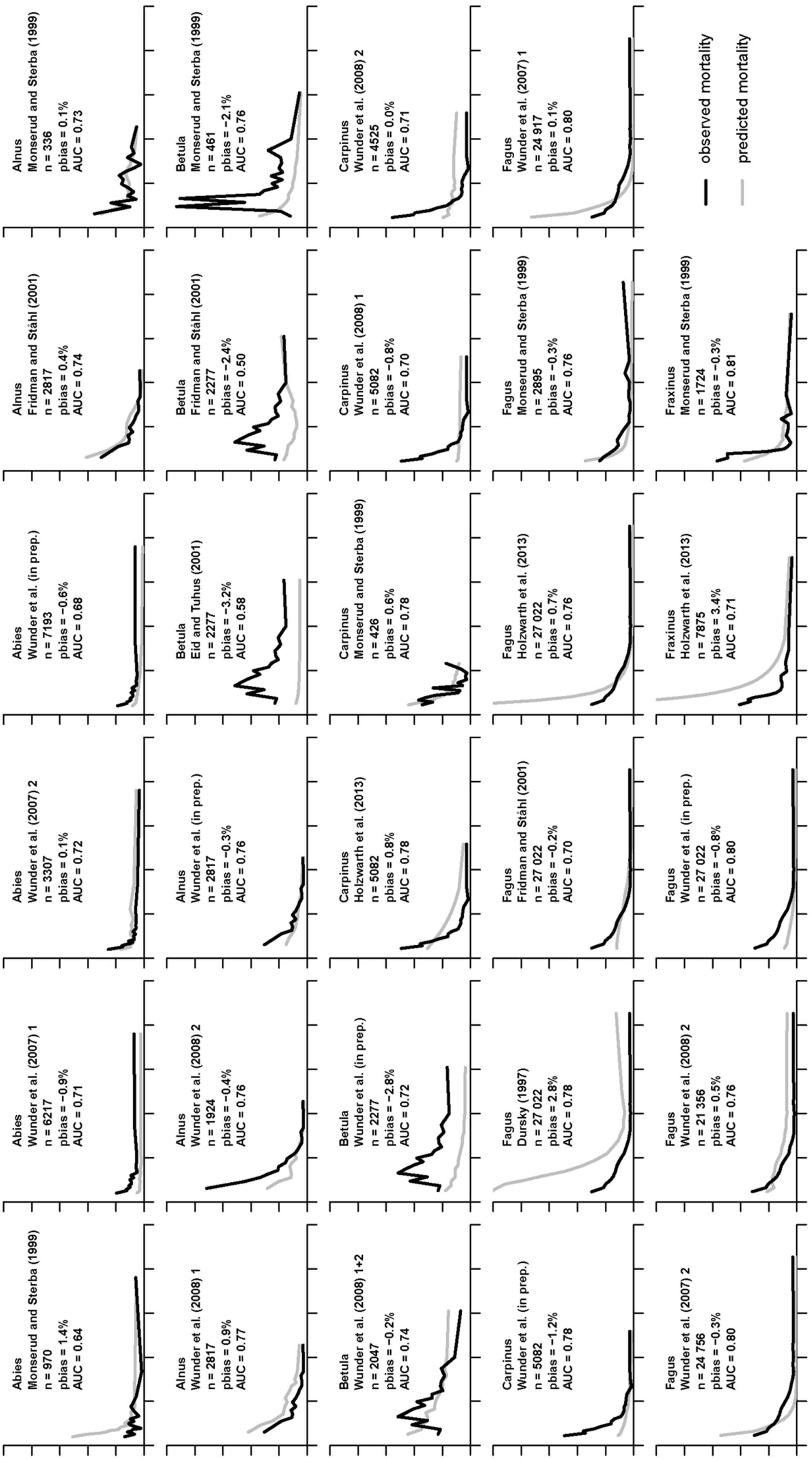

Fig. S12a Observed and predicted annual mortality rates as a function of *DBH* separately for each model-species combination.

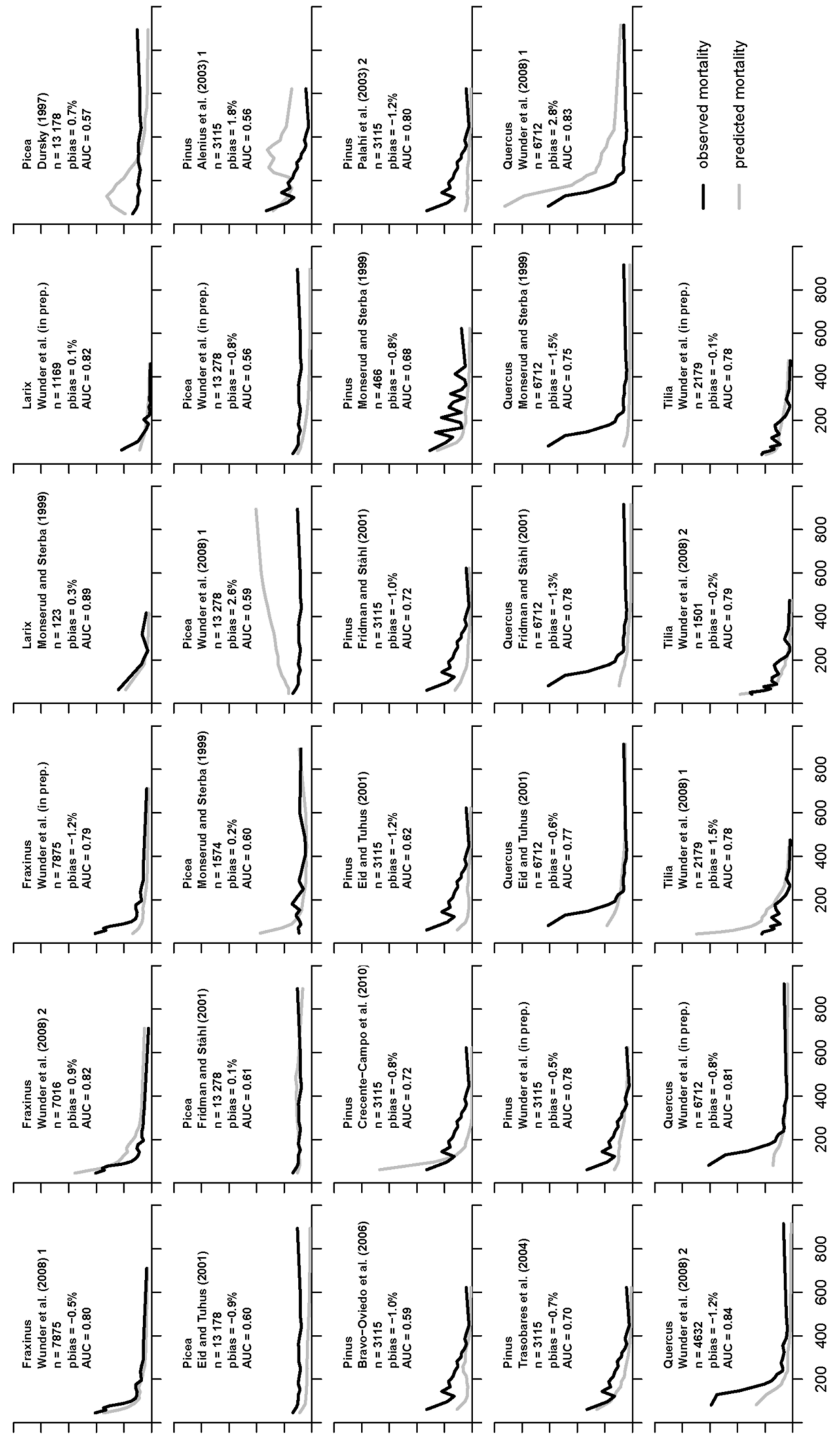

Fig. S12b Observed and predicted annual mortality rates as a function of *DBH* separately for each model-species combination.

Appendix B – Extended material and methods

In the following, we describe the tree, stand and site characteristics that were used to explain the tree status (dead or alive) in the third inventory (cf. Table 2). Herein, tree growth was derived for the interval between the first and the second inventory. All other tree and stand characteristics were calculated based on data from the second inventory.

Tree characteristics

Besides *DBH* as a measure for tree size, the annual increment of the diameter (*DI*) and of the basal area (*BAI*) were calculated to account for tree growth. In addition, a diameter-independent growth variable of *BAI* was derived, i.e. annual relative basal area increment (*relBAI*, cf. Wunder *et al.*, 2008a). Tree height (*h*) has been measured only for 17.7 % of the records. For the remaining, *h* was derived based on species- and site-specific allometric height curves (where possible, separately for each inventory year) as a function of *DBH* following Michailoff (1943). Crown ratio (*CR*) defined as the proportion of the crown length to *h* was not deduced from *DBH* and/or *h* since it reflects not only the dimensions of a tree but also its vitality state. Thus, *CR* was only available for 12.9 % of all records. As a measure of one-sided competition (Cannell *et al.*, 1984), the basal area of larger trees than the subject tree (*BAL*) and its relative counterpart *relBAL* being the share of *BAL* of the stand basal area (*BA*) were calculated. Spatially explicit competition indices could not be calculated because tree coordinates were only available for a subset of the reserves.

Stand characteristics

For *DBH*, two averages were calculated per permanent plot: the arithmetic (*mDBH*) and the quadratic mean (*qmDBH*, cf. Curtis & Marshall, 2000). As a measure of variance of the diameter distribution, the coefficient of variance was calculated using $CVd = sdDBH / mDBH$ with *sdDBH* being the standard deviation of *DBH* (Bravo-Oviedo *et al.*, 2006). Dominant height (*hdom*) was determined as the mean height of the hundred largest trees per hectare. Furthermore, basal area (*BA*) and the number of trees per hectare (*N*) were calculated. Species composition (*PBA*) was calculated as the percentage of the basal area of the subject species (i.e. *Betula*, *Picea* and *Pinus*) of the total stand *BA*.

Site characteristics

The geographical location of the permanents plots was described by their latitude (*LAT*) and altitude (*ALT*). The latter was taken from digital elevation models (DEM25m) provided by the State Agency for Spatial Information and Land Surveying of Lower Saxony (Landesamt für Geoinformation und Landesvermessung Niedersachsen LGLN) and the Swiss Federal Office of Topography (Swisstopo) for German and Swiss reserves, respectively. Since linear distance to the Mediterranean Sea as a measure of continentality (*CON*, cf. Trasobares *et al.*, 2004) is not meaningful for our data as it would result in severe extrapolation, we used the maximum value of *CON* = 186.6 km in the calibration dataset for all reserves. Mean growing degree-days (*GDD*) for the period between the first and second inventory were calculated based on interpolated annual temperature data following Baskerville and Emin (1969) using R code available online (http://geog.uoregon.edu/envchange/software/ GDD_calculator.txt). For the German reserves, temperature data from climate stations of the German Weather Service were interpolated following the WaSiM-ETH protocol (http://www.wasim.ch/downloads/ doku/wasim/interpolation_meteodata_2009_en.pdf). For the Swiss reserves, temperature data were derived following Rasche *et al.* (2012) based on the DAYMET model (Thornton *et al.*, 1997; available from Landscape Dynamics, WSL). The variable *moist* indicating moist or wet conditions (Fridman & Ståhl, 2001), which was only required for *Pinus* (cf. Table S4), was set to 0 for all relevant stands since the German reserve 'Ehrhorner Dünen' is dominated by dry conditions and none of the relevant Swiss permanent plots belongs to a moist or wet plant sociological association (Ellenberg & Klötzli, 1972). The site index (*SI*) for *Picea* and *Pinus* in Switzerland was derived from the topographical position, the exposition (both based on DEM25m) and large ecological regions following Keller (1978). Resulting dominant height at the age of 50 years was scaled to the age of 40 and 100 using yield tables by Badoux (1983) and the Landesforstanstalt Eberswalde (2000) for *Picea* and *Pinus*, respectively. For Germany, no such eco-topographic information on the growing conditions is available but *SI* was derived using estimates of tree age and Lorey's mean height of the respective species in the inventory data by applying suitable yield tables (Schober, 1995 for *Picea*; Landesforstanstalt Eberswalde, 2000 for *Pinus*). For all covariates associated with clear cut or other forest interventions (cf. Table S4), no management in the reserves was assumed.

Model application

Mortality model j calibrated to data of species k was used to predict the mortality probability p of tree i of the same species following

$$p_{i,j,k} = logit^{-1}\left(X_i\beta_{j,k}\right) = \frac{\exp(X_i\beta_{j,k})}{1+\exp(X_i\beta_{j,k})} = \frac{1}{1+\exp(-X_i\beta_{j,k})}$$

with X_i denoting the design matrix of the linear predictor and $\beta_{j,k}$ the respective parameter vector. Herein, k can also be a group of species when the model was calibrated, e.g. to a set of broadleaf species (Table S3). Since some models predict survival rather than mortality and in addition, the formulation of the logistic model was not always the same, and the equation above was modified respectively:

Model structure	**prediction of mortality**	**prediction of survival**
Type I	$\frac{1}{1+\exp(X_i\beta_{j,k})}$	$\frac{1}{1+exp(-X_i\beta_{j,k})}$
Type II	$\frac{1}{1+\exp(-X_i\beta_{j,k})}$	$\frac{1}{1+exp(X_i\beta_{j,k})}$

However, the proposed mortality models predict the status of the tree for unequal intervals Δt_j (cf. Table S3). Therefore, the mortality probability valid for Δt_j was rescaled to the census interval (Δt) of the respective permanent plot using

$$p_{i,j,k,\Delta t} = 1 - \left(1 - p_{i,j,k,\Delta t_j}\right)^{\frac{\Delta t}{\Delta t_j}}$$

Prediction bias

To quantify the degree of prediction accuracy (correct mortality rates), we defined prediction bias (p_{bias}) as the absolute difference of the mean predicted mortality probability (‘simulated mortality’) $\overline{p}_{\Delta t}$ and the mean mortality rate (‘observed mortality’) $\overline{y}_{\Delta t}$ over $\Delta t = 1$ year. To this end, the ‘simulated mortality’ $\overline{p}_{\Delta t} = \sum p_{i,\Delta t}/n$ and the ‘observed mortality’ $\overline{y}_{\Delta t} = \sum y_i/n$ were averaged for observations and predictions with the same cencus interval Δt. To render the values comparable, mean simulated and observed mortality rates were re-scaled to 1 year. Taking the example of the 'simulated mortality', this can be formulated as

$$\overline{p}_{\Delta t=1} = 1 - \left(1 - \overline{p}_{\Delta t}\right)^{\frac{1}{\Delta t}}$$

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2

A genealogy of mortality models based on inventory and tree-ring data

Technical report, not intended for publication:

Hülsmann L[1,2], Bugmann H[2], Cailleret M[2], Brang P[1]. A genealogy of mortality models based on inventory and tree-ring data.

[1] Research Unit Forest Resources and Management, WSL Swiss Federal Institute of Forest, Snow and Landscape Research, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

[2] Forest Ecology, Institute of Terrestrial Ecosystems, ETH Zurich, Universitätstrasse 16, 8092 Zurich, Switzerland

Abstract

Tree mortality models based on long-term datasets are increasingly available for a large set of species and from various geographical areas. However, they differ considerably regarding the type of data used for calibration and the approach for statistical modeling. Moreover, a large variability of mortality patterns predicted by various inventory-based models was identified (Chapter 1; cf. Hülsmann *et al.*, 2017). To evaluate the nature of these differences in greater detail, the predicted mortality probabilities of a large set of inventory- and tree-ring-based models were analyzed using hierarchical cluster analysis. The results of this analysis reflect the diversity of approaches in mortality modeling and emphasize that these differences do not modify mortality predictions in a systematic way. Nevertheless, the approaches underlying model development, i.e., the field design as well as the approach for statistical modeling, have a crucial influence on model predictions. In addition, mortality probabilities predicted by tree-ring-based models depend strongly on the sampling scheme. Due to the large differences in approaches, it was not possible to evaluate the need for species-specific models, nor to identify a reasonable grouping of species with similar mortality patterns. Overall, the results emphasize – once more – that tree mortality is highly variable in space and time, and that our knowledge on the mechanisms behind this variability is limited.

Key-words

Dendrochronological data; Empirical mortality models; Forest inventory data; Hierarchical cluster analysis; Mortality probability; Predictive behavior; Systematic review; Tree growth

Introduction

Tree mortality models that are developed using long-term datasets are increasingly available for a large set of species and from various geographical areas. However, they differ considerably regarding the type of data used for calibration (forest inventories or dendrochronological data), the sample size, the management intensity in the stands used for calibration and the handling of disturbance-related mortality (e.g., exclusion of certain plots or trees, cf. Bravo-Oviedo *et al.*, 2006; Wunder *et al.*, 2007). In addition, diverse sampling schemes have been applied in tree-ring-based models (paired sampling (*P*) or considering all available observations (*T*); cf. Cailleret *et al.*, 2016). Finally, a wide range of predictors including different competition and growth variables have been used (cf. Hawkes, 2000; Cailleret *et al.*, 2016). It is very likely that such differences influence the simulated probability of tree death. However, little is known on the (dis)similarities between the approaches and the general predictive behavior of the models. Since advice regarding the suitability of empirically-based mortality models is limited, such mortality algorithms tend to be selected by availability and chance, thus not necessarily increasing the reliability of Dynamic Vegetation Models (DVMs; e.g., Bircher, 2015).

Moreover, the majority of the mortality studies that are currently available proposed species-specific mortality formulations. Only a few authors attempted to group tree species, e.g., regarding their distribution (Fridman & Ståhl, 2001) or functional traits such as shade tolerance (Wunder *et al.*, in prep.). Although species-specific approaches appear reasonable in view of the differences in life history strategies (Franklin *et al.*, 1987; Harcombe, 1987), their necessity has not been proven.

As shown in Chapter 1 (cf. Hülsmann *et al.*, 2017), inventory-based mortality models differ considerably in their predictions of mortality patterns. To evaluate the nature of these differences in greater detail, we decided to assess the predicted mortality probabilities of a large set of mortality models using hierarchical cluster analysis (Masson & Knutti, 2011). For this purpose, we extended the scope of the analysis and used both inventory- and tree-ring-based models. The resulting dendrograms of mortality models were inspected to identify drivers that influence the similarity of mortality predictions. We hypothesized that (1) species or at least functional traits (e.g., deciduous vs. evergreen, shade tolerance), (2) predicted mortality type, i.e., 'regular' vs. 'irregular' mortality, (3) geographical origin of the calibration data, (4) management intensity and (5) the sampling scheme in tree-ring data should be influential model characteristics.

Material and methods

Mortality models

We used the same 46 inventory-based mortality models for European tree species as in the systematic model assessment in Chapter 1. The models based on tree-ring data were identified following Cailleret *et al.* (2016) thus extending the scope to formulations that have been developed all over the world since much fewer dendrochronological mortality models are available compared to inventory-based approaches. For the same reason, we used all models that the authors considered as ‘good’ even if the models were based on the same dataset and differed with respect to their covariates only. Models from the same publication and for the same species were identified using a numerical index following the numbering in the publications. Those models that rely on covariates that were not available in the validation dataset (e.g., canopy position) were discarded, resulting in 52 models based on dendrochronological data of 15 tree species (Table 1). Mixed-effects mortality models were applied by setting all random effects to zero (Rose *et al.*, 2006; Skrondal & Rabe-Hesketh, 2009).

Table 1 Tree-ring-based mortality models, related calibration species, number of all and dead trees in the calibration datasets (N_{cal}, N_{dead}) and the sampling scheme applied for model fitting. Sampling T considers all growth information and tree status observations from each tree, while the number of dying and living observations is almost equivalent in a paired sampling P, and sampling S is based on a more or less paired sampling that was subsequently scaled to mortality rates at the population level (Das *et al.*, 2007). The information ‘predicted status’ is required to apply the mortality models (cf. Chapter 1; the ‘type’ of logistic regression was II for all models). Note that the models Das *et al.* (2007) 1 and 2 refer to trees with $DBH > 20$ cm and $DBH < 20$ cm, respectively. Hartmann *et al.* (2007) used either un-truncated (*UT*) and truncated (*T*) ring-width series of living trees. The model by Macalady and Bugmann (2014) included study site and period as random effects. The sampling used by Senecal *et al.* (2004) remained unclear.

Publication	**Calibration species**	**Predicted status**	N_{cal} (N_{dead})	**Sampling scheme**
Bigler *et al.* (2004)	*Abies alba*	survival	70 (32)	*T*
Bigler *et al.* (2006)	*Pinus sylvestris*	survival	140 (70)	*T*
Bigler and Bugmann (2003)	*Picea abies*	survival	119 (59)	*P*
Bigler and Bugmann (2004) 5	*Picea abies*	survival	119 (59)	*T*
Bigler and Bugmann (2004) 8	*Picea abies*	survival	119 (59)	*T*
Bigler and Bugmann (2004) 9	*Picea abies*	survival	119 (59)	*T*
Bigler and Bugmann (2004) 10	*Picea abies*	survival	119 (59)	*T*
Bigler and Bugmann (2004) 11	*Picea abies*	survival	119 (59)	*T*
Bigler and Bugmann (2004) 12	*Picea abies*	survival	119 (59)	*T*
Carus (2010) 3	*Abies cilicica*	survival	44 (22)	*P*
Carus (2010) 7	*Abies cilicica*	survival	44 (22)	*P*
Carus (2010) 10	*Abies cilicica*	survival	44 (22)	*P*
Carus (2010) 12	*Abies cilicica*	survival	44 (22)	*P*
Das *et al.* (2007) 1	*Abies concolor*	survival	106 (45)	*S*
Das *et al.* (2007) 2	*Abies concolor*	survival	81 (36)	*S*
Das *et al.* (2007)	*Pinus lambertiana*	survival	155 (78)	*S*
Gillner *et al.* (2013) 1	*Fagus sylvatica*	survival	38 (18)	*P*
Gillner *et al.* (2013) 2	*Fagus sylvatica*	survival	38 (18)	*P*
Hanna and Kulakowski (2012) 1	*Populus tremuloides*	survival	37 (22)	*P*
Hanna and Kulakowski (2012) 2	*Populus tremuloides*	survival	40 (18)	*P*
Hanna and Kulakowski (2012) 3	*Populus tremuloides*	survival	41 (21)	*P*
Hanna and Kulakowski (2012) 4	*Populus tremuloides*	survival	28 (14)	*P*
Hanna and Kulakowski (2012) 5	*Populus tremuloides*	survival	37 (18)	*P*
Hanna and Kulakowski (2012) 6	*Populus tremuloides*	survival	48 (15)	*P*
Hanna and Kulakowski (2012) 7	*Populus tremuloides*	survival	33 (20)	*P*
Hanna and Kulakowski (2012) 8	*Populus tremuloides*	survival	33 (25)	*P*
Hanna and Kulakowski (2012) 9	*Populus tremuloides*	survival	41 (24)	*P*
Hanna and Kulakowski (2012) 10	*Populus tremuloides*	survival	42 (23)	*P*
Hanna and Kulakowski (2012)	*Populus tremuloides*	survival	120 (60)	*P*
Hartmann *et al.* (2007) UT	*Abies balsamifera*	mortality	60 (30)	*P*
Hartmann *et al.* (2007) T	*Abies balsamifera*	mortality	60 (30)	*P*
Hartmann *et al.* (2007) UT	*Acer saccharum*	mortality	60 (30)	*P*
Hartmann *et al.* (2007) T	*Acer saccharum*	mortality	60 (30)	*P*
Hartmann *et al.* (2007) UT	*Picea abies*	mortality	60 (30)	*P*
Hartmann *et al.* (2007) T	*Picea abies*	mortality	60 (30)	*P*
Hartmann *et al.* (2007) UT	*Picea glauca*	mortality	60 (30)	*P*
Hartmann *et al.* (2007) T	*Picea glauca*	mortality	60 (30)	*P*
Hartmann *et al.* (2007) UT	*Picea mariana*	mortality	60 (30)	*P*
Hartmann *et al.* (2007) T	*Picea mariana*	mortality	60 (30)	*P*
Kane and Kolb (2014) 1	*Abies concolor*	survival	56 (28)	*P*
Kane and Kolb (2014) 2	*Abies concolor*	survival	56 (28)	*P*
Kane and Kolb (2014) 3	*Abies concolor*	survival	56 (28)	*P*
Kane and Kolb (2014) 1	*Pinus flexilis*	survival	48 (24)	*P*
Kane and Kolb (2014) 2	*Pinus flexilis*	survival	48 (24)	*P*
Kane and Kolb (2014) 3	*Pinus flexilis*	survival	48 (24)	*P*
Kane and Kolb (2014) 4	*Pinus flexilis*	survival	48 (24)	*P*
Kane and Kolb (2014) 1	*Populus tremuloides*	survival	122 (61)	*P*
Kane and Kolb (2014) 2	*Populus tremuloides*	survival	122 (61)	*P*
Kane and Kolb (2014) 3	*Populus tremuloides*	survival	122 (61)	*P*
Kane and Kolb (2014) 1	*Pseudotsuga menziesii*	survival	142 (71)	*P*
Macalady and Bugmann (2014)	*Pinus edulis*	survival	265 (147)	*T*
Senecal *et al.* (2004)	*Picea glauca*	mortality	- (480)	?

Study sites and validation data

Inventory-based mortality models were applied to the inventory data from 54 strict forest reserves in Switzerland and Germany (for further details on the data and the derivation of variables used as model covariates cf. Chapter 1). For the application of tree-ring-based models, data from a recent dendrochronological campaign in 13 Swiss reserves including 671 dead trees of seven species were used (cf. Table 2, Vanoni *et al.*, 2016a; Vanoni *et al.*, 2016b). To this end, we calculated the required growth variables using measured ring widths (*RW*). Field measurements of diameter at breast height (*DBH*) and at the height of coring were used to derive variables that were based on basal area increment (*BAI*, cf. LeBlanc, 1996). Different growth variables calculated over several time windows were considered in terms of growth level, trend, variation, sensitivity and abrupt change over several time windows (for details cf. Appendix, Table S1 and the respective mortality studies). Age was derived based on an estimate of the number of missing rings to the pith using a geometric model (Duncan, 1989; Pirie *et al.*, 2015).

Table 2 Characteristics of tree-ring data (cf. Vanoni *et al.*, 2016a; Vanoni *et al.*, 2016b).

Species	Number of trees	Number of growth values per tree		Maximum age (years)
		median	range	
Abies alba	134	87	37 - 204	210
Acer pseudoplatanus	39	83	41 - 139	142
Fagus sylvatica	135	108	43 - 183	183
Larix decidua	51	121	34 - 432	432
Picea abies	124	97.5	40 - 415	435
Pinus cembra	39	111	47 - 388	388
Quercus spp.	149	88	57 - 192	194

Application of mortality models and assessment of their (dis)similarities

Since we were interested in the predictive behavior of the models but not in their accuracy, inventory and tree-ring datasets were used as ‘test data’ for model application, i.e., each model was considered as a valid realization of mortality patterns for the respective calibration species irrespective of its performance for the calibration or validation datasets. Therefore, the models were applied to all trees irrespective of their species.

Based on the model coefficients (cf. Chapter 1, Table S4 and this Chapter, Table S1) and the mathematical formulation of the logistic regression (Chapter 1, Table S3 and this Chapter

Table 1), the annual mortality probability for each observation, i.e., the set of two inventories or a tree ring from dendrochronological data, was calculated following eqn 1 in Chapter 1.

Subsequently, the difference between two mortality models was quantified using the Euclidian distance of predicted mortality probabilities at the level of individual observations. This requires a mortality prediction by every model for every single observation, which was not always feasible due to variables such as crown ratio (*CR*) or site index (*SI*) in some inventory-based models, or variables with a long time lag (e.g., *RW40*) in some tree-ring-based models. Therefore, a compromise had to be found between the number of observations and models in the full matrix of mortality probabilities. This resulted in 36 inventory- and 38 tree-ring-based models that were applied to 78 714 and 51 273 observations in the inventory and tree-ring datasets, respectively.

Based on the resulting distance matrices, the models were hierarchically clustered and their proximity was shown using dendrograms. To explore the patterns of predicted mortality with respect to the most common covariates in mortality models, i.e., tree size and growth, the mortality predictions for each observation were averaged within the clusters. Subsequently, median and 0.05- and 0.95-quantiles of each cluster were plotted as a function of *DBH* and relative basal area increment (*relBAI*), i.e., a measure of tree growth that is only weakly correlated with tree size. To this end, growth values were log-transformed with all no-growth observations set to the minimum of *relBAI*. We selected the number of clusters to be six to allow for a reasonable degree of distinction and aggregation at the same time. The dendrograms were visually interpreted regarding the factors that are expected to influence the predicted mortality probability, i.e., calibration species, geographical origin of the data, type of mortality intended by the authors, management intensity in the calibration data, use of growth covariates and the sampling scheme.

All computations were performed within R (R Core Team 2015, R Foundation for Statistical Computing. Vienna, Austria). Hierarchical clustering was performed using the function *hclust()* with the method *ward.D2*. Nonparametric quantile regression as implemented in the function *rqss()* was used to derive the quantiles of the mortality probabilities as a function of tree size and growth.

Results and discussion

Inventory-based mortality models

In the dendrogram of inventory-based mortality models (Fig. 1), three single models clustered alone and thus strongly differed from the others (i.e., Fridman & Ståhl, 2001, *Betula*; Alenius *et al.*, 2003, *Pinus*; Crecente-Campo *et al.*, 2010, *Pinus*). The models derived by Fridman and Ståhl (2001) and Crecente-Campo *et al.* (2010) were characterized by exceptionally high mortality probabilities for large (*DBH* > 60 cm) and small (*DBH* < 20 cm) trees, respectively. Except for these models, mortality rates were relatively low and typically showed a reverse J-shaped pattern over tree size. The growth influence on mortality appeared weaker than the effect of *DBH*, and no clear pattern could be identified except for Cluster 5, which showed higher mortality risk for slow growing trees. The unexpected double-humped pattern of mortality over *relBAI* for Clusters 2 and 6 was most presumably not caused by the growth covariates themselves, but may be an artifact of the correlation structure of *relBAI* and other mortality predictors in the test data (e.g., small trees with a high mortality risk dominantly had *relBAI* within the range of that values).

None of the considered model characteristics, i.e., calibrated species, mortality type, ecological zone or management intensity, could explain the differences between clusters and the similarities within clusters, or the overall structure of the dendrogram (cf. Fig. 2). With some exceptions, mortality models developed by the same author team were usually more similar, irrespective of the species.

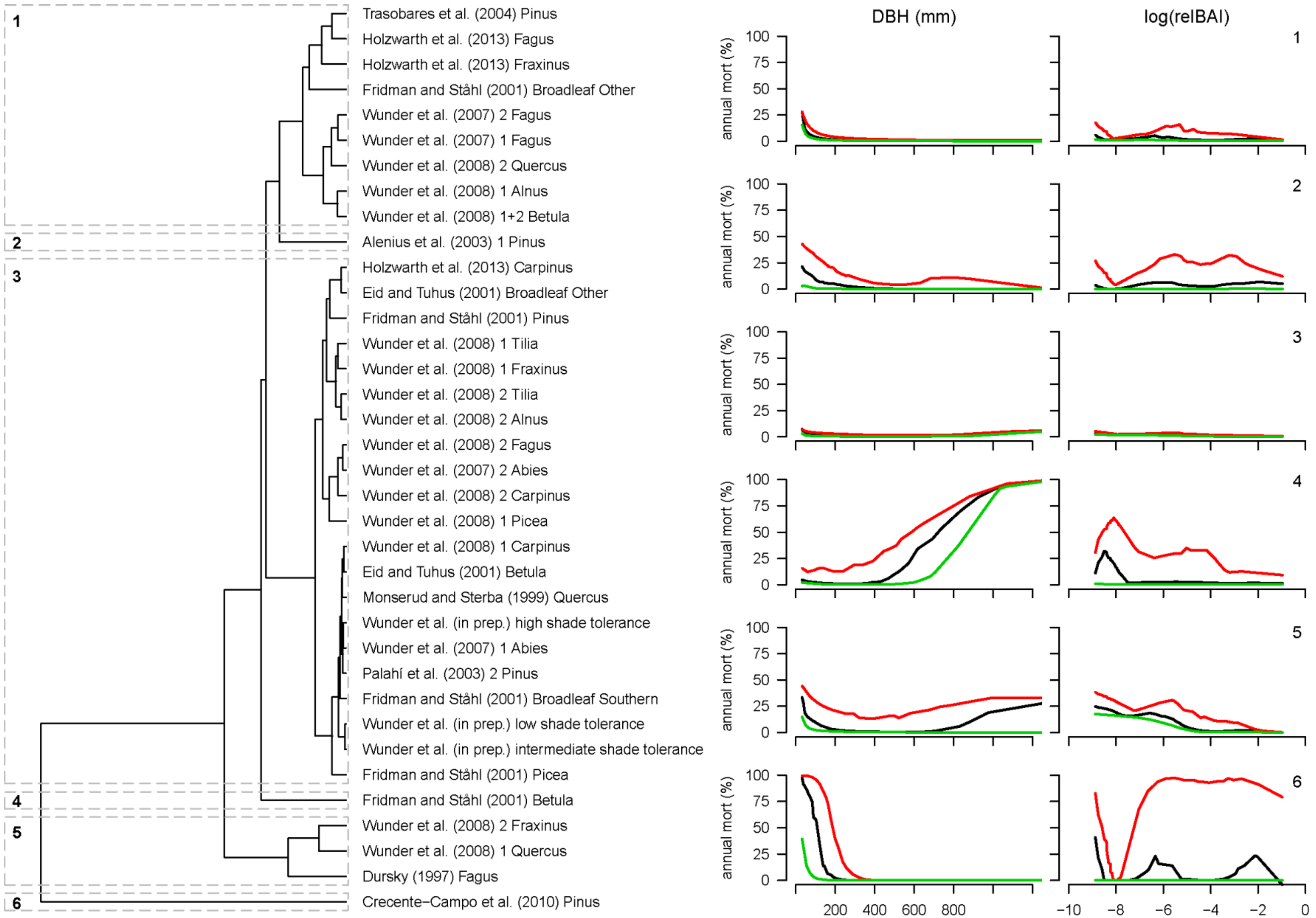

Fig. 1 Hierarchical clustering of inventory-based models into six clusters (boxes with gray dashed lines). For each cluster, quantiles of the mean annual mortality predictions are plotted as a function of tree size (*DBH*) and growth (*relBAI*). black = median, green = 0.05-quantile, red = 0.95-quantile.

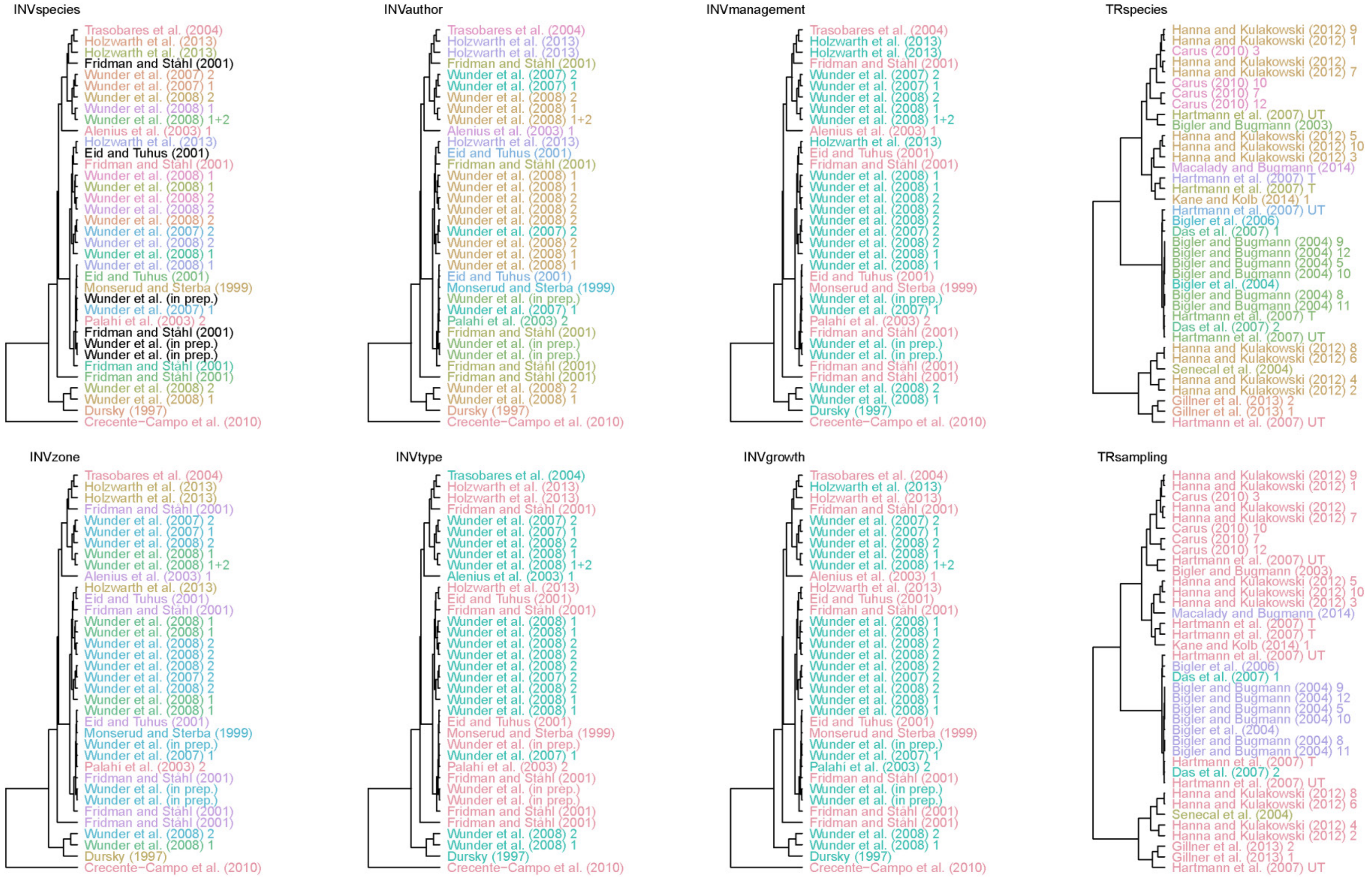

Fig. 2 Dendrograms of inventory- (INV) and tree-ring-based (TR) mortality models differentiated by color codes according to their main characteristics. The colors indicate different 'species' (species groups are shown in black), ecological 'zones' (cf. Chapter 1), 'author' teams, mortality 'types' (regular, irregular), 'management' intensities, consideration of tree 'growth' (yes, no), and 'sampling' schemes (purple = total number of years *T*, pink = paired sampling *P*, cyan = scaled to mortality rates *S*, brown = sampling unknown). Except for the sampling scheme, the color codes were not detailed, as model characteristics did not explain the obtained clustering.

Tree-ring-based mortality models

Compared to the inventory-based models, the influence of *DBH* was less obvious but growth shaped the mortality probability much more strongly, with higher mortality probabilities towards lower *relBAI* values (Fig. 3). This is related to the mortality predictors that were considered, i.e., inventory-based models dominantly relied on tree size (cf. Chapter 1) while tree-ring-based models mainly used growth information (Table S1). Mortality probabilities in the tree-ring-based models were often much higher than in the inventory-based models, since the magnitude of predicted mortality probabilities is defined by the ratio of dead over total trees in the calibration data (cf. Table 1). For example, mortality probabilities predicted by models based on a paired sampling (*P*) vary around 50 %. Predictions of models calibrated with the sampling scheme *T* revealed mortality probabilities closer to stand-scale mortality rates, albeit with an increase of mortality over *DBH* (cf. clusters 1 and 4), which was likely due to the increase in the proportion of dying observations compared to living ones towards high *DBH* (Cailleret *et al.*, 2016).

Based on the dendrograms, we observed a clustering of the models fitted with the same sampling approach (i.e., *T* and *P;* Fig. 2, TRsampling). Mortality predictions of models calibrated on the same species but not the same dataset sometimes differed strongly (e.g., Hanna & Kulakowski, 2012). In contrast, all mortality models calibrated on the same datasets were highly similar irrespective of the explanatory growth variables used (e.g., Bigler & Bugmann, 2004). Since the sampling scheme turned out to be exceedingly important for the clustering, it was impossible to identify other influences on the predictive behavior of the models, and the screening was stopped.

Alternatively, I tried to identify model similarities by:

- analyzing logit-transformed mortality probabilities in the hierarchical clustering,
- using regression trees with model covariates as fixed and single trees as random effects,
- calibrating new models with the same covariate structure using the predictions of each model to allow for the comparison of model coefficients (while some models achieved only a low performance, most of the models performed relatively well; an analysis of the model coefficients revealed no new insights compared to the original mortality predictions, however).

Yet, no clear patterns emerged that would have been helpful to group the mortality models by species, modeling approaches or other criteria.

Conclusion

The hierarchical regression trees of mortality probabilities predicted by a large set of inventory- and tree-ring-based mortality models did not reveal any clear pattern regarding the proposed hypotheses, i.e., calibration species, geographical origin of the data, type of mortality intended by the authors, management intensity in the calibration data and use of growth covariates. Since no promising patterns could be identified, no further analyses were carried out regarding this approach, e.g., by applying both inventory- and tree-ring-based mortality models to the same dataset, i.e., the intersection of inventory and tree-ring data from the Swiss forest reserves, and building a unified genealogy of mortality models, in combination with theoretical growth-based mortality models (e.g., the one used in the forest gap model ForClim; Bugmann, 1996).

The results of this analysis reflect the diversity of approaches in mortality modeling based on growth data and emphasize that these differences do not modify mortality predictions in a systematic way. Nevertheless, the field design as well as the statistical modeling, have a crucial influence on model predictions, since predictions from the same study were more similar. In addition, the mortality probabilities predicted by tree-ring-based models depend strongly on the sampling scheme. Due to the large differences in approaches, it was not possible to evaluate the need for species-specific models, nor to analyze which species are characterized by similar mortality patterns. Overall, the results suggest – once more – that tree mortality is highly variable in space and time, and that our knowledge on the mechanisms behind this variability is limited.

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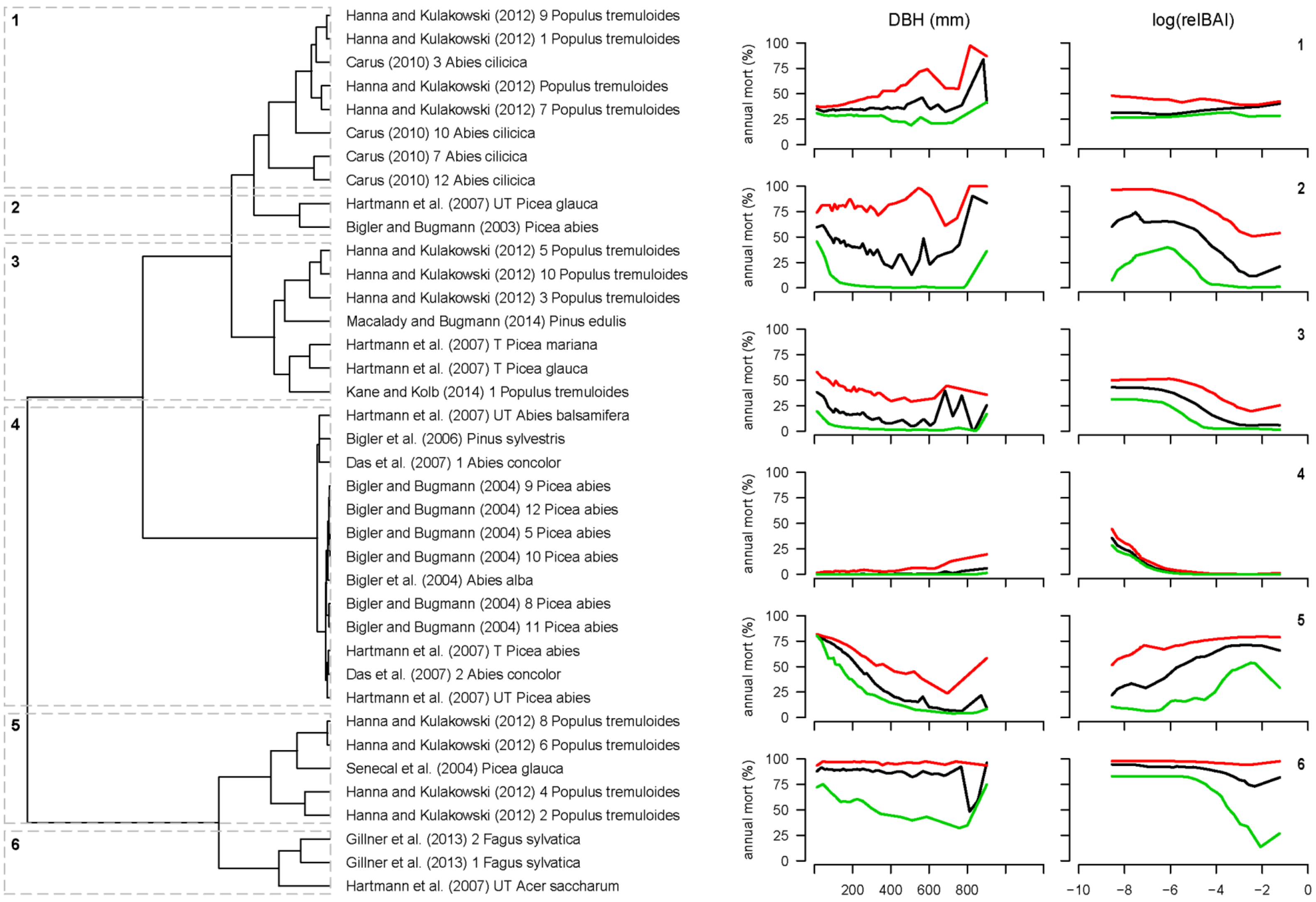

Fig. 3 Hierarchical clustering of tree-ring-based models into six clusters (boxes with gray dashed lines). For each cluster, quantiles of the mean annual mortality predictions are plotted as a function of tree size (*DBH*) and growth (*relBAI*). black = median, green = 0.05-quantile, red = 0.95-quantile.

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Appendix

Table S1 Coefficients and respective units for the tree-ring-based models. Abbreviations: *DBH* = diameter at breast height, *RW_* = mean ring width, *RW_med* = median ring width, *cvRW_* = coefficient of variation of ring width, *msRW_* = mean sensitivity of ring width, *sloRW_* = slope of local regression of ring width series, *DI_* = mean diameter increment, *DI3x* = diameter increment at a time lag of three years (Senecal *et al.*, 2004), *BAI_* = mean basal area increment, *sloBAI_* = slope of local regression of basal area increment series (*sloBAI_*), *relBAI_* = mean relative basal area increment, *relBAID_* = mean basal area increment divided by *DBH* (Gillner *et al.*, 2013), *NGC_* = number of years with a negative growth change, *PGC_* = number of years with a positive growth change. '_' indicates the length of the time window (given in years) for which the growth variables were calculated.

Publication	**Calibration species**	**Covariate**	**Coefficient**	**Unit**
Bigler et al. (2004)	*Abies alba*	INTERCEPT	2.277	-
Bigler et al. (2004)	*Abies alba*	relBAI1	534.84	-
Bigler et al. (2004)	*Abies alba*	sloBAI5	0.21	cm^2/a*a
Bigler et al. (2006)	*Pinus sylvestris*	INTERCEPT	11.415	-
Bigler et al. (2006)	*Pinus sylvestris*	log(relBAI1)	1.456	-
Bigler et al. (2006)	*Pinus sylvestris*	sloBAI5	0.816	cm^2/a*a
Bigler and Bugmann (2003)	*Picea abies*	INTERCEPT	-0.568	-
Bigler and Bugmann (2003)	*Picea abies*	log(BAI3)	0.898	cm^2/a
Bigler and Bugmann (2003)	*Picea abies*	sloBAI25	4.507	cm^2/a*a
Bigler and Bugmann (2004) 5	*Picea abies*	INTERCEPT	16.104	-
Bigler and Bugmann (2004) 5	*Picea abies*	log(relBAI1)	2.004	-
Bigler and Bugmann (2004) 8	*Picea abies*	INTERCEPT	16.003	-
Bigler and Bugmann (2004) 8	*Picea abies*	sloBAI5	0.431	cm^2/a*a
Bigler and Bugmann (2004) 8	*Picea abies*	log(relBAI1)	1.965	-
Bigler and Bugmann (2004) 9	*Picea abies*	INTERCEPT	15.68	-
Bigler and Bugmann (2004) 9	*Picea abies*	sloBAI25	0.872	cm^2/a*a
Bigler and Bugmann (2004) 9	*Picea abies*	log(relBAI1)	1.915	-
Bigler and Bugmann (2004) 10	*Picea abies*	INTERCEPT	15.646	-
Bigler and Bugmann (2004) 10	*Picea abies*	log(BAI3)	0.104	cm^2/a
Bigler and Bugmann (2004) 10	*Picea abies*	log(relBAI1)	1.938	-
Bigler and Bugmann (2004) 11	*Picea abies*	INTERCEPT	14.688	-
Bigler and Bugmann (2004) 11	*Picea abies*	sloBAI5	0.577	cm^2/a*a
Bigler and Bugmann (2004) 11	*Picea abies*	log(BAI3)	0.319	cm^2/a
Bigler and Bugmann (2004) 11	*Picea abies*	log(relBAI1)	1.769	-
Bigler and Bugmann (2004) 12	*Picea abies*	INTERCEPT	14.528	-
Bigler and Bugmann (2004) 12	*Picea abies*	sloBAI25	1.29	cm^2/a*a
Bigler and Bugmann (2004) 12	*Picea abies*	log(BAI3)	0.244	cm^2/a
Bigler and Bugmann (2004) 12	*Picea abies*	log(relBAI1)	1.736	-
Carus (2010) 3	*Abies cilicica*	INTERCEPT	0.524	-
Carus (2010) 3	*Abies cilicica*	sloBAI25	2.175	cm^2/a*a
Carus (2010) 7	*Abies cilicica*	INTERCEPT	2.224	-
Carus (2010) 7	*Abies cilicica*	log(BAI3)	-0.714	cm^2/a
Carus (2010) 7	*Abies cilicica*	sloBAI25	1.608	cm^2/a*a
Carus (2010) 10	*Abies cilicica*	INTERCEPT	-2.467	-
Carus (2010) 10	*Abies cilicica*	sloBAI25	1.32	cm^2/a*a
Carus (2010) 10	*Abies cilicica*	log(relBAI1)	-0.73	-
Carus (2010) 12	*Abies cilicica*	INTERCEPT	-0.589	-
Carus (2010) 12	*Abies cilicica*	log(BAI3)	-0.536	cm^2/a
Carus (2010) 12	*Abies cilicica*	sloBAI25	1.084	cm^2/a*a
Carus (2010) 12	*Abies cilicica*	log(relBAI1)	-0.586	-

Publication	**Calibration species**	**Covariate**	**Coefficient**	**Unit**
Das et al. (2007)	*Pinus lambertiana*	INTERCEPT	2.43	-
Das et al. (2007)	*Pinus lambertiana*	RW10	0.99	mm/a
Das et al. (2007)	*Pinus lambertiana*	sloRW40	35.53	mm/a*a
Das et al. (2007)	*Pinus lambertiana*	NGC5	-1.01	-
Das et al. (2007) 1	*Abies concolor*	INTERCEPT	4.47	-
Das et al. (2007) 1	*Abies concolor*	RW20	0.91	mm/a
Das et al. (2007) 1	*Abies concolor*	NGC5	-1.99	-
Das et al. (2007) 2	*Abies concolor*	INTERCEPT	3.24	-
Das et al. (2007) 2	*Abies concolor*	RW25	4.82	mm/a
Das et al. (2007) 2	*Abies concolor*	NGC25	-0.17	-
Gillner et al. (2013) 1	*Fagus sylvatica*	INTERCEPT	-4.519	-
Gillner et al. (2013) 1	*Fagus sylvatica*	relBAID20	4.862	cm^2/cm*a
Gillner et al. (2013) 2	*Fagus sylvatica*	INTERCEPT	-0.46584	-
Gillner et al. (2013) 2	*Fagus sylvatica*	relBAID20	3.51875	cm^2/cm*a
Gillner et al. (2013) 2	*Fagus sylvatica*	msRW20	-0.08261	-
Hanna and Kulakowski (2012) 1	*Populus tremuloides*	INTERCEPT	0.5025	-
Hanna and Kulakowski (2012) 1	*Populus tremuloides*	sloBAI15	0.0109	mm^2/a*a
Hanna and Kulakowski (2012) 2	*Populus tremuloides*	INTERCEPT	-3.1859	-
Hanna and Kulakowski (2012) 2	*Populus tremuloides*	age	0.0158	a
Hanna and Kulakowski (2012) 2	*Populus tremuloides*	DBH	0.0602	cm
Hanna and Kulakowski (2012) 3	*Populus tremuloides*	INTERCEPT	-2.4524	-
Hanna and Kulakowski (2012) 3	*Populus tremuloides*	log(BAI3)	0.5082	mm^2/a
Hanna and Kulakowski (2012) 3	*Populus tremuloides*	age	0.0161	a
Hanna and Kulakowski (2012) 4	*Populus tremuloides*	INTERCEPT	-4.7528	-
Hanna and Kulakowski (2012) 4	*Populus tremuloides*	sloBAI5	0.0033	mm^2/a*a
Hanna and Kulakowski (2012) 4	*Populus tremuloides*	age	0.0466	a
Hanna and Kulakowski (2012) 5	*Populus tremuloides*	INTERCEPT	-0.136	-
Hanna and Kulakowski (2012) 5	*Populus tremuloides*	log(BAI3)	0.4311	mm^2/a
Hanna and Kulakowski (2012) 5	*Populus tremuloides*	sloBAI5	0.0022	mm^2/a*a
Hanna and Kulakowski (2012) 5	*Populus tremuloides*	age	-0.00521	a
Hanna and Kulakowski (2012) 6	*Populus tremuloides*	INTERCEPT	-0.7708	-
Hanna and Kulakowski (2012) 6	*Populus tremuloides*	sloBAI10	0.00409	mm^2/a*a
Hanna and Kulakowski (2012) 6	*Populus tremuloides*	DBH	0.036	cm
Hanna and Kulakowski (2012) 7	*Populus tremuloides*	INTERCEPT	0.1995	-
Hanna and Kulakowski (2012) 7	*Populus tremuloides*	sloBAI10	0.00495	mm^2/a*a
Hanna and Kulakowski (2012) 8	*Populus tremuloides*	INTERCEPT	-0.7263	-
Hanna and Kulakowski (2012) 8	*Populus tremuloides*	sloBAI10	0.00483	mm^2/a*a
Hanna and Kulakowski (2012) 8	*Populus tremuloides*	DBH	0.0319	cm
Hanna and Kulakowski (2012) 9	*Populus tremuloides*	INTERCEPT	0.447	-
Hanna and Kulakowski (2012) 9	*Populus tremuloides*	sloBAI15	0.0134	mm^2/a*a
Hanna and Kulakowski (2012) 10	*Populus tremuloides*	INTERCEPT	-1.2051	-
Hanna and Kulakowski (2012) 10	*Populus tremuloides*	log(BAI5)	0.5999	mm^2/a
Hanna and Kulakowski (2012) 10	*Populus tremuloides*	sloBAI10	0.00502	mm^2/a*a
Hanna and Kulakowski (2012)	*Populus tremuloides*	INTERCEPT	0.414727	-
Hanna and Kulakowski (2012)	*Populus tremuloides*	sloBAI10	0.006135	mm^2/a*a
Hartmann et al. (2007) UT	*Abies balsamifera*	RW3med	-0.01923	0.001mm/a
Hartmann et al. (2007) T	*Abies balsamifera*	RW10med	-0.01596	0.001mm/a
Hartmann et al. (2007) T	*Abies balsamifera*	sloRW35	0.16283	0.001mm/a*a
Hartmann et al. (2007) UT	*Acer saccharum*	RW3med	0.00422	0.001mm/a
Hartmann et al. (2007) UT	*Acer saccharum*	sloRW25	-0.14174	0.001mm/a*a
Hartmann et al. (2007) T	*Acer saccharum*	RW5med	0.0002561	0.001mm/a
Hartmann et al. (2007) T	*Acer saccharum*	sloRW35	-0.0723448	0.001mm/a*a
Hartmann et al. (2007) UT	*Picea abies*	RW10med	-0.08507	0.001mm/a
Hartmann et al. (2007) UT	*Picea abies*	sloRW25	0.71304	0.001mm/a*a
Hartmann et al. (2007) T	*Picea abies*	RW10med	-0.08957	0.001mm/a

Publication	**Calibration species**	**Covariate**	**Coefficient**	**Unit**
Hartmann et al. (2007) UT	*Picea glauca*	RW10med	-0.001917	0.001mm/a
Hartmann et al. (2007) UT	*Picea glauca*	sloRW25	-0.050886	0.001mm/a*a
Hartmann et al. (2007) T	*Picea glauca*	RW3med	-0.002641	0.001mm/a
Hartmann et al. (2007) T	*Picea glauca*	sloRW3	-0.004504	0.001mm/a*a
Hartmann et al. (2007) UT	*Picea mariana*	RW5med	-0.003828	0.001mm/a
Hartmann et al. (2007) UT	*Picea mariana*	sloRW35	0.028764	0.001mm/a*a
Hartmann et al. (2007) T	*Picea mariana*	RW3med	-0.003527	0.001mm/a
Hartmann et al. (2007) T	*Picea mariana*	sloRW3	-0.012734	0.001mm/a*a
Kane and Kolb (2014) 1	*Abies concolor*	INTERCEPT	-0.4	-
Kane and Kolb (2014) 1	*Abies concolor*	RW5	1.6	mm/a
Kane and Kolb (2014) 1	*Abies concolor*	sloRW50	44.6	mm/a*a
Kane and Kolb (2014) 2	*Abies concolor*	INTERCEPT	-0.4	-
Kane and Kolb (2014) 2	*Abies concolor*	RW10	1.5	mm/a
Kane and Kolb (2014) 2	*Abies concolor*	sloRW50	49	mm/a*a
Kane and Kolb (2014) 3	*Abies concolor*	INTERCEPT	2.5	-
Kane and Kolb (2014) 3	*Abies concolor*	sloRW50	27.3	mm/a*a
Kane and Kolb (2014) 3	*Abies concolor*	cvRW40	-4.9	-
Kane and Kolb (2014) 1	*Pinus flexilis*	INTERCEPT	0.04	-
Kane and Kolb (2014) 1	*Pinus flexilis*	RW40	-4.3	mm/a
Kane and Kolb (2014) 1	*Pinus flexilis*	cvRW20	2.8	-
Kane and Kolb (2014) 2	*Pinus flexilis*	INTERCEPT	-0.03	-
Kane and Kolb (2014) 2	*Pinus flexilis*	RW50	-4.3	mm/a
Kane and Kolb (2014) 2	*Pinus flexilis*	cvRW20	2.8	-
Kane and Kolb (2014) 3	*Pinus flexilis*	INTERCEPT	0.4	-
Kane and Kolb (2014) 3	*Pinus flexilis*	RW50	2.8	mm/a
Kane and Kolb (2014) 3	*Pinus flexilis*	cvRW20	-4	-
Kane and Kolb (2014) 3	*Pinus flexilis*	NGC10	-0.4	-
Kane and Kolb (2014) 4	*Pinus flexilis*	INTERCEPT	0.5	-
Kane and Kolb (2014) 4	*Pinus flexilis*	RW40	2.8	mm/a
Kane and Kolb (2014) 4	*Pinus flexilis*	cvRW20	-4.1	-
Kane and Kolb (2014) 4	*Pinus flexilis*	NGC10	-0.4	-
Kane and Kolb (2014) 1	*Populus tremuloides*	INTERCEPT	-1.5	-
Kane and Kolb (2014) 1	*Populus tremuloides*	RW5	5.4	mm/a
Kane and Kolb (2014) 1	*Populus tremuloides*	cvRW30	-0.4	-
Kane and Kolb (2014) 1	*Populus tremuloides*	sloRW5	8.8	mm/a*a
Kane and Kolb (2014) 2	*Populus tremuloides*	INTERCEPT	-2	-
Kane and Kolb (2014) 2	*Populus tremuloides*	RW5	5.7	mm/a
Kane and Kolb (2014) 2	*Populus tremuloides*	cvRW40	0.4	-
Kane and Kolb (2014) 2	*Populus tremuloides*	sloRW5	9	mm/a*a
Kane and Kolb (2014) 3	*Populus tremuloides*	INTERCEPT	-0.7	-
Kane and Kolb (2014) 3	*Populus tremuloides*	RW5	4.8	mm/a
Kane and Kolb (2014) 3	*Populus tremuloides*	NGC50	-0.2	-
Kane and Kolb (2014) 1	*Pseudotsuga menziesii*	INTERCEPT	-0.005	-
Kane and Kolb (2014) 1	*Pseudotsuga menziesii*	RW10	3.8	mm/a
Kane and Kolb (2014) 1	*Pseudotsuga menziesii*	cvRW40	-2.2	-
Kane and Kolb (2014) 1	*Pseudotsuga menziesii*	sloRW50	62.4	mm/a*a
Macalady and Bugmann (2014)	*Pinus edulis*	INTERCEPT	4.851	-
Macalady and Bugmann (2014)	*Pinus edulis*	log(RW30)	3.089	mm/a
Macalady and Bugmann (2014)	*Pinus edulis*	msRW15	-3.46	-
Macalady and Bugmann (2014)	*Pinus edulis*	PGC10	0.224	-
Senecal et al. (2004)	*Picea glauca*	INTERCEPT	1.6459	-
Senecal et al. (2004)	*Picea glauca*	DBH	-0.1095	cm
Senecal et al. (2004)	*Picea glauca*	DI1	-0.7663	mm
Senecal et al. (2004)	*Picea glauca*	DI3x	0.9145	mm

3

Does one model fit all? Patterns of beech mortality in natural forests of three European regions

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[1] Research Unit Forest Resources and Management, WSL Swiss Federal Institute of Forest, Snow and Landscape Research, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

[2] Forest Ecology, Institute of Terrestrial Ecosystems, ETH Zurich, Universitätstrasse 16, 8092 Zurich, Switzerland

[3] Sachgebiet Waldnaturschutz/Naturwald, Nordwestdeutsche Forstliche Versuchsanstalt NW-FVA, Grätzelstrasse 2, 37079, Göttingen, Germany

[4] Research Unit Forest Soils and Biogeochemistry, WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

Abstract

Large uncertainties characterize forest development under global climate change. Although recent studies have found widespread increased tree mortality, the patterns and processes associated with tree death remain poorly understood, thus restricting accurate mortality predictions. Yet, projections of future forest dynamics depend critically on robust mortality models, preferably based on empirical data rather than theoretical, not well-constrained assumptions. We developed parsimonious mortality models for individual beech (*Fagus sylvatica* L.) trees and evaluated their potential for incorporation in Dynamic Vegetation Models (DVMs). We used inventory data from nearly 19’000 trees from unmanaged forests in Switzerland, Germany and Ukraine, representing the largest dataset used to date for calibrating such models. Tree death was modelled as a function of size and growth, i.e., stem diameter (*DBH*) and relative basal area increment (*relBAI*), using generalized logistic regression accounting for unequal re-measurement intervals. To explain the spatial and temporal variability in mortality patterns, we considered a large set of environmental and stand characteristics. Validation with independent datasets was performed to assess model generality. Our results demonstrate strong variability in beech mortality that was independent of environmental or stand characteristics. Mortality patterns in Swiss and German strict forest reserves were dominated by competition processes as indicated by J-shaped mortality over tree size and growth. The Ukrainian primeval beech forest was additionally characterized by windthrow and a U-shaped size-mortality function. Unlike the mortality model based on Ukrainian data, the Swiss and German models achieved good discrimination and acceptable transferability when validated against each other. We thus recommend these two models to be incorporated and examined in DVMs. Their mortality predictions respond to climate change via tree growth, which is sufficient to capture the adverse effects of water availability and competition on the mortality probability of beech under current conditions.

Key words

Climate change, Dynamic Vegetation Models, External validation, *Fagus sylvatica*, Forest inventory data, Forest reserves, Generalized logistic regression, Individual tree mortality

Introduction

Increasing tree mortality in response to global climate change is receiving particular attention (Allen *et al.*, 2010; Steinkamp *et al.*, 2015). However, tree mortality and particularly its spatial patterns and temporal variability remain poorly understood (Hawkes, 2000), partly due to its “stochastic, rare and irregular” nature (Eid & Tuhus, 2001). Consequently, the future development of forests, which depends critically on tree mortality (Friend *et al.*, 2014), is highly uncertain. Robust, widely applicable models of individual tree mortality are sorely needed as they allow for insights into mortality patterns and at the same time for projections of future tree mortality. Although several attempts towards model improvement have been made, robust, climate-sensitive tree mortality models continue to be lacking (Weiskittel *et al.*, 2011; Bircher *et al.*, 2015). In particular, Dynamic Vegetation Models (DVMs) at stand, landscape and global scales, which are a key tool to quantify future changes of forest ecosystems, typically include theoretical mortality algorithms that lack mechanistic and/or empirical justification. This strongly hampers the reliability of DVM projections (Keane *et al.*, 2001; Reyer *et al.*, 2015).

Fully mechanistic tree mortality models still have a long way to go due to insufficient understanding of the underlying physiological processes (Wang *et al.*, 2012). Therefore, a promising approach for progress in mortality models appears to be empirical, i.e., using different kinds of datasets to elucidate the relationship between the likelihood of tree death and variables that are internal or external to the tree (Weiskittel *et al.*, 2011). To date, three distinct strategies have been pursued to this end: (1) using tree size, vitality and competition within the stand (e.g., Monserud & Sterba, 1999), (2) using tree size and tree growth (e.g., Holzwarth *et al.*, 2013) and (3) using tree age in combination with environmental variables (e.g., Neuner *et al.*, 2015).

In all three approaches, tree age or attributes characterizing tree size such as diameter at breast height (*DBH*) account for the increased mortality risk of young or small trees that are often suppressed. The U-shaped relationship between *DBH* and mortality probability that has sometimes been found accounts for higher mortality of large trees as a consequence of mechanical instability and higher susceptibility to disturbance and, finally, ‘senescence’ (Harcombe, 1987). Growth rates are used as a predictor of mortality probability to capture that trees exposed to ‘stress’ allocate, in comparison to vigorous individuals, fewer resources to radial stem growth, which has low priority compared to photosynthetic tissue and root growth over short time scales (Waring, 1987).

In the absence of larger disturbances, tree mortality rates are typically low, i.e., 0.5-3 % per year (Peterken, 1996), and therefore datasets for deriving the relationship between tree size, growth and ‘regular’, i.e., non-catastrophic mortality considering species and site differences must be large (Metcalf *et al.*, 2009; Lutz, 2015). Such datasets are available from long-term re-measurements of permanent plots (e.g., Wunder *et al.*, 2008) or from increment cores (e.g., Bigler & Bugmann, 2003). Although inventory data have a lower temporal resolution than dendrochronological data, they allow for the estimation of both individual mortality probabilities and population-based mortality rates (Weiskittel *et al.*, 2011). Several models focusing mainly on ‘regular’ tree mortality were developed for European beech (*Fagus sylvatica* L.), one of the most widespread species of Central Europe. Most of them are based on inventory datasets, e.g., from Switzerland (Dobbertin & Brang, 2001; Wunder *et al.*, 2007; Wunder *et al.*, 2008), Germany (Dursky, 1997; Ahner & Schmidt, 2011; Holzwarth *et al.*, 2013; Nothdurft, 2013; Boeck *et al.*, 2014; Neuner *et al.*, 2015) or Austria (Hasenauer, 1994; Monserud & Sterba, 1999). Mortality models for beech based on dendrochronological data were developed by Gillner *et al.* (2013) for eastern Germany. Most of the datasets used in these efforts were relatively lean due to sparse geographical coverage and a small sample size in terms of total tree number and particularly the number of dead trees (Wyckoff & Clark, 2002). Large inventory datasets from strict forest reserves are of particular value for the calibration of mortality models as forest management was given up several to many decades ago, such that natural mortality is higher than in managed forests (Bravo-Oviedo *et al.*, 2006).

Tree mortality is characterized by high temporal and spatial variability due to complex interactions of multiple factors (Franklin *et al.*, 1987). This variability remains poorly understood (Wunder *et al.*, 2008; Dietze & Moorcroft, 2011) and thus complicates the derivation of generally applicable mortality models (Hawkes, 2000). We identified three areas where important knowledge gaps should be filled.

First, although mortality models based on tree size and growth alone have achieved good performance at the site to regional levels and thus appear promising for application, e.g., in forest gap models (Bircher *et al.*, 2015), the potential of additional environmental or stand characteristics (e.g., water availability, competition) for explaining the temporal and spatial variability of mortality over larger areas has not been studied in detail. Specifically, it remains unclear whether growth sufficiently integrates the effects of climate, soil and stand structure on mortality probability, or whether such covariates could increase the performance of growth-based tree mortality models. In particular, drought has been identified as an important driver of growth decline and tree mortality of European beech (Jung, 2009; Lakatos & Molnár, 2009; Scharnweber *et al.*, 2011; Zimmermann *et al.*, 2015), and its impacts are hotly debated in the context of climate change (Geßler *et al.*, 2007).

Second, the processes relevant for a tree's death vary during its lifetime (Holzwarth *et al.*, 2013), and thus the reliability of mortality predictions given a particular model structure may vary with tree size. Although the relative importance of the formulations contained in DVMs against the backdrop of uncertainties in the data, model parameters and process representations (Lek, 2007) is more and more investigated using sensitivity analysis (Wernsdörfer *et al.*, 2008), the impact of tree size on model accuracy has not been evaluated to date.

Third, the application of empirical mortality models in DVMs must inevitably be based on the assumption of a stable relationship between the explanatory variables and mortality (Keane *et al.*, 2001). However, current empirical mortality models are strongly restricted by their calibration domain in terms of space, time and resolution, referred to as the 'scope of inference' (Woolley *et al.*, 2012) or 'temporal and spatial inflexibility' (Hawkes, 2000). Therefore, a rigorous external validation of the mortality functions is required to assess their applicability beyond the conditions for which they have been calibrated. Since to date all beech mortality models except for the one developed by Dobbertin and Brang (2001) are lacking an external validation with independent data, it is simply unknown whether such empirical models are appropriate for the application across larger areas or over longer time spans.

Therefore, the main objective of this study was to develop parsimonious models for 'regular' beech mortality based on extensive inventory data from strict forest reserves, and to comprehensively evaluate their performance. Specifically, we aimed to answer three questions: (1) Does the growth-mortality relationship vary with site and stand characteristics, and particularly with water availability and competition? (2) How strongly does the prediction and classification accuracy of mortality models vary with tree size and between different sites? (3) How well do mortality models perform when applied outside their calibration range, i.e., in other forest reserves and in a primeval beech forest?

Material and methods

Study areas and sites

Datasets from inventories with similar design in strict forest reserves in Switzerland and Germany (Lower Saxony) were used (Fig. S1, see Appendix A for all additional Tables and Figures; cf. Meyer *et al.*, 2006; Brang *et al.*, 2011). Every reserve included up to 10 permanent plots ranging from 0.09 to 1.8 ha in size, with slightly irregular re-measurement intervals (Table 1). Permanent plots with pure or mixed beech stands were selected from the reserves of both networks. Reserves with considerable wind disturbance during the monitored intervals were excluded from the analysis. The Swiss and German reserves had been established in the period of 1961-1975 and 1971-1974, respectively. Former management ranged from no or only weak thinning to regular thinning from above and coppice with standards in Switzerland (Heiri *et al.*, 2009), and thinning from below in Germany. In addition to data from the Swiss and German reserves, data from a 10 ha plot in the primeval beech forest Uholka in Western Ukraine were used (Table 1; cf. Commarmot *et al.*, 2005).

Table 1 Extent of the inventory data from Swiss, German and Ukrainian strict forest reserves. The reduced Swiss dataset with available soil profile data was used to assess the influence of additional environmental and stand characteristics on beech mortality. Since for a considerable proportion of the Swiss and German permanent plots (54.3 and 33.3 %, respectively) more than three inventories were available, individual trees can appear more than once in the dataset (compare number of trees and records). 32.1 % of the Swiss and German records are such 'repeated measures'.

Reserve (network)	Interval length (years)	Number of reserves	Number of plots	Number of trees	Number of records	Number of dead trees	Size of permanent plots (ha)	Application
Switzerland (reduced)	5-18	13	43	7640	12 822	2414	0.09-1.32	influence of environmental and stand characteristics
Switzerland	5-18	15	81	12 114	18 369	3194	0.09-1.32	calibration / validation
Germany (Lower Saxony)	4-24	13	21	4377	5938	503	0.48-1.80	calibration / validation
Ukraine (Uholka)	5	1	1	2511	2511	208	10	calibration / validation

Climatic conditions of the Swiss and German reserves are similar in terms of mean annual air temperature (Switzerland: 5.4-9.1 °C, Germany: 6.1-9.0 °C for 1961-90; cf. DAYMET model below and Gauer & Aldinger, 2005), but mean annual precipitation sums of the German reserves are lower (Switzerland: 922-1842 mm, Germany: 618-1312 mm), whereas the

Ukrainian forest has intermediate climatic conditions (7.7 °C for 1990-2010, 1134 mm for 1980-2010; Commarmot *et al.*, 2013). Stand characteristics of the reserves indicate moderate structural differences with higher basal area (*BA*) but lower mean *DBH* in the Swiss reserves compared to the German and Ukrainian forests (Table S1). Accordingly, also the stand density index (*SDI*) calculated following Reineke (1933) was larger in Swiss reserves. The German forests are mixed with spruce (*Picea abies* Karst, 8.4 % of *BA* on average) and oak (*Quercus petraea* Liebl. and *Q. robur* L., 5.1 %) and have a larger proportion of beech (78.6 %) than the Swiss stands (43 %), which feature considerable shares of oak (16.3 %), spruce (7.5 %), ash (*Fraxinus excelsior* L., 7.3 %) and fir (*Abies alba* Mill., 7.2 %). The Ukrainian forest is an almost pure beech stand. Ten-year tree mortality rates were highly variable between reserves, ranging from 2.7 to 21.5 % (calculated for trees with a *DBH* > 8 cm). Mortality rates in the German reserves were approximately half the mortality rates in the Swiss and Ukrainian stands (Table S1).

Mortality information and tree characteristics

A set of three consecutive inventories was used to generate records for the calibration of mortality models based on trees that were alive in the first and second inventory and either dead or alive in the third inventory. Since for a considerable proportion of the Swiss and German permanent plots (54.3 and 33.3 %, respectively) more than three inventories were available, individual trees can appear more than once in the dataset as all possible sets of inventory data were used for model development (Table 1; 32.1 % of the records are such 'repeated measures'). Multiple records per tree were treated as independent (cf. Fig. S2 for further details). The inventory data provide diameter measurements at breast height (*DBH*) for revisited trees with a diameter of more than 4, 7 and 6 cm for Switzerland, Germany and Ukraine, respectively.

As an explanatory variable, the annual relative basal area increment (*relBAI*, cf. Bigler & Bugmann, 2004) was calculated based on the first and the second *DBH* measurement as the compound annual growth rate of the trees basal area BA_i using

$$relBAI_i = \left(\frac{BA_{i,2nd}}{BA_{i,1st}}\right)^{\frac{1}{\Delta t}} - 1 \qquad \text{eqn 1}$$

with Δt denoting the number of years of the growth period.

Tree *DBH* in the second inventory was used in addition to *relBAI* to model tree status (alive or dead) of the third inventory. First-aid transformations were applied as suggested for only-positive data (Mosteller & Tukey, 1977) to improve the relationship of the explanatory variables and mortality. Thus, *DBH* was log-transformed. *relBAI* was transformed using a modified log-transformation (logst) to achieve finite values even for those 11 % of the trees for which no growth ($relBAI \leq 0$) was observed (Stahel, 2008). The respective transformation threshold c was calibrated to the combined *relBAI* values of Switzerland, Germany and Ukraine.

Environmental and stand characteristics

To increase the generality of the mortality models, we selected environmental variables that are known to have a considerable influence on growth and mortality of beech because they challenge the plant's physiological system, e.g., frost (cf. Charrier *et al.*, 2013) and drought (increased transpiration, reduced photosynthesis along with excessive respiration, cf. McDowell *et al.*, 2013), or because they influence resource availability, e.g., soil properties and competition. We emphasized the effects of water availability using a large set of drought characteristics that were calculated based on the local site water balance. Following Nothdurft (2013) and Neuner *et al.* (2015), we also related beech mortality to temperature and precipitation. The time available for annual tree growth was considered using growing degree-days. Nutrient supply, which influences tree growth but is less critical for survival, was considered by using the proxy variable soil *pH*. The database and derivation of the environmental variables are described in detail in Appendix B. Climate and drought variables were calculated for the entire year and/or for the growing season, i.e., from April to September (*G*) (Table 2). Temperature was additionally averaged for the months January to March (*W*). Since drought and other climatic drivers may have a delayed effect on mortality (Berdanier & Clark, 2016), all variables were calculated for the 'growth' period (i.e., between the first and the second inventory) and the 'mortality' period (i.e., between the second and third inventory period).

Table 2 Environmental and stand characteristics considered within the beech mortality model for the reduced Swiss dataset. Note the varying seasonal level of the covariates considering the entire year, the growing season from April to September (*G*) and the winter month January to March (*W*). All climatic covariates were calculated for both the 'growth' (2) and the 'mortality' period (3). The stand covariates were derived for the second inventory of each record (2). The transformation (log/logst, square root or none, as applicable) that resulted in the best performance is indicated. All covariates were included as an additional term and in interaction with logst(*relBAI*).

Covariates	Abbreviation	Type	Seasonal level	Period or inventory	Transformation	Range	Unit
Mean diameter at breast height	*DBH.mean.2*	stand	-	second	sqrt	100-373	mm
Interquartile range of diameter at breast height	*DBH.IQR.2*	stand	-	second	sqrt	41-324	mm
Median diameter at breast height	*DBH.median.2*	stand	-	second	sqrt	67-370	mm
Basal area per hectare	*BA.2*	stand	-	second	log	30-59	m^2 ha^{-1}
Number of trees per hectare	*N.2*	stand	-	second	log	281-2780	ha^{-1}
pH-value	*pH*	nutrient supply	-	-	log	3.5 - 7.7	-
Available water capacity in the soil	*AWC*	water availability	-	-	log	59 - 238	mm
Mean annual precipitation sum	*P.2*	water availability	annual	growing	log	959 - 1931	mm
	P.3			mortality	log	978 - 1781	
Mean precipitation sum during growing season	*PG.2*	water availability	growing season	growing	log	483 - 1077	mm
	PG.3			mortality	sqrt	515 - 1020	
Mean annual air temperature	*mT.2*	temperature	annual	growing	sqrt	5.3 - 9.5	°C
	mT.3			mortality	-	5.9 - 10.2	
Mean air temperature during growing season	*mTG.2*	temperature	growing season	growing	log	10.0 - 15.1	°C
	mTG.3			mortality	sqrt	10.8 - 15.8	
Mean air temperature during winter months	*mTW.2*	temperature	winter	growing	-	-0.9 - 2.8	°C
	mTW.3			mortality	-	-0.9 - 3.6	
Mean growing degree-days	*GDD.2*	temperature	growing season	growing	log	1169 - 2150	-
	GDD.3			mortality	log	1305 - 2279	
Mean number of months during growing season with water deficit	*mDEFdurG.2*	water availability	growing season	growing	logst	0.0 - 2.5	-
	mDEFdurG.3			mortality	logst	0.0 - 2.5	
Mean annual maximum water deficit	*mDEFmax.2*	water availability	annual	growing	logst	0 - 17	mm
	mDEFmax.3			mortality	logst	0 - 28	
Overall maximum of the annual maximum water deficit	*maxDEFmax.2*	water availability	annual	growing	logst	0 - 74	mm
	maxDEFmax.3			mortality	sqrt	0 - 288	
Mean of cumulative water deficit during growing season	*mDEFcumG.2*	water availability	growing season	growing	logst	0 - 31	mm
	mDEFcumG.3			mortality	logst	0 - 35	
Overall maximum of cumulative water deficit during growing season	*maxDEFcumG.2*	water availability	growing season	growing	logst	0-152	mm
	maxDEFcumG.3			mortality	sqrt	0-351	
Percentage of years with at least one month water deficit	*percDEF.2*	water availability	annual	growing	logst	0-100	%
	percDEF.3			mortality	logst	0-100	

Since not only climate and soil may affect growth and mortality, we additionally considered stand characteristics that reflect the development stage, competition and structure of the forests (Table 2; Gendreau-Berthiaume *et al.*, 2016). As a proxy for stand age and structural complexity, the mean, median and interquartile range (*IQR*) of *DBH* were calculated. To capture stand density, *BA* and the number of trees per ha (*N*) were derived. Stand characteristics were calculated for the second inventory of each record based on all living trees. We did not include variables based on maximum size-density concepts (e.g., Yoda *et al.*, 1963) since their application to complex, uneven-aged, and mostly multi-species stands such as those in our study is not appropriate.

Overall, thirty-one environmental and stand characteristics were used to examine the influence of climate, site factors and stand properties on the relationship of *DBH* and *relBAI* to beech mortality probability. Due to data availability, these in-depth analyses could be performed for a subset of the Swiss sites only (cf. Appendix B and Table 2).

Mortality model

Mortality probability p was modeled using logistic regression (Weiskittel *et al.*, 2011) where p is related to the inverse logit transformation of the linear predictor

$$p_{i,\Delta t=1} = logit^{-1}(X_i\beta) = \frac{\exp(X_i\beta)}{1+\exp(X_i\beta)} \qquad \text{eqn 2}$$

with $p_{i,\Delta t=1}$ denoting the annual mortality probability of tree i, X_i the design matrix of the linear predictor and β the respective parameter vector. Since the length of the mortality period was not constant for all observations in the inventory datasets, $p_{i,\Delta t=1}$ was scaled to the length of the respective mortality period of Δt years following Monserud (1976) using

$$p_{i,\Delta t} = 1-\left(1-p_{i,\Delta t=1}\right)^{\Delta t} \qquad \text{eqn 3}$$

resulting in a generalized logistic regression approach (Yang & Huang, 2013). The scaled mortality probability $p_{i,\Delta t}$ was used as a predictor for tree status y_i (1 = dead, 0 = alive), which was assumed to be binomially distributed. To estimate the parameters of β, the log-likelihood LL matching $p_{i,\Delta t}$ and y_i after Δt years was maximized:

$$LL\ (\beta) = \sum_{i=1}^{n} \{ y_i * \ln(p_{i,\Delta t}) + (1 - y_i) * \ln(1 - p_{i,\Delta t}) \} \qquad \text{eqn 4}$$

Standard errors, confidence intervals and p-values were calculated based on the Fisher information taken from the Hessian matrix.

Performance criteria

The performance of the models was assessed as good calibration (i.e., correct mortality rates) and good discrimination (i.e., correct attribution of dead/alive status). During model selection, the Brier Score (*BS*) defined as

$$BS = \frac{1}{n} \sum_{i=1}^{n} (p_{i,\Delta t} - y_i)^2 \qquad \text{eqn 5}$$

was applied, indicating good calibration and discrimination when being small (Steyerberg *et al.*, 2010).

Since calibration and discrimination skills of a model are not necessarily correlated (Bravo-Oviedo *et al.*, 2006), the prediction bias (p_{bias}) and the Area Under the receiver operating characteristic Curve (*AUC*) were used to examine model performance in more detail. p_{bias}, which indicates calibration accuracy, is defined as the difference of the mean predicted mortality probability (‘simulated mortality’) $\overline{p}_{\Delta t=10}$ and the mean mortality rate (‘observed mortality’) $\overline{y}_{\Delta t=10}$ over a time period of 10 years (cf. Appendix B). *AUC* is a widely used, threshold-independent measure of classification accuracy (Hosmer & Lemeshow, 2000). In our models, it corresponds to the probability that the model predicts a larger mortality probability for a randomly chosen dead tree than for a randomly chosen living tree (Fawcett, 2006). *AUC* ranges between 0 and 1 and equals 0.5 for randomly assigned tree status. Following Hosmer and Lemeshow (2000), the discriminative ability can be rated as acceptable ($0.7 \leq AUC < 0.8$), excellent ($0.8 \leq AUC < 0.9$) or outstanding ($AUC \geq 0.9$).

p_{bias} and *AUC* were calculated for the entire datasets as well as for a range of subsets by applying the models calibrated with the full data to individual reserves and specific diameter classes. This in-depth analysis provides further information on the variability of model performance.

Calibration and validation scheme

Based on the reduced Swiss dataset, the importance of environmental and stand characteristics for the prediction of tree mortality was assessed using 10-fold cross-validation and the 'one standard error rule' to avoid over-fitting (cf. Appendix B for further details, Breiman *et al.*, 1984; Hastie *et al.*, 2001). A basic model comprising log(*DBH*), logst(*relBAI*) and their interaction was compared with more sophisticated models, each additionally including one environmental or stand characteristic and its interaction with *relBAI*.

Since to our surprise no considerable benefit of including environmental and stand characteristics was found, the dataset for Switzerland was expanded to all beech-dominated reserves (Table 1). For each of the datasets from Switzerland, Germany and Ukraine, 10-fold cross-validation with a modified selection criterion resulting in less simplified models (cf. Appendix B) was applied to select an optimal combination of covariates and their respective transformations. Terms considered in the model formulae were log(*DBH*) and logst(*relBAI*). Additionally, the quadratic terms of the transformed variables and the interaction of log(*DBH*) and logst(*relBAI*) were included (Table S2). A comprehensive assessment of model performance was carried out for the models that achieved high discriminative accuracy. Additionally, each model was validated with data from the inventory datasets that had not been used for its calibration (Table 4).

All computations were performed within R (R Core Team 2015, R Foundation for Statistical Computing. Vienna, Austria). *relBAI* was transformed using *logst()* from the package *regr0* (Version 1.0-4/r46, 2015). Maximum likelihood estimation was carried out using the function *optim()* with the fitting method *BFGS*. *AUC* calculations were based on the function *auc()* from the package *SDMTools* (Version 1.1-221, 2014). Since *auc()* prevents values below 0.5, which is not appropriate for *AUC* calculations using partial datasets, the corresponding part of the code was removed.

Results

Environmental and stand influences on mortality

The results of the 10-fold cross-validation revealed no considerable model improvement by any of the environmental and stand characteristics (Fig. S3). Twenty-nine out of 31 covariates resulted in an improved *BS*, most strongly by mean and median *DBH*, winter temperature and stem density, whereas *pH* and *BA* did not cause a decrease in *BS*. The best model included median *DBH* as an additional covariate. In spite of these improvements, mean *BS* of the basic model without additional variables was still below the limit of the 'one standard error rule', i.e., the mean *BS* plus the standard error of *BS* of the best model (cf. Appendix B). Consequently, none of the additional covariates can be expected to substantially improve mortality predictions. To avoid the risk of over-fitting, the model including *DBH*, *relBAI* and their interaction was selected as the best parsimonious model, and subsequent models did not include additional environmental or stand variables.

Mortality patterns

The model selection procedure for the datasets from Switzerland, Germany and Ukraine resulted in three different model shapes (Table 3, for the results of model selection cf. Table S2). Beech mortality in the Swiss reserves was best described by the combination of log(*DBH*), logst(*relBAI*), the quadratic term of logst(*relBAI*) and the interaction of *DBH* and *relBAI*. In Germany, the interaction and the quadratic term were not required, thus resulting in a simpler model based on log(*DBH*) and logst(*relBAI*). In Ukraine, tree growth was not required to predict tree mortality, but models including a quadratic term for log(*DBH*) achieved highest accuracy. Thus, the most parsimonious model for the Ukrainian data included only log(*DBH*) and its quadratic term.

Table 3 Parameter estimates, standard errors, significance levels (*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$) and confidence intervals of the calibrated models for Switzerland, Germany and Ukraine. *DBH* = diameter at breast height (mm), *relBAI* = annual relative basal area increment. The transformation threshold *c* for the logst-transformation of *relBAI* was calibrated to the combined *relBAI* values of Switzerland, Germany and Ukraine ($c = 0.002333$).

Coefficient	*β*	*se*	*t*	*p*	Significance	Confidence intervals
			Switzerland			
Intercept	-0.204	0.816	-0.25	0.802		[-1.80, 1.40]
log(*DBH*)	-2.302	0.141	-16.36	0.000	***	[-2.58, -2.03]
logst(*relBAI*)	-1.922	0.482	-3.99	0.000	***	[-2.87, -0.98]
$(\text{logst}(relBAI))^2$	-0.698	0.078	-8.95	0.000	***	[-0.85, -0.55]
log(*DBH*) × logst(*relBAI*)	-0.616	0.057	-10.74	0.000	***	[-0.73, -0.50]
			Germany			
Intercept	0.917	0.592	1.55	0.122		[-0.24, 2.08]
log(*DBH*)	-1.281	0.086	-14.97	0.000	***	[-1.45, -1.11]
logst(*relBAI*)	-0.537	0.084	-6.36	0.000	***	[-0.7 , -0.37]
			Ukraine			
Intercept	14.201	3.708	3.83	0.000	***	[6.93, 21.47]
log(*DBH*)	-6.859	1.380	-4.97	0.000	***	[-9.56, -4.15]
$(\log(DBH))^2$	0.625	0.125	5.02	0.000	***	[0.38, 0.87]

For a beech tree with median growth, the probability to die within 10 years ranged between 1 and 32 % depending on its *DBH*, with considerable differences between the three models (Fig. 1). In the Swiss and German reserves, the mortality probability for beech was highest for small, slow-growing trees and decreased with increasing *DBH* and *relBAI*. However, the effect of growth on the mortality probability was less pronounced for the German model. Still, the Swiss and the German model predicted similar mortality probabilities over the entire *DBH* range for trees with average growth. In the Ukrainian forest, mortality patterns differed from those in the Swiss and German reserves. While the mortality probability similarly decreased with *DBH* for small trees, the risk of death increased again for trees with a *DBH* > 25 cm. The resulting U-shaped relationship between *DBH* and mortality probability was independent of tree growth.

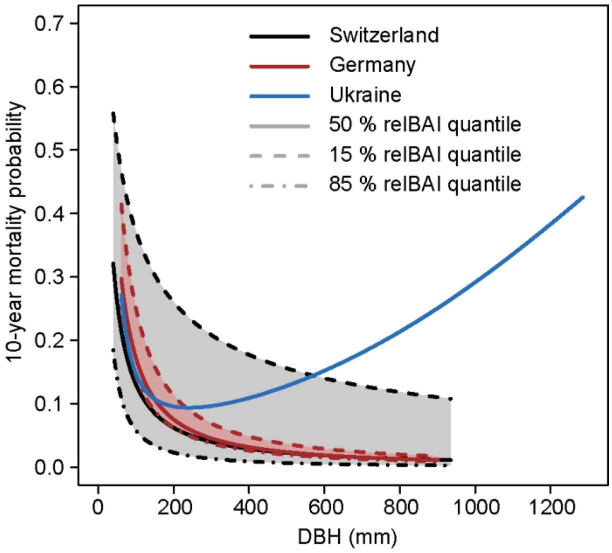


Fig. 1 Simulated 10-year mortality probability as a function of *DBH* for three growth levels as predicted by the Swiss, German and Ukrainian models. Median and quantiles at 15 and 85 % of annual *relBAI* were selected based on the combined *relBAI* values of all three datasets: median = 0.012, 15 % quantile = 0.002, 85 % quantile = 0.028. Predictions are restricted to the available *DBH* range of each dataset to avoid extrapolation.

Internal performance of mortality models

All three models predicted nearly unbiased overall mortality rates, as indicated by p_{bias} of approximately zero, thus confirming successful calibration (Table 4). According to the criteria by Hosmer and Lemeshow (2000), the Swiss model achieved excellent discrimination with an *AUC* of 0.83. The discriminative power of the German model was acceptable (*AUC* = 0.79), while the Ukrainian model performed only somewhat better than a random mortality assignment (*AUC* = 0.60). Therefore, only the performance of the Swiss and the German model, which attained sufficient discrimination of living and dead trees, was analyzed in more detail for their calibration domain.

Table 4 Calibration and validation performance of the Swiss, German and Ukrainian models. The respective performance measures 10-year p_{bias} and AUC were calculated for the calibration dataset and additionally when each of the three models was applied to the datasets of the two other countries (external evaluation) to assess the transferability of the mortality models.

Calibration dataset	Performance criterion	Performance of calibration dataset	Performance of external evaluation		
			Switzerland	Germany	Ukraine
Switzerland	p_{bias} (%)	-0.23	-	3.45	-8.00
	AUC	0.83	-	0.76	0.54
Germany	p_{bias} (%)	-0.10	-0.57	-	-5.71
	AUC	0.79	0.79	-	0.51
Ukraine	p_{bias} (%)	0.00	0.20	5.75	-
	AUC	0.60	0.68	0.63	-

The discriminative ability of the models clearly varied with tree size (Fig. 2). The Swiss model best distinguished between dead and living trees of small to medium size, whereas the death of trees with a $DBH > 35$ cm was predicted less successfully. This pattern was only partially evident for the German model with a lower overall discriminative power. Again, trees with diameters between 30 and 50 cm featured lower AUC values than smaller trees. However, unlike the Swiss model, the German model was able to discriminate acceptably between living and dead trees with a $DBH > 50$ cm. The discriminative power of the two models was influenced not only by tree size, but it also differed considerably among the reserves (Table S3). For the Swiss dataset, AUC values in the range 0.71-0.94 indicated acceptable to outstanding discrimination. In Germany, the model achieved acceptable to excellent performance for most of the reserves ($AUC = 0.74$-0.89), but the discrimination of living and dead trees was unsatisfactory in three reserves ($AUC < 0.7$).

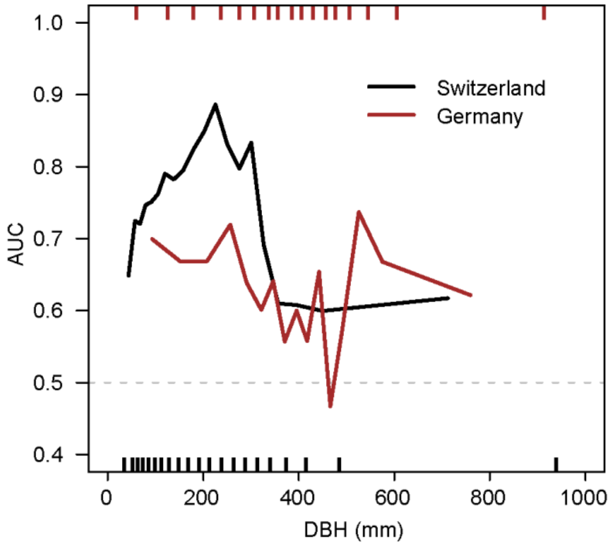
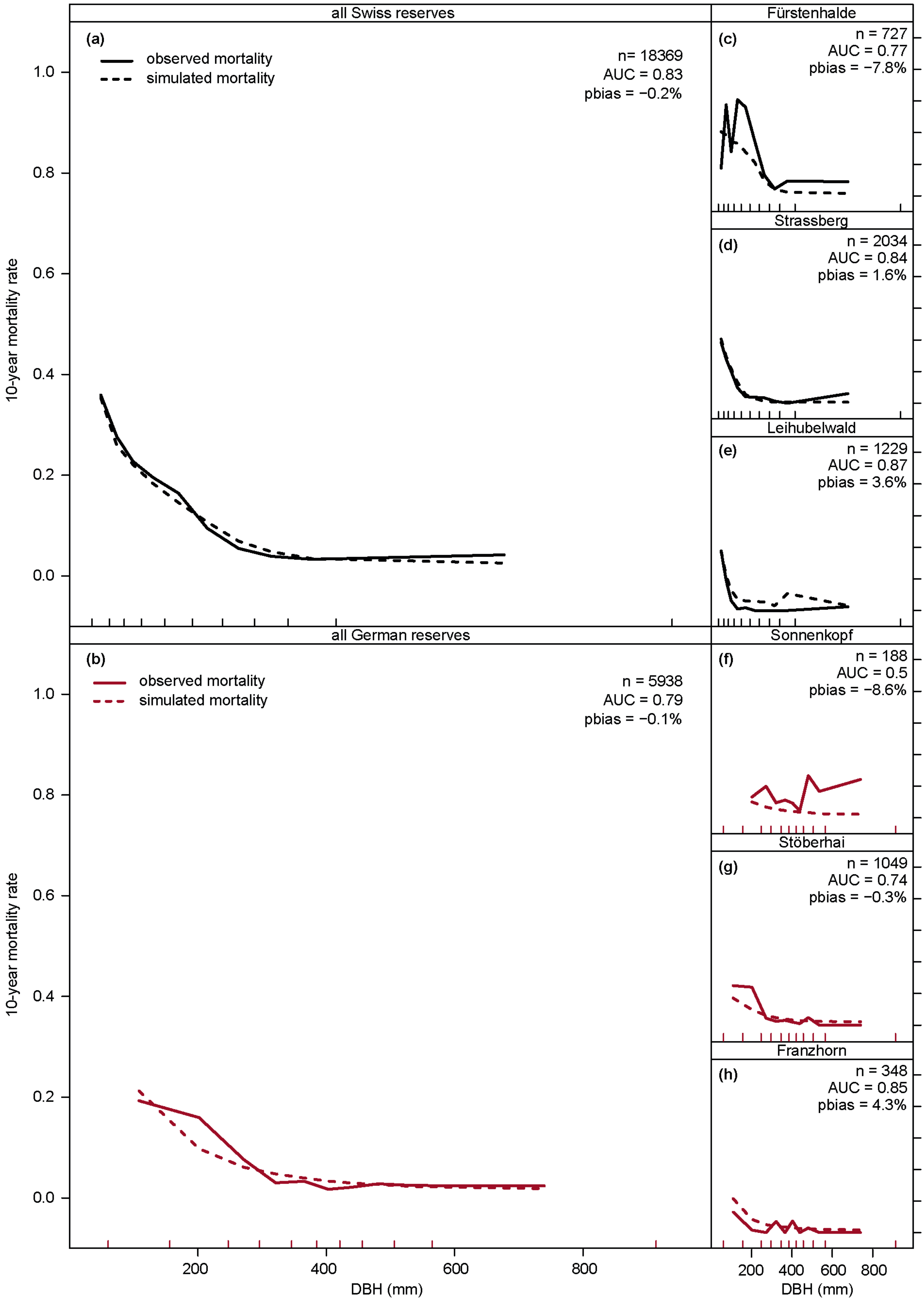


Fig. 2 *AUC* values for the Swiss and the German model calculated separately for *DBH* classes of the respective calibration dataset to assess the influence of tree size on discriminative power. *DBH* classes are approximately equally-sized (Switzerland: $n_{classes}$ = 20, Germany: $n_{classes}$ = 16). The limits of the *DBH* classes for both datasets are indicated as rugs in the respective color. The grey dashed line at $AUC = 0.5$ indicates a discrimination as good as random mortality assignment.

To assess the influence of tree size on prediction bias, observed and simulated mortality rates were analyzed as a function of *DBH* (Fig. 3), revealing that the Swiss and the German models predicted consistent mortality rates over the entire *DBH* range when considering the full dataset (Fig. 3a,b). However, p_{bias} for single reserves varied between -8.0 and 3.7 % in Switzerland, and between -8.6 and 4.3 % in Germany (Table S3). Positive and negative p_{bias} values were caused by deviations of observed and simulated mortality rates in all diameter classes, without any tree size tending to show a particularly large mismatch (Fig. 3c-h). Only the p_{bias} pattern of the German reserve Sonnenkopf (Fig. 3f) showed increased mortality of trees > 50 cm that was not captured by the model.

Fig. 3 Observed and simulated 10-year mortality rates of the Swiss and the German model plotted as a function of *DBH* to assess the influence of tree size on the prediction bias. Mortality rates are shown for the full datasets (a,b) as well as for three typical example reserves with under- and overestimation and with a nearly unbiased overall mortality prediction (c-h) to reveal which tree sizes resulted in substantial p_{bias} values. For each sub-plot, the number of records (*n*) included in the respective dataset and the performance measures *AUC* and p_{bias} are indicated. *DBH* classes are approximately equally-sized with $n_{classes}$ = 10. The limits of the *DBH* classes for both datasets are indicated as rugs in the respective color.


all Swiss reserves
(a)
observed mortality
simulated mortality
n= 18369
AUC = 0.83
pbias = −0.2%
10-year mortality rate
1.0
0.8
0.6
0.4
0.2
0.0
all German reserves
(b)
observed mortality
simulated mortality
n = 5938
AUC = 0.79
pbias = −0.1%
10-year mortality rate
1.0
0.8
0.6
0.4
0.2
0.0
200
400
600
800
DBH (mm)
Fürstenhalde
(c)
n = 727
AUC = 0.77
pbias = −7.8%
Strassberg
(d)
n = 2034
AUC = 0.84
pbias = 1.6%
Leihubelwald
(e)
n = 1229
AUC = 0.87
pbias = 3.6%
Sonnenkopf
(f)
n = 188
AUC = 0.5
pbias = −8.6%
Stöberhai
(g)
n = 1049
AUC = 0.74
pbias = −0.3%
Franzhorn
(h)
n = 348
AUC = 0.85
pbias = 4.3%
1.0
0.8
0.6
0.4
0.2
0.0
200
400
600
800
DBH (mm)

External evaluation of mortality models

When the Swiss and the German model were validated against each other, *AUC* values of both models indicated acceptable discriminative power (Table 4). However, when validated with the Ukrainian data, both models achieved very poor *AUC* values. In contrast, the Ukrainian model was more successful in discriminating living vs. dead trees for the German and the Swiss dataset than within its calibration domain.

The analysis of p_{bias} as a function of tree size (Fig. 4; cf. Table 4 for overall p_{bias} values) revealed that mortality rates in the Swiss reserves were reproduced quite well by the German model, showing only a weak underestimation for average-sized and large trees, thus resulting in an overall p_{bias} value close to zero. In contrast, the Swiss model was less successful in predicting mortality rates for the German dataset, especially for small and average-sized trees, resulting in an overestimation of mortality (p_{bias} = 3.45 %). The U-shaped mortality pattern in the Ukrainian model resulting from the quadratic term of *DBH* caused a clear overestimation of mortality for larger trees in the Swiss as well as in the German datasets. Vice versa, when the Swiss and the German model were used to predict mortality rates for the Ukrainian dataset, the mortality of large trees was far too low.

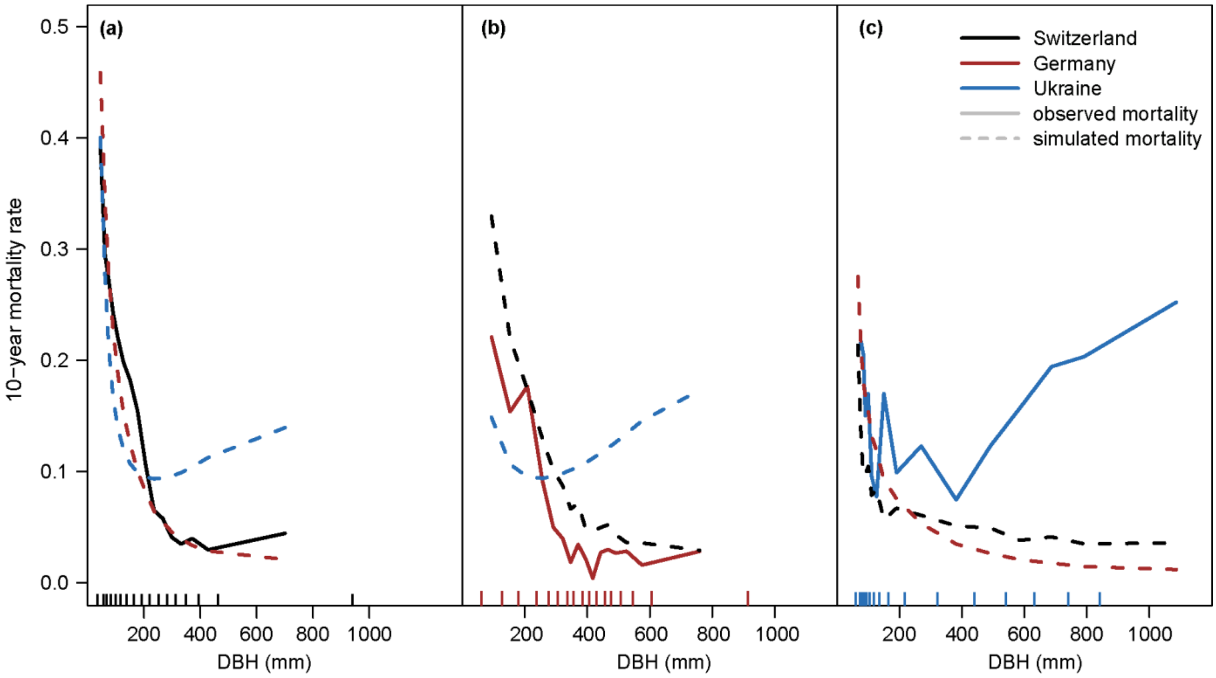


Fig. 4 Ten-year mortality rates as the result of external validation plotted as a function of *DBH* for the datasets from Switzerland (a), Germany (b) and Ukraine (c). Observed mortality is shown with solid lines, mortality simulated by models of the respective other countries is shown in dashed lines. *DBH* classes are approximately equally-sized ($n_{classes}$ = 16). The limits of the *DBH* classes for the datasets are indicated as rugs in the respective color.

Discussion

Environmental and stand influences on mortality

The integration of covariates beyond tree growth and size in tree mortality models to improve their accuracy and applicability to variable site conditions has been suggested in a number of studies (e.g., Monserud & Sterba, 1999; Dietze & Moorcroft, 2011), but these conjectures could not be tested due to insufficient sample sizes. For the first time we were able to evaluate this using a very large dataset for a widespread European tree species. Contrary to expectations (cf. Nothdurft, 2013; Neuner *et al.*, 2015), none of the environmental or stand variables markedly enhanced the accuracy of mortality predictions. Nevertheless, this does not mean that environmental and stand characteristics do not influence beech mortality, but rather that our models consider these effects via the integrating variable growth. In addition, it should be taken into account that our dataset does not feature annual resolution, i.e., the lack of model improvements when including climate and drought variables may be due to the inability to detect impacts of climate or competition over shorter time scales (Dobbertin, 2005). Because of their high temporal resolution, dendrochronological data are likely to have higher potential for contributing to the understanding of the interactions between environment, growth and tree mortality (e.g., Bigler *et al.*, 2004; Gillner *et al.*, 2013; Cailleret *et al.*, 2016). Also, the lack of any direct influence of environmental covariates on mortality in our models may partly have been caused by the low spatial resolution of the climatic and especially the soil data, such that these covariates did not effectively represent drought conditions at the tree level.

Growth, which integrates not only the effects of competition, but also those of the environment (Dobbertin, 2005) was not considered as a covariate in the models by Nothdurft (2013) and Neuner *et al.* (2015). Conversely, in none of the growth-based beech mortality models (e.g., Dursky, 1997; Wunder *et al.*, 2008; Holzwarth *et al.*, 2013) the influence of climate, soil or competition was taken into account. Our novel approach combines growth and environmental data in unified models, indicating that tree size (*DBH*) and stem growth (*relBAI*) sufficiently integrate the adverse effects of water availability and competition on the vitality of beech, and that the influence of growth on mortality is stable even under varying environmental conditions. We expect our results to be reliable since the Swiss reserves cover a large portion of the natural gradient of site characteristics for beech forests, encompassing dry to moist and warm to cool conditions (Table 2), and yet not even drought, which we consider as the environmental driver with the largest potential to influence the growth-mortality relationship (Geßler *et al.*, 2007), explained spatial and temporal differences of mortality. Thus, we suggest *DBH* and *relBAI* as meaningful and unifying predictors of beech mortality based on inventory data with decadal resolution.

Mortality patterns

The similarities in mortality predictions of the Swiss and the German model indicate that mortality processes were similar in pattern and magnitude in the reserves of both networks. Thus, mortality was driven mainly by competition, and the competitive status and vitality of a tree could be expressed well using tree size and growth. This is in line with mortality relationships for beech found in Swiss reserves (Wunder *et al.*, 2007; Wunder *et al.*, 2008), in a nature reserve in Eastern Germany (Gillner *et al.*, 2013) and in the German National Park Hainich (Holzwarth *et al.*, 2013). In contrast to Holzwarth *et al.* (2013), however, we did not find a U-shaped mortality relationship between *DBH* and mortality, most presumably due to the low importance of advanced ‘decay’ phenomena in the reserves of our dataset as a result of previous management and their comparatively low age (Heiri *et al.*, 2011; Meyer & Schmidt, 2011).

In contrast to the comparable influence of tree size on mortality probability, the growth variable *relBAI* more strongly affected mortality in the Swiss than in the German reserves. As discussed below, this may be related to (1) different climatic conditions, (2) differences in species composition and/or (3) differences in stand structure and competition. However, we decided not to include further site and stand covariates into these models since, when doing so for the reduced Swiss dataset, no marked model improvement was achieved.

Although the climate of the Swiss and German reserves is similar, mean annual precipitation sums are higher in Switzerland, potentially contributing to the different relationship between growth and mortality (Monserud & Sterba, 1999). Under better growing conditions, which may apply to the Swiss reserves, the same reduction in growth could lead to a larger increase of mortality risk than under less favorable conditions, where trees are adapted to lower growth. However, we demonstrated that climate and drought could not explain the variability in beech mortality for a subset of the Swiss data.

Species composition was found to be related to beech mortality (Jutras *et al.*, 2003; Boeck *et al.*, 2014; Neuner *et al.*, 2015). Possibly, the higher proportion of spruce and fir in the Swiss reserves may explain the pronounced effect of low growth on mortality. However, the quantification of such effects is everything but straightforward and should be based on spatially explicit, species-specific competition indices.

Lower *BA*, *N* and *SDI* in the German reserves suggest lower competition compared to the Swiss reserves. Although a trend of increasing importance of tree growth for mortality in denser stands (i.e., higher *BA*) was confirmed within both datasets, no marked improvement resulted when *BA* or an interaction of *BA* and *relBAI* were included in a model for the combined Swiss and German data (results not shown). This suggests that slower growth is less important in stands with lower density, such as in the German reserves, but the processes altering the influence of growth on mortality are not sufficiently explained with stand density alone. Differences in mortality may originate from the type of management regime prior to reserve designation (i.e., in Germany mainly thinning from below) and the time since the last management intervention, factors that are not evident directly from stand structural attributes.

Compared to the Swiss and German mortality models, the Ukrainian model reflected entirely different mortality patterns. The U-shaped size-dependent mortality and the absence of any influence of growth on mortality were most striking. High mortality rates for small as well as for large trees have long been proposed as a general pattern (Buchman *et al.*, 1983; Lorimer & Frelich, 1984) and have recently been disentangled into different mortality ‘modes’, thus providing improved insights on the mechanisms associated with beech mortality (Holzwarth *et al.*, 2013). Our findings coincide with this mortality pattern, as processes that may act to amplify the mortality of large trees, such as stem rot or wind breakage, were reported for the Uholka forest (Trotsiuk *et al.*, 2012; Hobi *et al.*, 2015). This may have been the cause for the lack of a growth-related component in the mortality model, i.e., also trees with high growth rates may have died.

However, it should be taken into account that the Uholka data derive from one single (albeit large) plot monitored during 10 years, whereas the German and Swiss data cover not only a much larger set of environmental conditions but also a much longer period. Thus, conclusions derived from this single plot with only one mortality period should be drawn with care, as mortality is highly variable in space and time (cf. Wunder *et al.*, 2008). Still, several lines of evidence indicate that it may be representative of primeval beech forests in general, including the U-shaped mortality pattern in the German National Park Hainich (Holzwarth *et al.*, 2013) and the high amounts of deadwood in all decay stages in the Uholka-Shyrokyi Luh primeval beech forest, indicating regularly occurring small-scale disturbances (Hobi *et al.*, 2015).

Internal performance of mortality models

The good to excellent overall discriminative performance achieved by the German and Swiss models substantiates the suitability of tree size and growth for the prediction of natural mortality of beech. In comparison, the Ukrainian model performed much worse. Besides the additional source of variability due to wind disturbances, it is possible that tree mortality in primeval forests can generally be described less accurately by size and growth due to the concurrence of all successional stages. The considerable variation in individual tree growth histories (Nagel *et al.*, 2014) and increased susceptibility of trees to factors that are hard to predict, such as stem rot or other diseases, may render the process of tree mortality and the relationship between vigor, competitiveness and mortality more complex (Franklin *et al.*, 1987).

Owing to the large number of records included in our datasets, the performance criteria *AUC* and p_{bias} could be calculated not only for the entire dataset, but also (1) as a function of tree size and (2) for individual reserves. Both elements provide novel insights, as discussed below.

On the one hand, *AUC* patterns indicate that the high overall model performance was driven particularly by the excellent discrimination of small- to mid-diameter trees, while the predictive power of the covariates available in our study decreased with tree size. This suggests that competition was the main driver for beech mortality as captured in the Swiss and German mortality model. Competition decreases in importance for larger trees (Franklin *et al.*, 1987), but it is reasonable to surmise that mortality of large trees is more complex and thus harder to predict as the result of, e.g., wind, pathogens and wood-decaying fungi (Trotsiuk *et al.*, 2012; Holzwarth *et al.*, 2013). Additionally, mortality processes for such trees may not be covered well in our datasets due to the comparatively small number of trees with $DBH > 50$ cm.

On the other hand, the performance criteria calculated separately for each reserve revealed large differences in predictive as well as in discriminative ability. In combination with the graphical representation of observed and simulated mortality over *DBH*, performance measures calculated per reserve allowed us to relate the influence of development stage and disturbance to the observed mortality patterns. For example, the underestimation of the mortality of trees with $DBH > 50$ cm in the German reserve Sonnenkopf (Fig. 3f) was possibly caused by a small-scale wind disturbance (Meyer *et al.*, 2015). However, this was the only example where an under- or overestimation of mortality could be related to a particular historical event. Similarly, it was not possible to group the reserves according to p_{bias} patterns, and the variability in mortality patterns at the level of individual permanent plots could not be linked to climate, soil or stand structure, either. Thus, tree mortality remains a highly variable and multi-factorial process.

External evaluation of mortality models

Validation with independent data is an important step to rigorously test the transferability of mortality models, e.g., for application in DVMs (Hawkes, 2000; Woolley *et al.*, 2012), be it at the species level (stands and landscapes) or for generalization into a broad suite of 'Plant Functional Types' (global level). To assess the general applicability of a model, the importance of the performance measures AUC and p_{bias} should be weighted differently than in an internal assessment. p_{bias} should be evaluated first since it is more sensitive to under- and overestimation of mortality rates than the discrimination measure AUC. However, overall p_{bias} values are only helpful if the mortality pattern across tree size is reflected adequately (cf. Table 4 and Fig. 4; Ukrainian model applied to Swiss data). Thus, it is important to graphically represent the observed and simulated mortality rates as a function of tree size.

The limited informative value of AUC regarding validation performance is clearly evident from the Ukrainian model, which better discriminated living and dead trees for the Swiss and German datasets than for its own calibration data. Thus, the discriminative power of a model strongly depends on the dataset to which it is applied, and hence AUC values reported for validation are primarily an indicator of the discrimination of dead vs. living trees in the dataset itself, and only secondarily of the general suitability of model structure and parameterization.

p_{bias} from the external validation reflected the mortality patterns identified by the three mortality models, showing similarities for the Swiss and the German networks but a deviating pattern for the Ukrainian forest. Due to the increased mechanical instability of larger trees in the Ukrainian forest, the models calibrated with data from Swiss and German reserves were not transferable to the Ukrainian data, and vice versa. The overestimation of mortality by the Swiss model when applied to German data traces back to the larger effect of tree growth on mortality in the Swiss model, which penalized more strongly for low *relBAI* values and thus reduced the survival of slow-growing trees. Still, the low p_{bias} values of 3.33 and -0.53 % for a period of 10 years and acceptable *AUC*s suggest that the similarities of mortality patterns in Switzerland and Germany allow for a meaningful application of the models to the other country, or the derivation of a joint model based on the combined datasets.

Implications for mortality algorithms in DVMs

A major limitation for the analysis of long-term forest processes such as mortality is data availability (Bugmann, 1996; Hawkes, 2000). Generalized logistic regression is helpful to make effective use of inventory data from permanent plots of forest reserves for mortality modeling, even in the case of irregular measurement intervals. Although we found that the bias in mortality predictions introduced by ignoring the dependency structure is negligible (cf. Fig. S2), the approach of generalized logistic regression could be further improved by including random effects to account for the hierarchical data structure (Yang & Huang, 2013). Empirical mortality models are strongly needed to improve projections of DVMs (Adams *et al.*, 2013). However, the derivation of such predictive models requires different strategies for (1) model selection and (2) performance assessment compared to mortality models that are built for inferring the effects of a set of covariates on mortality.

Models designed for mortality prediction in DVMs should be based on a model selection procedure that avoids the risk of over-fitting, which can be particularly problematic when a mortality model is derived from a spatially and/or temporally limited dataset. We used a very large dataset, and ensured model parsimony by applying a 10-fold cross-validation combined with the ‘one standard error rule’ (Breiman *et al.*, 1984).

The combined analysis of p_{bias} and *AUC* enables a comprehensive screening of the performance of tree mortality models in terms of calibration and discrimination. In particular, it provides insights on often neglected aspects of spatial variability and validity and thus provides essential information regarding the uncertainty of mortality algorithms in DVMs. We suggest that p_{bias} and *AUC* should be preferred over confusion matrices or sensitivity and specificity; threshold-dependent metrics should be avoided since they strongly depend on the choice of the threshold (Lawson *et al.*, 2014). Moreover, thresholds are not required for the implementation of mortality algorithms in DVMs when stochastic approaches are employed, which were found to be more promising for the classification of tree status than deterministic approaches (Fortin & Langevin, 2011; Bircher *et al.*, 2015). Thus, we suggest *AUC* as a key measure to assess the calibration performance while p_{bias} and its graphical representation as a function of tree size should be used to characterize validation performance. For internal performance assessments based on subsets of the calibration data, a combination of both performance criteria is recommended to assess the spatial variability of mortality. We also recommend the analysis of *AUC* patterns that are calculated by *DBH* class, thus revealing the accuracy of predictions for different tree sizes.

The mortality models presented here were derived with a view towards the requirements of DVMs, i.e., assuring parsimony, and that their internal as well as external performance was evaluated comprehensively. Acceptable p_{bias} and high *AUC* values show that these models allowed us to approximate tree mortality reasonably well by simple indicators of tree size and growth. Rather simple relationships of log-transformed covariates and their quadratic equivalent successfully described the covariate effect on mortality and make our models easily applicable. Nevertheless, potential model improvements by means of more flexible approaches, e.g., restricted cubic splines (Wunder *et al.*, 2008), could be assessed in the future. External model evaluation suggested rather accurate mortality predictions for the German and the Swiss mortality models when validated with data from the respective other country. Moreover, model robustness was fostered by the largest dataset ever used to calibrate beech mortality models, covering a wide range of environmental conditions and multiple decades. Therefore, the Swiss and German mortality models are promising candidates for inclusion in DVMs.

DVMs are widely used to anticipate future ecosystem development based on climate scenarios (Bonan, 2008). Although the mortality models developed here do not include climate variables explicitly, mortality depends on the growth variable *relBAI*, which itself responds to interannual variability in the environment, including climate. However, growth rates as simulated in a DVM may not have the same features as those from inventory or tree-ring data, e.g., regarding the absolute level of simulated growth, the magnitude of interannual variability or temporal autocorrelation (cf. Rasche *et al.*, 2012; Anderegg *et al.*, 2015). Thus, the interaction of growth and mortality predictions warrants further scrutiny before simulated growth can be reliably used as a predictor for tree mortality (Wernsdörfer *et al.*, 2008;

Larocque *et al.*, 2011; Radtke *et al.*, 2012; Bircher *et al.*, 2015). Nevertheless, the growth-dependent mortality algorithms derived here are advantageous for implementation in DVMs as they follow the rule of parsimony and avoid undesirable interactions of climate-dependent growth and additional climate variables.

In conclusion, we developed models for regular mortality of individual beech trees that we can recommend for incorporation and examination in DVMs. They are highly promising for pushing the frontier of DVM development towards more reliable predictions that are congruent with observational data (Bircher *et al.*, 2015). However, for an adequate parameterization, mortality models for an extended set of tree species are required, taking into account their widely different life history strategies (Franklin *et al.*, 1987). We are confident that such models can be fitted and evaluated using the methodology developed here, provided that extensive datasets covering large gradients of site conditions are available. The limited availability of such data continues to constrain the development of robust models of crucial forest processes such as tree mortality and recruitment (Lutz, 2015). Thus we need to emphasize the invaluable nature of long-term monitoring data in the context of a growing need for better empirical foundations in the modeling of future vegetation dynamics.

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Appendix A – Table S1-3, Fig. S1-3

Table S1 Stand characteristics per reserve for the Swiss, German and Ukrainian data.

Switzerland	***N*** **(ha^{-1})**	***BA*** **(m^{2}ha^{-1})**	**mean *DBH* (mm)**	**10-year mortality (%)**	***SDI***	**Germany**	***N*** **(ha^{-1})**	***BA*** **(m^{2}ha^{-1})**	**mean *DBH* (mm)**	**10-year mortality (%)**	***SDI***
Adenberg	448	38.0	293	18.2	690	Franzhorn	286	31.1	334	5.9	533
Bannhalde	530	45.2	265	16.6	824	Großer Freeden	341	39.8	364	6.7	689
Bois de Chênes	557	34.2	248	13.1	662	Großer Staufenberg	392	34.2	315	9.6	640
Fürstenhalde	400	38.4	323	17.2	685	Hünstollen	298	35.0	339	8.3	609
Hüntwangenhalde	900	40.4	209	6.6	836	Limker Strang	166	26.6	427	5.2	469
Langgraben	723	44.5	246	19.7	858	Lohn	136	32.1	530	7.5	485
Leihubelwald	951	33.3	190	14.5	725	Meinsberg	220	35.2	437	5.8	680
Seldenhalde	647	52.0	247	9.0	955	Nordahner Holz	327	35.1	321	7.5	623
Strassberg	988	34.5	191	12.1	744	Oderhang	295	29.4	335	4.7	594
Tariche Bois Banal	1102	42.4	192	21.5	902	Rieseberg	241	32.0	377	8.7	555
Tariche Haute Côte	951	43.8	220	12.6	896	Sonnenkopf	181	29.6	432	11.5	636
Tutschgenhalden	717	44.0	243	10.1	854	Stöberhai	323	36.5	366	5.6	690
Unterwilerberg	577	46.8	296	10.0	862	Vogelherd	138	25.0	473	2.7	395
Vorm Stein	1357	40.4	178	16.2	905	**Ukraine**					
Weidwald	769	46.2	247	12.0	903	Uholka	228	37.3	357	15.0	599

Table S2 Mean Brier scores (*meanBS*) of the models considered during model selection using 10-fold cross-validation for the three calibration datasets from Switzerland, Germany and Ukraine. † = model achieving best performance. At the bottom, these models and the respective limits of *meanBS* plus 0.8 times its standard error (*seBS*) are indicated. All models that perform equally well considering the modified 'one standard error rule' are indicated in light grey. The best parsimonious model for each dataset, which was selected for further analysis, is framed.

Models evaluated during 10-fold cross-validation						***meanBS***		
Model number	**log (*DBH*)**	**(log (*DBH*))^2**	**logst (*relBAI*)**	**(logst (*relBAI*))^2**	**log(*DBH*) × logst(*relBAI*)**	**Switzerland**	**Germany**	**Ukraine**
1	X					0.1295	0.0687	0.0761
2	X	X				0.1293	0.0685	0.0752
3			X			0.1188	0.0720	0.0758
4			X	X		0.1181	0.0719	0.0759
5	X		X			0.1131	0.0678	0.0759
6	X	X	X			0.1128	0.0676 †	0.0752
7	X		X	X		0.1119	0.0678	0.0760
8	X	X	X	X		0.1117	0.0676	0.0752
9	X		X		X	0.1116	0.0678	0.0757
10	X	X	X		X	0.1117	0.0676	0.0750 †
11	X		X	X	X	0.1107 †	0.0678	0.0758
12	X	X	X	X	X	0.1108	0.0676	0.0750
Number of the model achieving best performance						**11**	**6**	**10**
***meanBS* + 0.8 × *seBS* of the best model**						**0.1114**	**0.0683**	**0.0754**

Table S3 Detailed internal performance of the Swiss and German models. Ten-year p_{bias} and *AUC* were calculated separately per reserve. Additionally, the number of records (*n*) is indicated.

Swiss reserves	p_{bias} (%)	*AUC*	*n*	German reserves	p_{bias} (%)	*AUC*	*n*
Adenberg	-4.6	0.82	2161	Franzhorn	4.3	0.85	348
Bannhalde	-1.6	0.80	297	Großer Freeden	-0.8	0.89	513
Bois de Chênes	1.8	0.85	3252	Großer Staufenberg	-0.5	0.74	417
Fürstenhalde	-7.8	0.77	727	Hünstollen	1.1	0.78	667
Hüntwangenhalde	3.7	0.94	415	Limker Strang	-0.7	0.83	995
Langgraben	-8.0	0.86	440	Lohn	-2.7	0.76	180
Leihubelwald	3.6	0.87	1229	Meinsberg	-2.1	0.81	657
Seldenhalde	3.3	0.81	644	Nordahner Holz	4.1	0.80	256
Strassberg	1.6	0.84	2034	Oderhang	3.5	0.62	262
Tariche Bois Banal	1.0	0.86	2105	Rieseberg	2	0.75	126
Tariche Haute Côte	1.8	0.83	2266	Sonnenkopf	-8.6	0.50	188
Tutschgenhalden	-3.8	0.85	281	Stöberhai	-0.3	0.74	1049
Unterwilerberg	-5.1	0.83	300	Vogelherd	-0.1	0.66	276
Vorm Stein	3.2	0.83	840				
Weidwald	-5.8	0.71	1378				

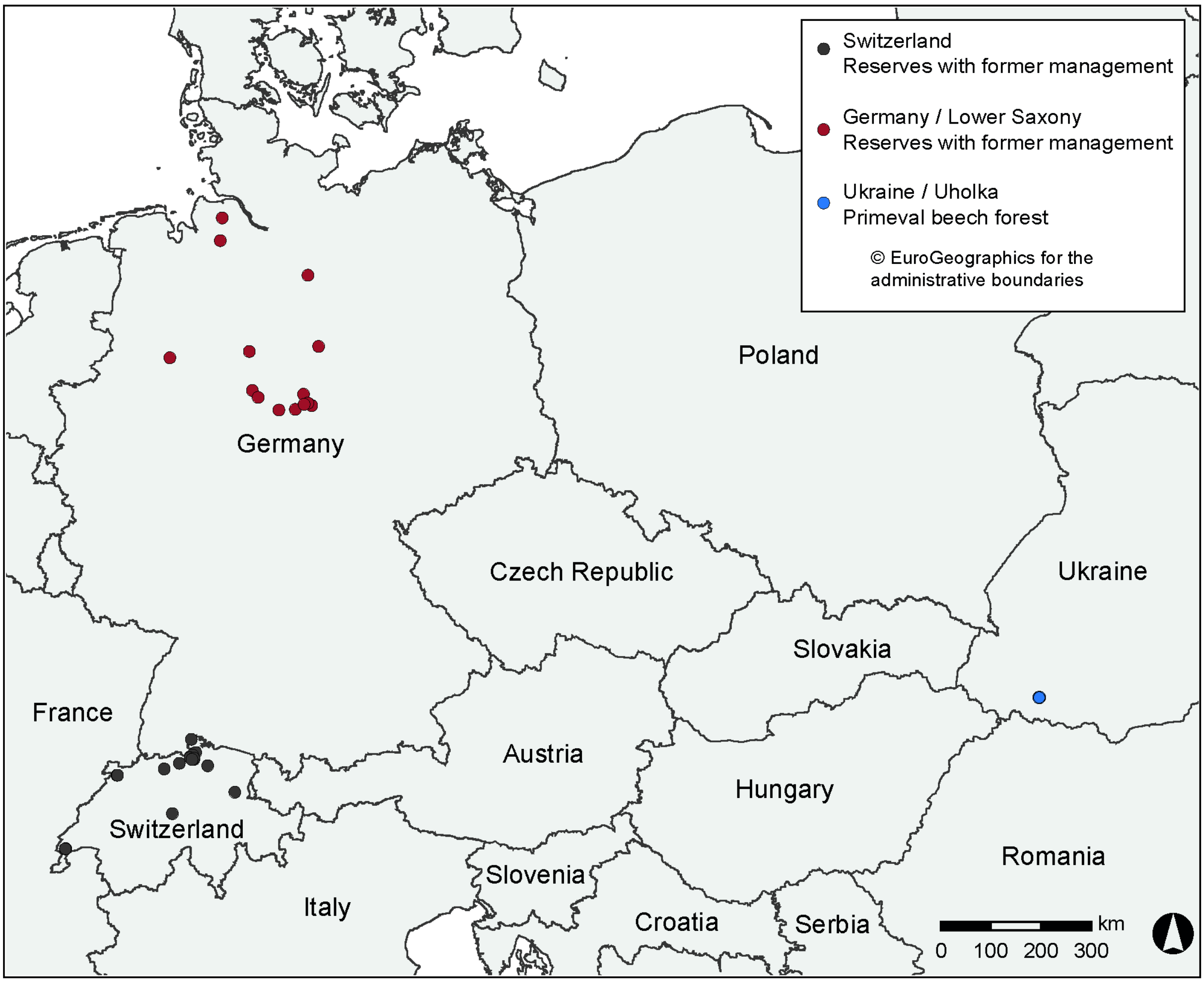

Fig. S1 Map of the strict forest reserves used for calibration and validation. Number of reserves per respective dataset: Switzerland n = 15, Germany n = 13, Ukraine n = 1.

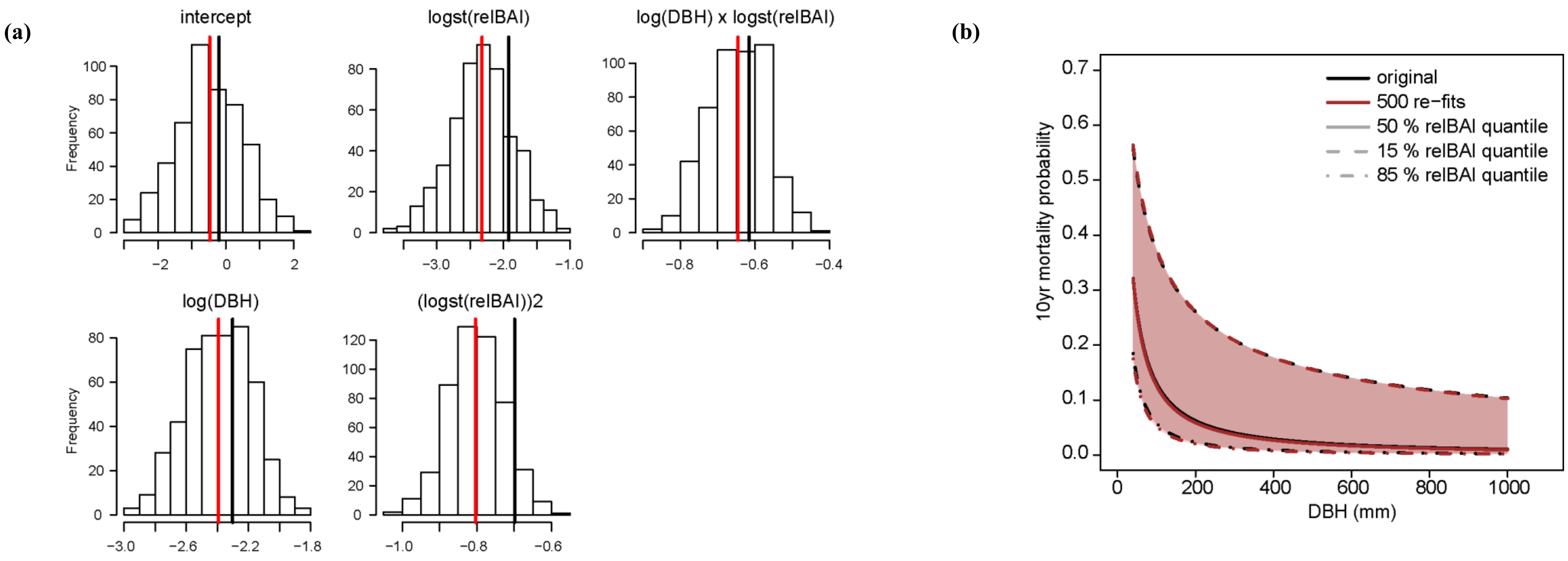

Fig. S2 To evaluate the influence of trees occurring more than once in the calibration dataset, parameter estimates and model predictions of the Swiss model (refer to Table 3) were compared with estimates and predictions of 500 re-fitted models. These were calibrated using randomly sampled inventory sets including only one set of three consecutive inventories per permanent plot, to ensure that trees occur only once per calibration dataset. Histograms of the re-fitted parameter estimates (a) are shown indicating their mean (red) and the original parameter estimate (black). While the estimates for the intercept, log(*DBH*) and the interaction of log(*DBH*) and logst(*relBAI*) do not indicate any bias, the estimates of logst(*relBAI*) and its quadratic term appear positively biased when the entire dataset is used for calibration. However, model predictions differ only marginally as indicated by the simulated 10-year mortality probability (b) predicted by the original model (black) and the model with parameter estimates averaged over the 500 re-fits (red) plotted as a function of *DBH* for three growth levels. For a period of ten years in the Swiss dataset, the original model overestimates the mortality probability on average by 0.2 % in comparison to the re-fitted mean model. In view of the uncertainty that is associated with mortality predictions, such a bias does not justify the use of more sophisticated regression techniques, which become laborious for data with unequal measurement intervals (generalized mixed logistic models, cf. Yang & Huang, 2013). Repeated model selection using 10-fold cross-validation revealed that the 'best' models considering the 'one standard error rule' always include the original combination of covariates and only some sampled datasets support the (not necessarily) more parsimonious model structure log(*DBH*) + $(\log(DBH))^2$ + logst(*relBAI*) + $(\text{logst}(relBAI))^2$ (results not shown). In favour of parsimony and simplicity, the use of repeated observations per tree seems sufficiently solid.

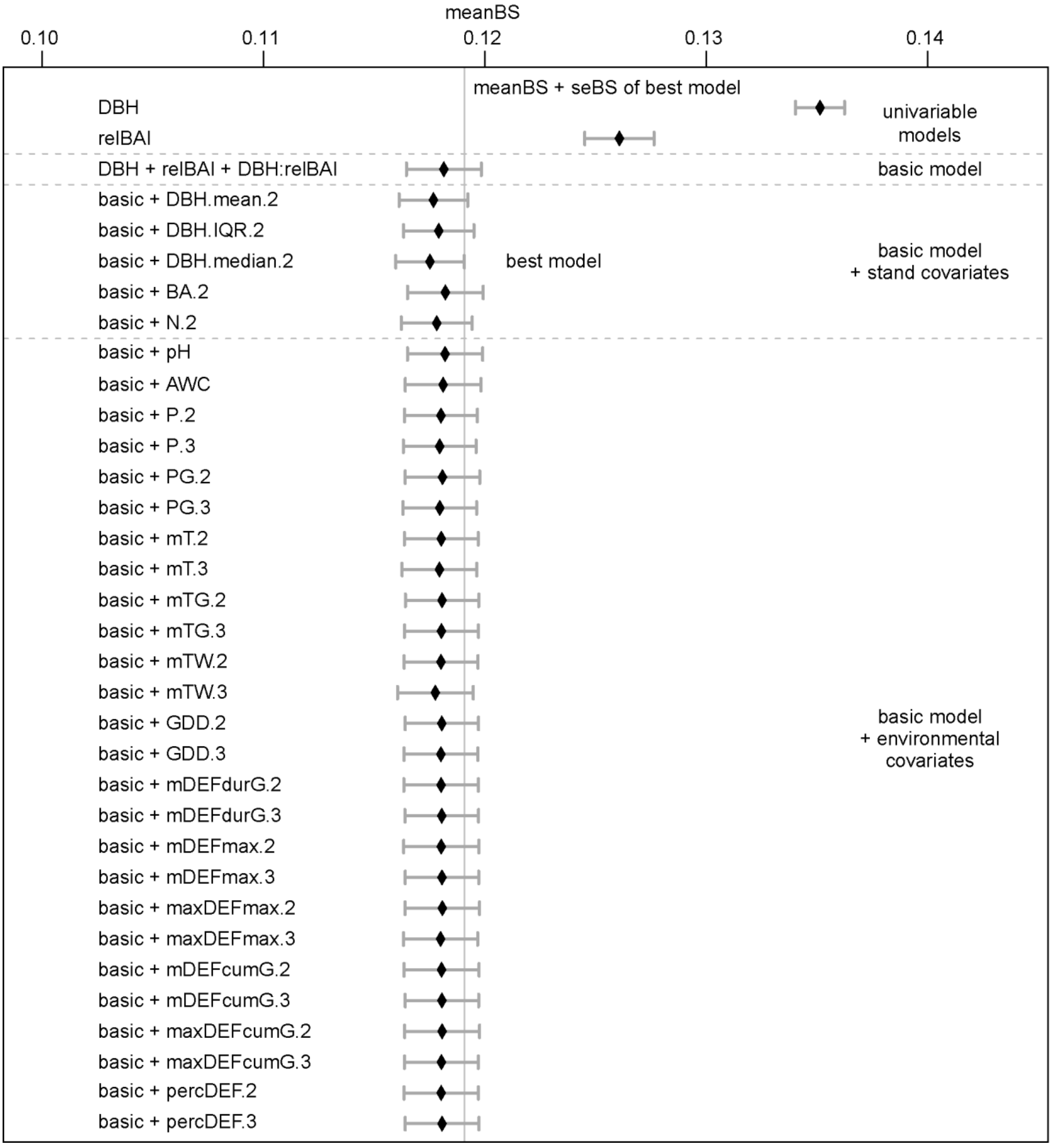

Fig. S3 Mean Brier Scores (*meanBS*) and corresponding standard error bars (*seBS*) resulting from 10-fold cross-validation for two univariable models, the basic model and the basic model with additional environmental and stand characteristics (cf. Table 2 for explanation and applied transformations). Transformed covariates are included as an additional term plus as an interaction with logst(*relBAI*). The grey line indicates *meanBS* + *seBS* ('one standard error rule') of the best model, which includes median *DBH* as an additional covariate. *meanBS* of the basic model is within this limit and was therefore chosen as the best parsimonious model.

Appendix B – Extended material and methods

Environmental characteristics

For a subset of the permanent plots from Switzerland (Table 1), a soil survey was conducted including one soil profile per permanent plot. Field capacity and available water capacity (*AWC*) were calculated by the use of pedotransfer functions (Teepe *et al*., 2003) based on soil texture, bulk density, organic carbon content and stone content of each soil horizon. Soil characteristics were accumulated to 1 m depth or down to the bedrock if soil depth was less than 1 m.

Temperature and precipitation data were derived using the DAYMET model (Thornton *et al*., 1997; available from Landscape Dynamics, WSL), interpolating MeteoSwiss station data to a grid of 1 ha cell size. Daily minimum and maximum temperatures as well as daily precipitation sums were derived for each permanent plot by calculating the average of the DAYMET cell that included the center of the permanent plot and the eight surrounding cells, following Rasche *et al*., (2012). In the mortality models, we considered mean temperature (*mT*) and mean precipitation sums (*P*). Growing degree-days (*GDD*) were calculated following Baskerville and Emin (1969) using R code available online (http://geog.uoregon.edu/envchange/software/GDD_calculator.txt).

The site water balance was determined using a climatic water balance model that derived monthly soil water deficit as the difference of potential and actual evapotranspiration (modified Thornthwaite method, cf. Willmott *et al*., 1985; code available online http://geog.uoregon.edu/envchange/software/AET_calculator.txt). To quantify the frequency and intensity of drought, six distinct drought characteristics were derived from the monthly soil water deficit (Table 2).

Performance criterion pbias

p_{bias}, which indicates calibration accuracy, is defined here as the difference of the mean predicted mortality probability ('simulated mortality') $\overline{p}_{\Delta t=10}$ and the mean mortality rate ('observed mortality') $\overline{y}_{\Delta t=10}$ over a time period of 10 years. To this end, the 'simulated mortality' $\overline{p}_{\Delta t} = \sum p_{i,\Delta t}/n$ and the 'observed mortality' $\overline{y}_{\Delta t} = \sum y_i/n$ were averaged for observations and predictions with the same mortality period length Δt. To render the values comparable, mean simulated and observed mortality rates were re-scaled to 10 years before calculating the overall mean. Taking the example of the 'simulated mortality', this can be formulated as

$$\overline{p}_{\Delta t=10} = 1 - \left(1 - \overline{p}_{\Delta t}\right)^{\frac{10}{\Delta t}}$$

Model selection

To assess the potential benefit of including environmental and stand characteristics in a mortality model while avoiding over-fitting, a 10-fold cross-validation scheme and the 'one standard error rule' (Breiman *et al.*, 1984; Hastie *et al.*, 2001) were applied for model selection. A stratified sampling scheme was employed in each fold to achieve roughly the original proportion of dead vs. living trees. Brier score (*BS*) values per fold were used to estimate the respective mean (*meanBS*) and standard error (*seBS*). To achieve robust estimates, the 10-fold cross-validation was repeated 20 times and *meanBS* and *seBS* were averaged, as suggested by De'ath and Fabricius (2000).

A basic model comprising log(*DBH*), logst(*relBAI*) and their interaction was compared with more sophisticated models, each additionally including one environmental or stand characteristic and its interaction with *relBAI*. For every additional covariate, the transformation (log/logst, square root or none, as applicable) was chosen that resulted in lowest *meanBS*. Environmental and stand characteristics were retained in the model if the corresponding *BS* distribution fulfilled the condition ($meanBS_{add} + seBS_{add}) < meanBS_{basic}$ with BS_{add} and BS_{basic} denoting the *BS* of the model with and without an additional covariate, respectively (Breiman *et al.*, 1984).

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4

How to kill a tree – Empirical mortality models for eighteen species and their performance in a dynamic forest model

In review as:

Hülsmann L[1,2], Bugmann H[2], Cailleret M[2,3], Brang P[1] How to kill a tree – Empirical mortality models for eighteen species and their performance in a dynamic forest model. Ecological Applications.

[1] Research Unit Forest Resources and Management, WSL Swiss Federal Institute of Forest, Snow and Landscape Research, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

[2] Forest Ecology, Institute of Terrestrial Ecosystems, ETH Zurich, Universitätstrasse 16, 8092 Zurich, Switzerland

[3] Research Unit Forest Dynamics, WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

Abstract

Dynamic Vegetation Models (DVMs) are suitable for simulating forest succession and species range dynamics under current and future conditions based on mathematical representations of the three key processes regeneration, growth and mortality. However, mortality formulations in DVMs are typically coarse and often lack an empirical basis, which increases the uncertainty of projections of future forest dynamics and hinders their use for developing adaptation strategies to climate change. Thus, sound tree mortality models are highly needed. We developed parsimonious, species-specific mortality models for 18 European tree species using > 90 000 records from inventories in Swiss and German strict forest reserves along a considerable environmental gradient. We comprehensively evaluated model performance and incorporated the new mortality functions in the dynamic forest model ForClim. Tree mortality was successfully predicted by tree size and growth. Only a few species required additional covariates in their final model to consider aspects of stand structure or climate. The relationships between mortality and its predictors reflect the indirect influences of resource availability and tree vitality, which are further shaped by species-specific attributes such as lifespan, shade and drought tolerance. Considering that the behavior of the models was biologically meaningful, and that their performance was reasonably high and not impacted by changes in the sampling design, we suggest that the mortality algorithms developed here are suitable for implementation and evaluation in DVMs. In the DVM ForClim, the new mortality functions resulted in simulations of stand basal area and species composition that were generally close to historical observations. However, ForClim performance was poorer than when using the original, coarse mortality formulation. The difficulties of simulating stand structure and species composition, which were most evident for Fagus sylvatica L. and in long-term simulations, resulted from feedbacks between simulated growth and mortality as well as from extrapolation to very small and very large trees. Growth and mortality processes and their species-specific differences should thus be revisited jointly, with a particular focus on small and very large trees in relation to their shade tolerance.

Key words

Dynamic Vegetation Models, Empirical mortality models, European tree species, Forest inventory data, Forest reserves, Generalized logistic regression, Individual tree mortality, Tree growth

Introduction

Tree mortality – one of the key demographic processes that shape forest ecosystems – has significant short- and long-term implications for a wide range of forest ecosystem services (Van Mantgem *et al.*, 2009; Millar & Stephenson, 2015). Management for ecosystem services therefore requires a good understanding of tree death and of its determinants, in particular since drought-induced dieback and other mortality hazards are likely to increase in response to future climate change (Allen *et al.*, 2010; Steinkamp *et al.*, 2015). Tree mortality is a highly complex and multifactorial process, and the scientific community still faces difficulties to understand the underlying mechanisms (Sala *et al.*, 2010) and predict mortality from the individual to the regional level (Weiskittel *et al.*, 2011; Adams *et al.*, 2013; McDowell *et al.*, 2013; Meir *et al.*, 2015).

This difficulty has implications for predictive mortality functions as an essential component of forest simulation models, which are used for short-term forest planning (growth-and-yield models; Hasenauer, 2006) and for assessing the long-term consequences of climate change (Dynamic Vegetation Models DVM; Bugmann, 2001; Smith *et al.*, 2001; Friend *et al.*, 2014). While much effort has been devoted to accurately predict tree growth, mortality formulations in DVMs are typically coarse and usually lack an empirical basis (Loehle & LeBlanc, 1996; Keane *et al.*, 2001) or robust mechanistic foundation (Allen *et al.*, 2015). The poor representation of tree mortality in DVMs has critical consequences for the accuracy of their predictions, and thus for the reliability of their projections (Keane *et al.*, 2001; Reyer *et al.*, 2015), which may impede the timely initiation of measures that maintain ecosystem services (De Groot *et al.*, 2002; Temperli *et al.*, 2012).

Besides theoretical ('data-free') and physiological process-based approaches (cf. Wunder *et al.* (2006), Weiskittel *et al.* (2011) and Meir *et al.* (2015) for respective advantages and drawbacks), empirical mortality models have been suggested as a valid and pragmatic alternative (Adams *et al.*, 2013). Such empirical mortality models are not only highly valuable for the reliable simulation of future forest dynamics, but also to improve our understanding of the mortality process (Cailleret *et al.*, 2016). Among other approaches, tree size and radial stem growth can be used as predictors of tree death (Cailleret *et al.*, 2017; Hülsmann *et al.*, 2017), which is supported by the assumption that the dimensions of a tree – typically expressed via its stem diameter – are a proxy for the access to resources and constraints on the hydraulic system (Grote *et al.*, 2016), and that radial growth provides an indication of individual-tree vitality (Harcombe, 1987; Dobbertin, 2005).

Growth-based mortality models have been fitted using forest inventory (Ruiz-Benito *et al.*, 2013) or dendrochronological data (Gillner *et al.*, 2013) and a variety of methodological approaches (Hawkes, 2000; Weiskittel *et al.*, 2011; Cailleret *et al.*, 2016). However, most of them (1) do not adequately consider species differences for a wide range of species, (2) are not sensitive to the variation in climate and site conditions, and (3) have not been implemented in DVMs and validated in this context (cf. Larocque *et al.*, 2011; Bircher *et al.*, 2015). The obstacles to achieve this arise from the fact that mortality of individuals having outgrown the seedling stage is rare and highly variable in space and time (Eid & Tuhus, 2001), and there is a general scarcity of data for describing long-term processes (Bugmann, 1996b; Hawkes, 2000).

In DVMs, tree regeneration, growth and mortality are modeled based on life history strategies, e.g. shade and drought tolerance and longevity (Bugmann, 1994), of individual tree species or of Plant Functional Types (PFTs; Bugmann, 1996a; Wullschleger *et al.*, 2014). By grouping species with similar ecological characteristics to PFTs, mortality models can be calibrated and validated even for rare species. Yet, modeling approaches are mostly limited to one or few species (Holzwarth et al. 2013, Neuner et al. 2015; but see Wunder et al. 2008). Thus, there is no comprehensive evidence that life history strategies determine the mortality patterns of tree species, and that PFTs are a useful and robust concept.

Moreover, only few studies have accounted for the spatial and temporal variability in size- and growth-mortality relationships (Wunder *et al.*, 2008; Dietze & Moorcroft, 2011) by including additional covariates in mortality models (but see Condés & Del Río, 2015). Climate or stand characteristics may be required as driving factors of mortality under conditions of drought or high competition, since they are only partly reflected in size or growth variables (Rowland *et al.*, 2015). However, datasets with a representative sampling along major environmental gradients and over long time periods that allow for a systematic analysis of environmental influences on the relationship between tree size, growth and mortality are rare.

To verify the suitability of growth-based empirical mortality functions for DVMs, their predictive performance, i.e. the accuracy of a model when applied to new data, should be evaluated using cross-validation approaches or by validation with independent external data (cf. Hülsmann *et al.*, 2016). Subsequently, such mortality models should be incorporated in DVMs, a step that is made only rarely (but see Wyckoff & Clark, 2002; Wernsdörfer *et al.*, 2008; Larocque *et al.*, 2011; Bircher *et al.*, 2015). Thus, a comprehensive and sound assessment of empirical mortality models in DVMs is still lacking, and it remains unclear whether more empiricism in mortality modeling would actually advance the quality of simulations from DVMs.

Thus, the overall objectives of this study were to develop parsimonious mortality models for a large set of European tree species, to comprehensively evaluate their performance, and to incorporate them in a specific DVM (ForClim; cf. Bugmann, 1996b). To this end, we used extensive inventory data from strict forest reserves in Switzerland and Germany along a large environmental gradient. We followed the approach of model calibration and evaluation that was established and tested for *Fagus sylvatica* L. by Hülsmann *et al.* (2016). Specifically, we addressed three main questions: (1) Can life history strategies such as lifespan and stress tolerance be used to group tree species into reasonable PFTs that account for species differences in mortality? (2) How successful are mortality models that are based on size and growth *alone* compared to models that include further climate or stand characteristics in accurately predicting tree mortality? (3) How do the new mortality functions perform when embedded in a DVM?

Material and methods

Study areas and inventory data

We used inventory data from 54 strict forests reserves in Switzerland and Lower Saxony / Germany to develop the mortality models (cf. Brang *et al.*, 2011; Meyer *et al.*, 2015). Measurements had been conducted repeatedly on up to 14 permanent plots per reserve for up to 60 years with re-measurement intervals of 4 - 27 years. The permanent plots vary in size between 0.03 and 3.47 ha. The inventories provide diameter measurements at breast height (*DBH*) and information on the species and status (alive or dead) of trees with *DBH* ≥ 4 cm for Switzerland and ≥ 7 cm for Germany. As ForClim does not explicitly simulate natural large-scale disturbances, only plots without substantial wind-throw, fire or bark beetle events at the stand scale were used to derive the mortality models. Mortality in the remaining stands was rather low, with a mean annual mortality rate of 1.5 % and strong variation between plots from 0 to 6.5 % (assessed for trees of all species with *DBH* ≥ 7 cm).

We only used data from permanent plots with at least 20 trees per species to obtain reliable plot-level mortality rates, and selected tree species occurring on at least 10 plots to cover sufficient ecological gradients. This led to a dataset of 197 permanent plots and 18 tree or shrub species: *Abies alba* Mill., *Acer campestre* L., *Acer pseudoplatanus* L., *Alnus incana* Moench., *Betula pendula* Roth, *Carpinus betulus* L., *Cornus mas* L., *Corylus avellana* L., *Fagus sylvatica*, *Fraxinus excelsior* L., *Picea abies* (L.) Karst, *Pinus mugo* Turra, *Pinus sylvestris* L., *Quercus pubescens* Willd., *Quercus* spp. (*Q. petraea* Liebl. and *Q. robur* L.; not properly differentiated in the Swiss inventories), *Sorbus aria* Crantz, *Tilia cordata* Mill. and *Ulmus glabra* Huds. (Table 1).

Table 1 Number of records per tree species. Numbers are given for the total dataset, per country and for those that resulted in tree death. Additionally, the number of reserves and permanent plots that are covered in the data of each species are indicated. Note: *Quercus* spp. refers to both *Q. petraea* and *Q. robur*.

Species	total	Germany	Switzerland	dead	Reserves	Permanent plots
Abies alba	7140	0	7140	1147	7	31
Acer campestre	1183	0	1183	256	5	19
Acer pseudoplatanus	1399	24	1375	255	12	26
Alnus incana	1252	0	1252	734	5	11
Betula pendula	1847	300	1547	723	7	14
Carpinus betulus	5789	1637	4152	1283	19	28
Cornus mas	1123	0	1123	215	1	10
Corylus avellana	1427	0	1427	739	8	14
Fagus sylvatica	26 645	6899	19 746	4018	40	118
Fraxinus excelsior	7645	142	7503	1715	19	52
Picea abies	12 965	458	12 507	2209	20	59
Pinus mugo	7376	0	7376	1250	4	21
Pinus sylvestris	2925	317	2608	519	10	24
Quercus pubescens	2968	0	2968	429	2	15
Quercus spp.	7250	832	6418	1536	22	48
Sorbus aria	1546	0	1546	492	8	23
Tilia cordata	1911	0	1911	344	8	16
Ulmus glabra	631	20	611	137	4	11
All	93 022	10 629	82 393	18 001	54	197

Mortality information and tree characteristics

We considered tree size and growth as key indicators for mortality risk (Monserud, 1976). Radial stem growth between the first and second inventory and *DBH* at the second inventory were used to predict tree status (alive or dead) at the third inventory. To this end, the annual relative basal area increment (*relBAI*$_i$, cf. Bigler & Bugmann, 2004) was calculated as the compound annual growth rate of the trees basal area (BA_i) using

$$relBAI_i = \left(\frac{BA_{i,2nd}}{BA_{i,1st}}\right)^{\frac{1}{\Delta t}} - 1 \qquad \text{eqn 1}$$

with Δt denoting the number of years of the growth period. Several sets of three inventories per tree were used if more than three inventories were available (45.0 %). Thus, 26.5 % of the trees appeared more than once in the dataset (for verification cf. Hülsmann *et al.*, 2016).

To improve the relationship between the explanatory variables and mortality, suitable transformations were applied (cf. Mosteller & Tukey, 1977), i.e., log(*DBH*) and logst(*relBAI*). The latter is a modified transformation based on the common logarithm that is applicable even to those 8.8 % of the records with *relBAI* = 0 (Stahel, 2015; cf. Appendix B).

Climate and stand characteristics

We included additional climate and stand characteristics in the mortality models to address spatial and temporal differences in mortality rates between permanent plots and inventories that cannot be explained by changes in growth rates alone (cf. Table S1, see Appendix A for all additional Tables and Figures). To this end, mean annual precipitation sum (*P*) and mean annual air temperature (*mT*) were calculated between the second and the third inventory (for their derivation cf. Appendix B).

As a proxy for stand age and structural complexity, the mean and the interquartile range of *DBH* were calculated at the permanent plot level (*mDBH*, *iqrDBH*). To account for stand density, basal area (*BA*) and the number of trees (*N*) per hectare were considered. These stand characteristics were calculated for the second inventory based on all living trees ≥ 7 cm. We did not further expand the set of climate and stand characteristics considered to keep the models simple and thus also applicable in DVMs.

Mortality models

Generalized logistic regression (Monserud, 1976; Weiskittel *et al.*, 2011; Yang & Huang, 2013) was used to model mortality probability. This was necessary to account for the unequal re-measurement intervals in the inventory data. The annual mortality probability of tree i ($p_{i,\Delta t=1}$) was defined as

$$p_{i,\Delta t=1} = logit^{-1}(X_i\beta) = \frac{\exp(X_i\beta)}{1+\exp(X_i\beta)} \qquad \text{eqn 2}$$

with X_i denoting the design matrix of the linear predictor and β the respective parameter vector. The annual probability was scaled to the length of the respective mortality period of Δt years using

$$p_{i,\Delta t} = 1 - \left(1 - p_{i,\Delta t=1}\right)^{\Delta t} \qquad \text{eqn 3}$$

and then fitted against the observed status of the tree (y_i; 1 = dead, 0 = alive) using maximum-likelihood estimation for the parameters of β. Standard errors, confidence intervals and p-values of the parameter estimates were derived using the Fisher information based on the Hessian matrix (cf. Hülsmann *et al.*, 2016).

Model selection and performance criteria

In a first step, the most promising climate or stand characteristic and its most suitable transformation (log, square root or none) were identified for each species. To this end, covariates were included in highly flexible models to capture linear, non-linear and interacting influences of log(*DBH*) and logst(*relBAI*) on mortality (cf. Table 2, Formula C12 with different transformations of the climate and stand characteristics). We selected the covariate that resulted in the smallest Brier Score (*BS*). *BS* corresponds to the mean squared error of the model defined as

$$BS = \frac{1}{n}\sum_{i=1}^{n}\left(p_{i,\Delta t} - y_i\right)^2 \qquad \text{eqn 4}$$

and ranges between 0 and 1, with low values indicating good model calibration and discrimination, i.e., correct mortality rates and attribution of dead/alive status (cf. Harrell, 2015). *BS* does, however, not allow for the comparison of models based on different datasets since it depends on the overall mortality rate that varies between species (Steyerberg *et al.*, 2010).

In a second step, the final model was selected from a large set of model formulae (cf. Table 2) with varying complexity and flexibility that are based on the terms log(*DBH*), logst(*relBAI*), their interaction and the respective quadratic terms (Formulae 1-12). These models were analyzed without an additional covariate (Formulae A1-12), with the most promising climate or stand characteristic (B1-12), and in interaction with logst(*relBAI*) (C3-12). To this end, we calculated *BS* in repeated 10-fold cross-validation and applied the 'one standard error rule' to avoid overfitting (cf. Appendix B for details, Breiman *et al.*, 1984; Hastie *et al.*, 2001). For models that included an additional climate or stand characteristic, an alternative model without that covariate was derived to compare its performance with the respective full model. These were selected by applying the 'one standard error rule' to Formulae A1-12 only.

Table 2 Model formulae considered during model selection and their degree of complexity. Model numbers 1-12 in the first column refer to formulae with increasing flexibility of the influence of the tree covariates *DBH* and *relBAI*. The letters A-C refer to the use of additional climate or stand characteristics: A = without an additional characteristic, B = with an additional characteristic, C = with an additional characteristic and its interaction with logst(*relBAI*). The numbers of 1-28 in columns A-C indicate increasing complexity of the formulae and were used to select the most parsimonious models during 10-fold cross-validation (cf. Appendix B). The complexity of a model was assigned considering the number of predictors and their flexibility (quadratic terms, interactions). Note that the additional characteristic was selected separately for each species (cf. Table S4).

		Use of additional climate or stand characteristics		
Number	**Formula**	**A**	**B**	**C**
1	$\log(DBH)$	1	11	
2	$\log(DBH) + (\log(DBH))^2$	2	12	
3	$\mathrm{logst}(relBAI)$	1	11	21
4	$\mathrm{logst}(relBAI) + (\mathrm{logst}(relBAI))^2$	2	12	22
5	$\log(DBH) + \mathrm{logst}(relBAI)$	3	13	23
6	$\log(DBH) + (\log(DBH))^2 + \mathrm{logst}(relBAI)$	4	14	24
7	$\log(DBH) + \mathrm{logst}(relBAI) + (\mathrm{logst}(relBAI))^2$	4	14	24
8	$\log(DBH) + (\log(DBH))^2 + \mathrm{logst}(relBAI) + (\mathrm{logst}(relBAI))^2$	5	15	25
9	$\log(DBH) * \mathrm{logst}(relBAI)$	6	16	26
10	$\log(DBH) * \mathrm{logst}(relBAI) + (\log(DBH))^2$	7	17	27
11	$\log(DBH) * \mathrm{logst}(relBAI) + (\mathrm{logst}(relBAI))^2$	7	17	27
12	$\log(DBH) * \mathrm{logst}(relBAI) + (\log(DBH))^2 + (\mathrm{logst}(relBAI))^2$	8	18	28

Several performance criteria were reported to take into account that calibration and discrimination are not necessarily correlated (Bravo-Oviedo *et al.*, 2006). In addition to *BS*, the Area Under the receiver operating characteristic Curve (*AUC*) was calculated, which is a threshold-independent measure of classification accuracy. Following Hosmer and Lemeshow (2000), the discriminative ability is rated as acceptable ($0.7 \leq AUC < 0.8$), excellent ($0.8 \leq AUC < 0.9$) or outstanding ($AUC \geq 0.9$).

Since all data were used for model development, no external validation of the models using independent data could be carried out. However, to correct for overfitting and assess the predictive behavior in external application, i.e., when applied to new data from the same domain, BS and AUC from cross-validation were reported (cf. Appendix B). Furthermore, AUC was calculated for diameter classes to assess the calibration success of the models with respect to tree size.

Commonly, performance criteria used in mortality studies do not convey an intuitive expectation of the predictive behavior of mortality models at the level of forest stands. Therefore, we selected an additional performance criterion that facilitates the evaluation of model performance with respect to the application in DVMs. We defined the prediction bias p_{bias} as the difference of the mean predicted annual mortality probability ('simulated mortality') $\overline{p}_{\Delta t=1}$ and the mean annual mortality rate ('observed mortality') $\overline{y}_{\Delta t=1}$ calculated at the level of single inventories of permanent plots (cf. Appendix B) and reported the mean absolute deviation (mad) of p_{bias}. This allowed us to quantify the variation in prediction accuracy, i.e., how well the models can deal with the high variability of mortality rates and patterns in space and time (Wunder *et al.*, 2008; Dietze & Moorcroft, 2011). Observed variability and $mad\ p_{bias}$ increase with increasing mortality rates. Therefore, we additionally calculated the respective relative value ($rmad\ p_{bias}$), i.e., the ratio of $mad\ p_{bias}$ and the observed annual mortality rate $\overline{y}_{\Delta t=1}$. Both values were used to evaluate the models with respect to their ability to predict correct mortality rates in space and time.

Model calibration and evaluation was performed with R (R Core Team 2015, R Foundation for Statistical Computing. Vienna, Austria). The function *logst()* from the package *regr0* (Version 1.0-4/r46, 2015) was used for the *relBAI* transformation. The function *optim()* and the *BFGS* method were applied for maximum-likelihood estimation. AUC was calculated using a modified version of the *auc()* function from the package *SDMTools* (Version 1.1-221, 2014) to allow for values below 0.5, which is necessary to calculate AUC in cross-validation.

Implementation of inventory-based mortality models in ForClim

Model description

To examine the performance and behavior of the new mortality functions in DVMs, we used the climate-sensitive forest gap model ForClim, which simulates the dynamics of forest stands on short and long time scales (Bugmann, 1996b). Establishment, growth and mortality for cohorts of individual trees are simulated on independent patches (~ 800 m^2) at an annual resolution based on species-specific parameters (e.g., shade and drought tolerance), environmental conditions (light availability, temperature, soil nitrogen and water availability) and tree characteristics (cf. Bugmann, 1996b; Didion *et al.*, 2011; Rasche *et al.*, 2012).

In the latest model version, ForClim 3.3 (Mina *et al.*, 2015), tree mortality is modeled as a combination of a constant 'background' mortality that depends on the species-specific maximum age and a stress-induced mortality that is activated if the annual diameter increment is lower than a threshold (3 mm or 10 % of the species-specific maximum growth rate at a given tree size) for more than two consecutive years. Mortality is modeled individually for each tree of a cohort based on a stochastic approach that results in tree death if a uniformly distributed random number between 0 and 1 is below the annual mortality probability. A more detailed description of the mortality function is provided in Bircher *et al.* (2015).

This mortality formulation was replaced by the new inventory-based models (IM) without environmental covariates, i.e., alternative models, based on tree size and growth only. The models were implemented following two approaches: (1) with mean parameter estimates (IM_mean) and (2) by randomly sampling the parameters using their mean and standard error to account for the uncertainty in model estimates (IM_sd, assuming a normal distribution of the parameters).

The mortality functions were applied to all trees irrespective of their *DBH* although this led to extrapolation at least for the small trees (initial *DBH* of trees in ForClim is 1.27 cm whereas the calipering threshold in the inventories is 4 cm or more). Since for some species in the validation data no mortality function could be developed, we used the models from species of the same genus: the model of *Acer pseudoplatanus* for *A. platanoides*, *Alnus incana* for *A. glutinosa* and *A. viridis*, *Sorbus aria* for *S. aucuparia* and *Tilia cordata* for *T. platyphyllos*. Simulation results for these species were jointly reported (e.g., *Tilia* spp.). Species for which no mortality model could be developed and that were present in minor abundance were excluded from the simulations (e.g., *Populus nigra*, *Taxus baccata*).

Simulation setup and model validation

We ran short- and long-term simulations to assess the performance and behavior of the two new mortality functions (IM_mean, IM_sd) and to compare them with the original model version (ForClim 3.3), as follows:

Short-term simulations. To validate the new mortality functions in ForClim, we simulated historical forest dynamics based on past climate data (cf. Appendix B) and compared the results against inventory measurements. To this end, permanent plots were selected from the Swiss forest reserves according to the following criteria: (1) inventory data should cover at least a period of 35 years, (2) plot size had to exceed 0.2 ha to ensure a representative structure and composition of the forest, and (3) recent dynamics had to be unaffected by severe natural disturbances, which are not accounted for in the model. We ended up with 28 permanent plots located in 13 forest reserves (Table S2) that were all part of the calibration dataset. ForClim was initialized with single-tree data (species, *DBH*) from the first available inventory of each permanent plot. As spatial information about tree positions on the plots was not available, trees were allocated randomly and evenly to an initial set of patches, each with a size of 800 m^2 (Wehrli *et al.*, 2005). Depending on the ratio of permanent plot area and patch size (Table S2), this resulted in the direct initialization of 2 to 44 patches. To average over the stochasticity across patches, the initial set of patches was replicated to 200. For evaluating the goodness-of-fit of the historical runs, we compared simulated and measured stand- and species-specific *BA* at the last inventory and the cumulative number of dead trees (N_{dead}) per hectare over the whole period. The root mean square error (*RMSE*) as well as the relative bias (*rbias*) were reported for both criteria separately per species and permanent plot.

Long-term simulations. As model validation is constrained by the short length of the empirical data series, we also simulated Potential Natural Vegetation (PNV), i.e., the species composition expected in a pseudo-equilibrium state in the absence of anthropogenic influences (Ellenberg, 2009), along a well-studied environmental gradient in Switzerland (cf. Bugmann & Solomon, 2000). Starting from bare ground, forest dynamics were simulated for 1500 years, and forest structure and composition at the end of the simulation were examined qualitatively for their plausibility (Rasche *et al.*, 2012). Since we were not able to calibrate a mortality model for *Pinus cembra* L., the sites Grande Dixence and Bever were excluded.

Results

Size and growth influences on mortality

Formulae of the final models varied between tree species with respect to the flexibility of the covariates *DBH* and *relBAI* (Table S3). Nevertheless, all models except for those of *Cornus mas*, *Pinus mugo* and *Ulmus glabra*, which were based on tree growth alone (Formulae 3 and 4), included both explanatory variables. Most common was Formula 7 with medium complexity and the terms log(*DBH*) + logst(*relBAI*) + $(\text{logst}(relBAI))^2$, which was selected for ten species. Mortality of three species was best predicted using Formula 5, including only *DBH* and *relBAI* without any quadratic term or interaction. Only for *Tilia cordata* (Formula 9) and *Fraxinus excelsior* (Formula 11), models were more complex and included also the interaction between log(*DBH*) and logst(*relBAI*).

In spite of the different model formulae, the overall pattern of simulated mortality with respect to the main predictors was very similar for most species, i.e., mortality risk decreased with increasing tree size and growth (Fig. 1). However, the models differed concerning (1) the respective influence of size and growth as characterized by the steepness of the slope of mortality over *DBH* and *relBAI*, and (2) the overall level of mortality probabilities. Four main patterns became evident: (1) low overall mortality and a slight effect of *DBH* and *relBAI*: *Abies alba*, *Cornus mas*, *Fagus sylvatica*, *Picea abies*, *Pinus mugo*, *Tilia cordata* and *Ulmus glabra*; (2) high overall mortality, also in large trees, and a strong growth influence on mortality: *Alnus incana*, *Betula pendula*, *Corylus avellana* and *Sorbus aria*; (3) strong impacts of *DBH* and *relBAI* on mortality: *Acer pseudoplatanus*, *Pinus sylvestris*, *Quercus pubescens* and *Quercus* spp.; and (4) intermediate impacts of *DBH* and *relBAI* on mortality: *Acer campestre*, *Carpinus betulus* and *Fraxinus excelsior*.

None of the species-specific models included a quadratic term for *DBH*, which would suggest a U-shaped mortality pattern, i.e., higher mortality for both small and larger trees. The quadratic term of logst(*relBAI*), which was included in 12 of the 18 final models, dominantly resulted in a pronounced decrease of mortality probability with increasing growth. For *Alnus incana*, *Fraxinus excelsior* and *Sorbus aria*, the quadratic growth term decreased the predicted mortality probability of trees with very slow growth ($relBAI < 0.002$), but did not modify the overall positive effect of growth on survival.

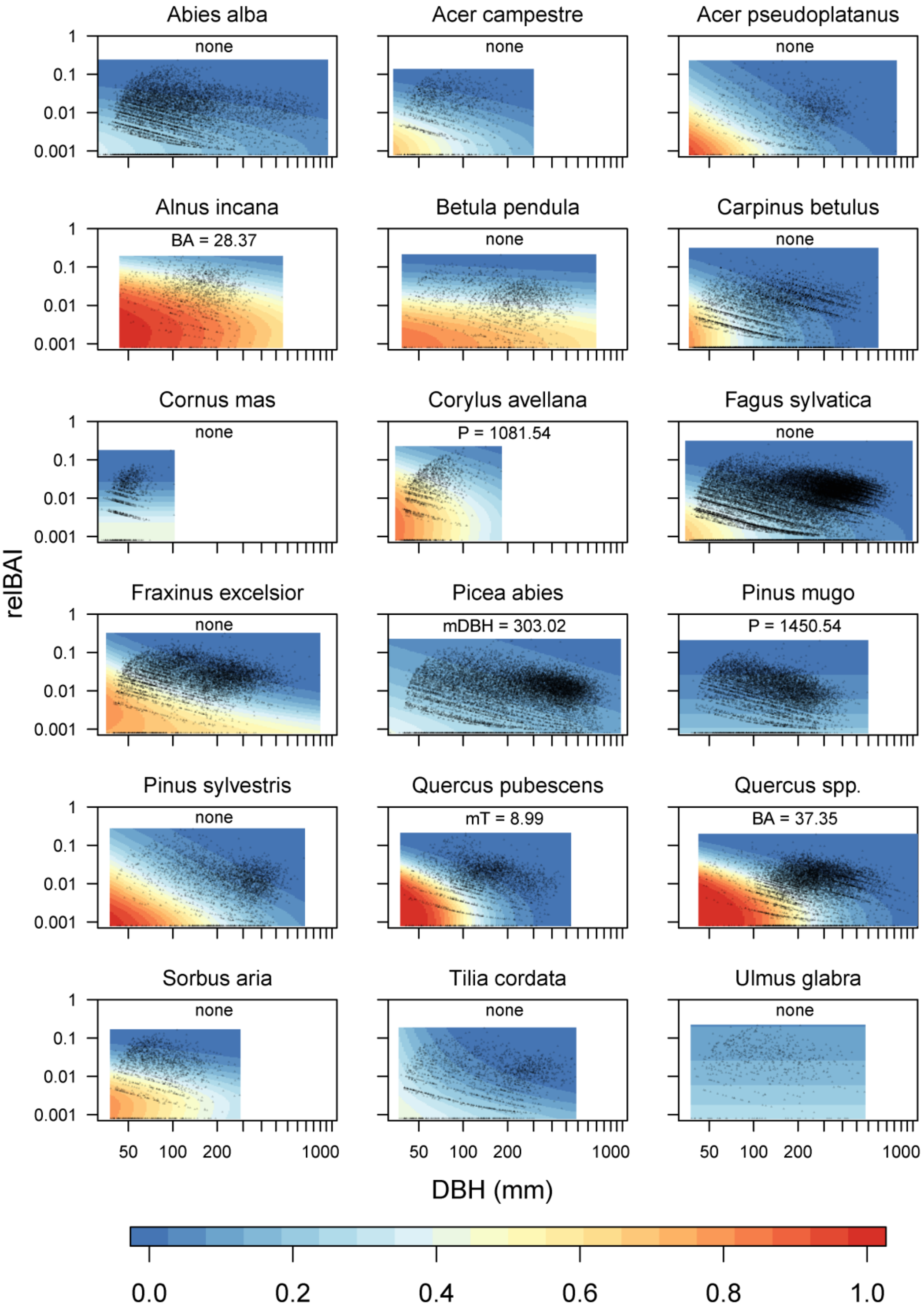

Fig. 1 Prediction maps of ten-year mortality probability as a function of *DBH* and *relBAI*. In accordance with the variable transformations applied in the models, logarithmic scales are used for plotting, i.e., natural logarithm for *DBH* and the common logarithm for *relBAI* (cf. logst transformation, Stahel, 2015). The interval $\Delta t = 10$ years for the mortality probability was selected to increase the contrast of the typically very low annual mortality probabilities. Predictions of models that included an additional climate or stand characteristic are shown for the additional covariate fixed at its medium value as indicated in the plot). Observations of *DBH* and *relBAI* are shown with black triangles. No-growth observations are located at the lower limit of the predictive map defined by back-transformed logst(0), i.e., 0.0008029.

Climate and stand influences on mortality

From the set of the most promising climate or stand characteristics selected for each species (cf. Table S4), only a few remained in the final models (Table S3). Additional covariates considerably improved the models of *Alnus incana* (improved by *BA*), *Corylus avellana* (*P*), *Picea abies* (*mDBH*), *Pinus mugo* (*P*), *Quercus pubescens* (*mT*) and *Quercus* spp. (*BA*). The two stand variables (*BA* and *mDBH*) were positively correlated with mortality (cf. Fig. S1). The effect of precipitation (*P*) was inconsistent. At high *P*, mortality probability was lower for *Pinus mugo* but higher for *Corylus avellana*. Higher mean temperature (*mT*) increased mortality of *Quercus pubescens*. None of the additional covariates that remained in the models required an interaction term with tree growth. Thus, the general relationship between *relBAI* and mortality was not altered.

Alternative models without the additional covariate were based on the same or a similar formula as the full model (cf. Table S5). Thus, they indicate a similar complexity and shape of the relationship between *DBH*, *relBAI* and mortality (cf. Fig. S2). For *Corylus avellana*, *Picea abies* and *Quercus pubescens* a formula with lower flexibility was selected for the alternative model, which resulted in size-independent mortality for *Picea abies*.

Calibration performance

Discrimination accuracy (*AUC*) was high for most species (Table 3). While the ability of the models to correctly identify tree status was acceptable for seven species ($0.7 \leq AUC < 0.8$), it was even excellent for nine species ($0.8 \leq AUC < 0.9$). Only the models of *Picea abies* and *Ulmus glabra* had no discriminative ability. The over-optimism assessed via cross-validation was low for all species, i.e., the relative difference between cross-validation *BS* and apparent *BS* was < 1 % of apparent *BS*, and cross-validation *AUC* was only < 0.003 lower than apparent *AUC* (Table 3).

AUC plotted as a function of *DBH* revealed that discrimination was not equally successful across tree size (Fig. S3). Mostly, *AUC* decreased with increasing *DBH*, indicating that the models had less or even no discriminative power for larger trees (cf. *Acer pseudoplatanus*, *Fagus sylvatica*, *Picea abies*, *Pinus mugo*, *Quercus pubescens*, *Quercus* spp. and *Ulmus glabra*). In contrast, an increasing *AUC* trend with tree size was identified for *Cornus mas* and *Corylus avellana*. The models of the remaining species either had the best *AUC* for mediumsized trees (cf. *Acer campestre* and *Fraxinus excelsior*) or achieved a constant discrimination over the considered *DBH* range.

Table 3 Performance criteria of the calibrated models. Brier Score (*BS*) and Area Under the receiver operating characteristic Curve (*AUC*) were calculated for the entire calibration dataset and during repeated 10-fold cross-validation (CV) to assess the predictive ability of the mortality models. To quantify the variation in prediction accuracy, the mean absolute deviation (*mad*) of the prediction bias (p_{bias}) defined as the difference of the mean predicted annual mortality probability ($\bar{\boldsymbol{p}}_{\Delta t=1}$) and the mean annual mortality rate ($\bar{\boldsymbol{y}}_{\Delta t=1}$) was calculated at the level of single inventories of permanent plots (cf. Appendix B). Observed variability and *mad* p_{bias} increase with increasing mortality rates. Therefore, we additionally calculated the respective relative value (*rmad* p_{bias}), i.e., the ratio of *mad* p_{bias} and the observed annual mortality rate ($\bar{\boldsymbol{y}}_{\Delta t=1}$). Both values were used to evaluate the models with respect to their ability to predict correct mortality rates in space and time. For species for which the final model included an additional covariate (highlighted in grey), also the performance of the best model without an additional covariate (A1-12) is given (alternative models).

Species	**Formula**	**Covariate**	***BS***	***BS* CV**	***AUC***	***AUC* CV**	$\bar{y}_{\Delta t=1}$ **(%)**	***mad* p_{bias} (%)**	***rmad* p_{bias}**
Abies alba	A7	-	0.1233	0.1235	0.721	0.720	1.3	0.7	0.53
Acer campestre	A7	-	0.1310	0.1323	0.815	0.813	2.2	1.5	0.68
Acer pseudoplatanus	A5	-	0.1114	0.1121	0.847	0.846	1.7	0.8	0.48
Alnus incana	B7	*BA*	0.1828	0.1843	0.790	0.788	9.1	2.7	0.30
Alnus incana	A7	-	0.1869	0.1881	0.778	0.777	9.1	4.6	0.51
Betula pendula	A7	-	0.1878	0.1886	0.766	0.765	4.5	2.3	0.51
Carpinus betulus	A7	-	0.1335	0.1337	0.806	0.806	2.2	1.3	0.59
Cornus mas	A4	-	0.1270	0.1280	0.790	0.789	1.8	0.6	0.32
Corylus avellana	B7	*P*	0.2024	0.2037	0.753	0.751	6.7	1.6	0.24
Corylus avellana	A5	-	0.2144	0.2152	0.725	0.724	6.7	3.2	0.48
Fagus sylvatica	A7	-	0.1032	0.1032	0.814	0.814	1.4	0.5	0.36
Fraxinus excelsior	A11	-	0.1326	0.1328	0.813	0.813	2.2	1.1	0.48
Picea abies	B5	*mDBH*	0.1348	0.1349	0.659	0.658	1.5	1.1	0.72
Picea abies	A3	-	0.1371	0.1372	0.616	0.616	1.5	1.0	0.68
Pinus mugo	B3	*P*	0.1217	0.1218	0.766	0.766	1.2	0.5	0.44
Pinus mugo	A3	-	0.1266	0.1267	0.720	0.720	1.2	1.0	0.84
Pinus sylvestris	A5	-	0.1128	0.1132	0.815	0.814	1.7	0.6	0.36
Quercus pubescens	B7	*mT*	0.0777	0.0782	0.892	0.891	1.6	0.4	0.22
Quercus pubescens	A5	-	0.0840	0.0843	0.884	0.884	1.6	0.7	0.46
Quercus spp.	B7	*BA*	0.1123	0.1125	0.842	0.842	2.0	1.0	0.51
Quercus spp.	A7	-	0.1150	0.1152	0.838	0.838	2.0	1.1	0.56
Sorbus aria	A7	-	0.1563	0.1573	0.821	0.821	3.3	1.8	0.55
Tilia cordata	A9	-	0.1233	0.1240	0.798	0.796	1.5	1.3	0.89
Ulmus glabra	A3	-	0.1658	0.1672	0.616	0.614	1.8	1.0	0.53

The variation of the prediction accuracy between sites and inventory periods, assessed as *rmad* p_{bias}, ranged between 0.22 and 0.89 (Table 3). Fairly large values resulted for *Acer campestre*, *Picea abies*, *Pinus mugo* and *Tilia cordata* (*rmad* $p_{bias} \geq 0.68$), while models of *Alnus incana, Cornus mas*, *Corylus avellana* and *Quercus pubescens* achieved lowest *rmad*

p_{bias} (≤ 0.32) and hence the most accurate prediction of mortality rates at the level of single inventories. The underlying values of *mad* p_{bias} indicate that the models estimate annual mortality rates at the level of single inventories with an average absolute bias of 0.4 to 4.6 % per year.

The alternative models that did not include additional covariates had reduced discriminative power, i.e., lower *AUC*, when compared to the corresponding full model (Table 3). Nevertheless, the reduction in *AUC* was small (< 0.03 except for *Picea abies* and *Pinus mugo*) and did not change the discriminative ability, as rated following Hosmer and Lemeshow (2000). However, the models' ability to accurately predict mortality rates in space and time was more severely affected when additional covariates were omitted. Models that included an additional covariate typically had a substantially lower *rmad* p_{bias} than the alternative models for the respective species. Only for *Picea abies*, *rmad* p_{bias} was not reduced by the additional covariate, which was in accordance with the poor discriminative ability of both model formulations of this species.

Implementation of inventory-based mortality models in ForClim

Short-term simulations

Compared with forest inventory data, the new model versions ForClim IM_mean and IM_sd performed slightly worse than ForClim 3.3 in predicting stand- and species-specific *BA* at the end of the historical runs (Fig. 2; Table 4; Table S6). Overall, the inventory-based models overestimated *BA*. Although *BA* of several species was too high, overestimation was particularly driven by *Fagus sylvatica* (*RMSE* > 11, *rbias* > 30 %) and occurred especially at permanent plots where this species dominates (e.g., Fürstenhalde and Weidwald; cf. Fig. 2; Table S6). *BA* was underestimated by the new mortality functions for *Alnus* spp., *Betula pendula*, *Corylus avellana*, *Fraxinus excelsior* and *Tilia* spp. (cf. Table 4). Accounting for uncertainty in model parameters resulted in pronounced underestimation of *BA*, so that the IM_mean approach achieved better *BA* performance than ForClim IM_sd. The reduction of *BA* caused by the random sampling of the parameters of the mortality formulation was especially strong for *Acer campestre*, *Carpinus betulus*, *Sorbus* spp. and *Tilia* spp. but negligible in the case of *Fagus sylvatica* (cf. Fig. 2, Table 4).

Table 4 Species-specific *RMSE* and *rbias* (%) of *BA* and N_{dead} simulated by the three ForClim versions 3.3, IM_mean and IM_sd at the last inventory of every permanent plot. For each species and variable of interest, the lowest *RMSE* and the *rbias* closest to zero were highlighted in bold. Trees with *DBH* < 4 cm were not considered.

Species	Basal area (*BA*)						Number of dead stems per ha (N_{dead})					
	3.3		IM_mean		IM_sd		3.3		IM_ mean		IM_sd	
	RMSE	*rbias*	*RMSE*	*rbias*	*RMSE*	*rbias*	*RMSE*	*rbias*	*RMSE*	*rbias*	*RMSE*	*rbias*
Abies alba	4.6	**7.2**	**4.2**	7.6	5.8	-14.3	4.0	-44.0	4.9	-56.3	**3.1**	**-33.9**
Acer campestre	0.1	241.5	0.1	311.7	**0.0**	**148.8**	**0.1**	**33.7**	0.2	-48.2	0.1	40.0
Acer pseudoplatanus	3.2	-31.2	**1.8**	**-16.0**	2.0	-23.5	1.3	-24.2	1.2	-32.9	**0.9**	**-16.0**
Alnus spp.	**0.3**	**-2.7**	0.5	-88.6	0.5	-97.2	0.6	**2.0**	0.2	-8.1	**0.2**	-10.4
Betula pendula	**1.4**	**-50.1**	1.8	-74.1	2.2	-99.0	**1.5**	-19.4	1.5	-16.3	1.6	**-12.5**
Carpinus betulus	3.0	-43.1	**1.3**	**9.3**	2.5	-38.2	**1.1**	29.0	1.3	-37.9	1.4	**26.3**
Corylus avellana	0.1	-94.4	**0.1**	**-94.3**	0.1	-97.8	0.6	-30.4	0.6	-31.9	**0.6**	**-28.6**
Fagus sylvatica	**6.4**	**5.7**	11.5	33.1	11.2	32.5	**3.0**	**-24.3**	5.2	-62.5	4.9	-58.3
Fraxinus excelsior	**2.8**	**-52.1**	3.6	-69.2	5.0	-95.1	1.0	-25.7	**0.9**	**-0.5**	1.4	44.0
Picea abies	**3.0**	**2.5**	3.2	-19.7	2.9	-17.4	1.6	-41.1	**1.4**	**-33.6**	1.4	-34.6
Pinus mugo	**2.1**	**171.9**	3.0	240.2	3.1	251.0	**3.1**	**-61.8**	3.7	-74.0	3.7	-74.2
Pinus sylvestris	3.4	**10.5**	**2.2**	24.3	2.3	17.7	**0.5**	**-23.2**	0.6	-30.2	0.5	-24.9
Quercus pubescens	**0.4**	**-95.9**	0.4	-100.0	0.4	-100.0	0.1	-22.8	**0.0**	**-21.0**	**0.0**	**-21.0**
Quercus spp.	2.7	24.3	**2.0**	**10.3**	2.8	-17.7	1.7	-66.3	1.0	-38.0	**0.4**	**-4.9**
Sorbus spp.	**0.3**	-53.1	0.5	**11.4**	0.4	-58.7	**0.4**	-18.4	0.7	-36.1	0.4	**-18.3**
Tilia spp.	**0.5**	**-17.6**	0.8	-32.2	2.7	-99.2	0.4	-45.5	**0.3**	**-16.5**	1.4	132.0
Ulmus glabra	0.4	262.8	**0.2**	**122.5**	0.3	172.5	0.1	-36.8	0.1	-30.6	**0.1**	**2.1**
Number of species with best performance	**9**	**10**	7	6	1	1	7	5	4	4	**9**	**10**

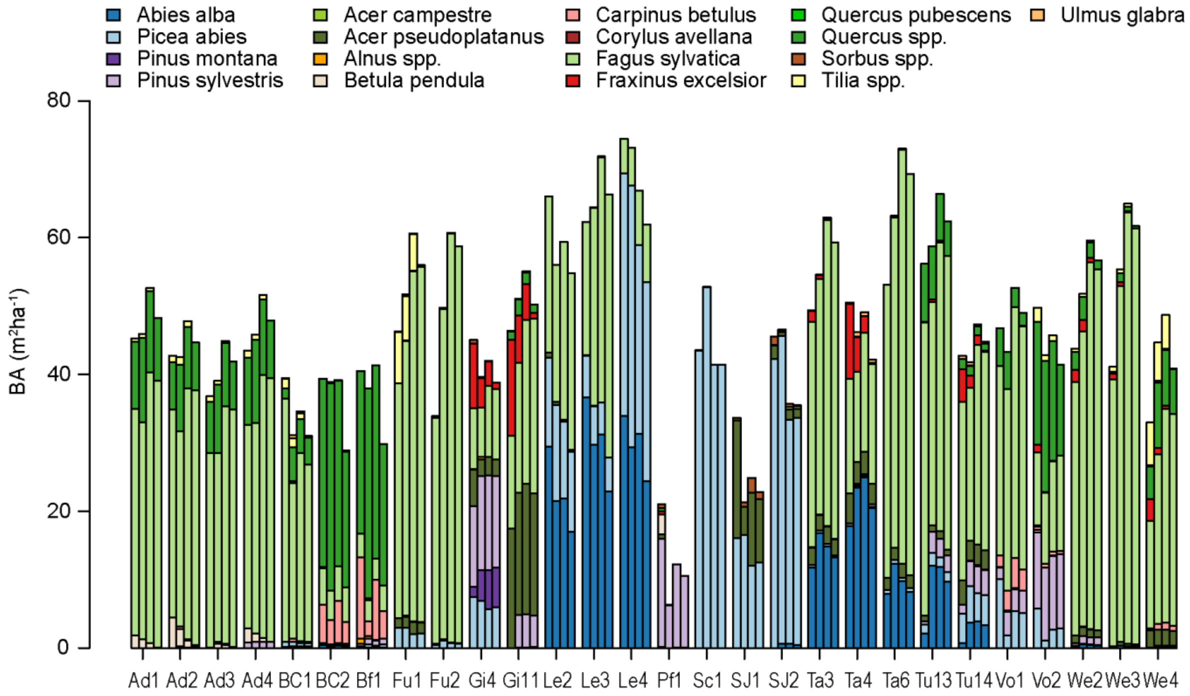

Fig. 2 Species-specific *BA* observed (leftmost bar; from inventory data) and simulated by the three model versions of ForClim (from left to right: ForClim 3.3, ForClim IM_mean; ForClim IM_sd) for each permanent plot at the last inventory. The acronyms of the permanent plots and the years of the last inventories are available in Table S2.

In contrast, IM_sd was superior to ForClim 3.3 in predicting accurate numbers of dead trees for most of the species (cf. Table 4), but the performance of ForClim 3.3 in predicting N_{dead} was better in the majority of the permanent plots (cf. Table S6) since most of them were dominated by *Fagus sylvatica*. For this species, mortality rates were strongly underestimated by both inventory-based mortality functions (cf. Table 4).

Based on the simulation results with the new mortality functions, three main types of disagreement between observed and simulated *BA* and N_{dead} could be distinguished. For their interpretation, the number of observed versus simulated N_{dead} as a function of *DBH* (cf. Fig. S6) must be considered, as follows.

First, simulated *BA* for *Fagus sylvatica*, *Pinus mugo* and *Pinus sylvestris* was overestimated since mortality was considerably underestimated, for *Fagus sylvatica* most markedly for trees with *DBH* < 20 cm. Second, the opposite was found for *Acer campestre*, *Carpinus betulus*, *Fraxinus* excelsior and *Tilia* spp. simulated by IM_sd since too many trees died, in particular between 16 and 40 cm *DBH* (e.g., Tariche Haute Côte, Weidwald). Finally, *BA* and N_{dead} were jointly underestimated for several other species including *Picea abies*, which is the result of considerably underestimated mortality of small trees (*DBH* < 8 cm) and overestimated mortality of large trees (e.g., Scatlè). However, the prediction accuracy of trees with large *DBH* varied among sites. In contrast to mortality patterns in the inventory data, simulated mortality over *DBH* of *Acer pseudoplatanus*, *Fagus sylvatica* and *Picea abies*, was not J-shaped but clearly hump-shaped (cf. Fig. S6).

Long-term simulations

Species composition and *BA* predicted after 1500 years differed considerably between ForClim 3.3 and the new mortality functions. In the center of the Swiss environmental gradient, the dominance of *Fagus sylvatica* as simulated by ForClim IM_mean and IM_sd was even more evident than in short-term simulations (Fig. 3). High *BA* of *Fagus sylvatica* was fostered by trees reaching very large *DBH* (e.g., > 280 cm in Bern). At the sites dominated by *Fagus sylvatica*, *Carpinus betulus* established in small numbers, but those trees reached great size and thus contributed strongly to total *BA*. In comparison, the *BA* of other species was negligible. This is in contrast to ForClim 3.3 and expected PNV under these conditions (Bugmann & Solomon, 2000). The consideration of uncertainty in model parameters (IM_sd) reduced *BA* of *Carpinus betulus* and increased the presence of *Picea abies* but did not change the strong prevalence of *Fagus sylvatica*.

In contrast to expectations and outputs from ForClim 3.3 (Rasche *et al.*, 2012), PNV in Sion simulated by ForClim IM_mean and IM_sd was not dominated by *Pinus sylvestris* but by *Pinus mugo*, and *BA* was comparably low. In addition, simulations of ForClim IM_mean resulted in an unexpected large presence of *Acer campestre*. The simulated biomass of *Picea abies* in Davos was lower than expected and suggested by ForClim 3.3, in particular for *DBH* > 115 cm.

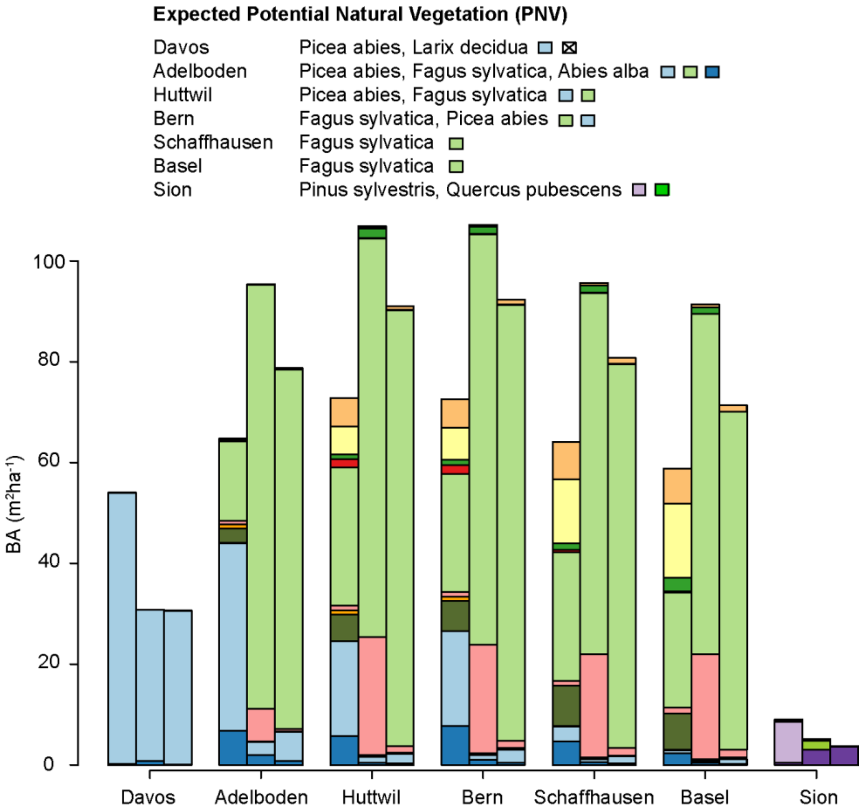

Fig. 3 Potential Natural Vegetation (PNV, *BA* per species) simulated along the Swiss environmental gradient at the end of a 1500-years run using ForClim 3.3 (left), ForClim IM_mean (middle) and ForClim IM_sd (right). The color code used to represent the different species is the same than in Fig. 2. Expectations of PNV according to Rasche *et al.* (2012). Note that *Larix decidua* Mill. was not simulated in ForClim since no mortality could be fitted for this species.

Discussion

The development of new inventory-based mortality models provided novel insights with respect to (1) species-specific differences of mortality patterns, (2) potential advances of growth-based mortality models that include climate and stand characteristics, and (3) the suitability of empirical mortality models for implementation in DVMs.

Species-specific patterns of mortality

Tree mortality over *DBH* and *relBAI* was J-shaped for nearly all species in our study. This is congruent with ecological theory of stress and vigor (Waring, 1987), which suggests that individuals with restricted access to resources, i.e., those that have a small rooting and crown system (small trees; Harcombe, 1987), and individuals that show reduced vitality (slow-growing trees; cf. Manion, 1981; Stephenson *et al.*, 2011), are exposed to higher stress and thus usually have a higher probability to die.

This general relationship between *DBH*, *relBAI* and mortality is modified by species-specific traits that are related to life history strategies (Grime, 1977; Brzeziecki & Kienast, 1994). Specifically, species that can reach high age show lower mortality rates than typical pioneers. In addition, species with high shade tolerance are expected to have a good ability to survive in the sub-canopy (Givnish, 1988), i.e., when being small, and to resist low-growth periods (cf. storage hypothesis, Valladares & Niinemets, 2008). Conversely, less shade-tolerant species are more likely to show increased mortality at low *DBH* and *relBAI* and thus a pronounced effect of size and growth on mortality (Kobe & Coates, 1997). The four distinct patterns that we identified for the influences of size and growth on mortality are related to these life history strategies, as discussed below.

The first group features low overall mortality and weak impacts of *DBH* and *relBAI*. It is dominated by relatively long-lived species with high shade tolerance (cf. Bugmann, 1994 for specifications of maximum age and shade tolerance). While this applies to *Abies alba*, *Fagus sylvatica*, *Picea abies* and *Tilia cordata*, the lifespan of *Ulmus glabra* is shorter, and thus the overall mortality rate we found appears low. However, the model for *Ulmus glabra* had only low discriminative ability, and thus this pattern is not necessarily reliable. In turn, *Cornus mas* and *Pinus mugo* are less shade-tolerant than the other species in this group, and the influences of *DBH* and *relBAI* arising from their models appear rather weak. Bearing in mind the shrubby shape and small size of *Cornus mas*, a maximum age of 300 years can be regarded as long-living (San-Miguel-Ayanz *et al.*, 2016). When taking into account the narrow *DBH* range of this species covered in the data, this may have led to weaker effects of *DBH* and *relBAI* than expected from species attributes. In contrast, *Pinus mugo* may not feature particularly high mortality rates for small and slow-growing trees due to its occurrence in relatively open stands under quite stressful conditions with respect to water and nutrient availability (Ellenberg, 2009; Brang *et al.*, 2014). As more competitive species are missing in these stands, the mortality patterns of *Pinus mugo* do not indicate high shade tolerance, but rather high tolerance of drought and lack of nutrients.

In contrast, high overall mortality was identified for the second group that consists mainly of short-living pioneers, i.e., *Alnus incana*, *Betula pendula*, *Corylus avellana* and *Sorbus aria*. The high mortality of slow-growing trees of these species is due to their low shade tolerance (for similar patterns cf. Wunder *et al.*, 2008; Moustakas & Evans, 2015). Given their low competitiveness, even large trees of these species experience high mortality risk (Brzeziecki & Kienast, 1994).

Species of the third group show a similarly strong influence of *relBAI* on mortality, as *Pinus sylvestris*, *Quercus pubescens* and *Quercus* spp. feature low shade tolerance as well. However, due to a higher maximum age, more large trees survive compared to the second group. In contrast, *Acer pseudoplatanus* is typically considered a shade-tolerant species, and its seedlings achieve high survival and low but sustained growth under low light conditions (Ammer, 1996). Nevertheless, shade tolerance considerably decreases when *Acer* seedlings become taller, which may explain why mortality decreased strongly with size and growth for this species (Hein *et al.*, 2008).

The fourth group of *Acer campestre*, *Carpinus betulus* and *Fraxinus excelsior* is characterized by medium life expectancy and medium to high shade tolerance. This is reflected in mortality patterns with average mortality effects of tree size and growth, which bridge between the second and the third group.

In contrast to the often proposed U-shaped mortality over tree size (Buchman *et al.*, 1983; Lorimer & Frelich, 1984), we did not find any evidence of a positive quadratic term for *DBH* in the models. This agrees with the results of Ruiz-Benito *et al.* (2013) and a recent assessment of inventory-based mortality models that revealed U-shaped mortality in four out of 58 cases only (Hülsmann *et al.*, 2017). Higher background mortality of large trees is typically associated with a number of additional mortality agents such as insect attacks, drought, rot or mechanical instability (Franklin *et al.*, 1987; Das *et al.*, 2016; Grote *et al.*, 2016). In the forest reserves studied here, the lack of U-shaped mortality is most likely related to the relatively short time without forest management (approximately 60 years, exceptionally > 200 in Derborence and Scatlè; cf. Heiri *et al.*, 2011; Meyer & Schmidt, 2011). Consequently, a large population of big trees that would show the right tail of the U-shaped mortality is not present yet, in contrast to true old-growth forests (Hülsmann *et al.*, 2016; cf. Appendix C for an extended discussion on U-shaped mortality over tree size and growth).

Climate and stand influences on mortality

The infrequency of additional covariates for climate or stand properties in the final models does not necessarily disprove any direct long- or short-term environmental effects on mortality. Rather, this suggests that they are considered, at least to a large degree, via tree size and growth. Our study provides ample evidence across a large number of tree species that size (*DBH*) and growth (*relBAI*) sufficiently capture the influences of climatic and stand conditions on mortality probability, and tree size and growth can thus be used as integrative indicators of vitality (cf. Dobbertin, 2005). In a previous study, we showed that not only precipitation and temperature but also a large variety of drought indices did not substantially improve mortality predictions for *Fagus sylvatica* (Hülsmann *et al.*, 2016), a result supported by the findings of this study. Nevertheless, we were unable to test the influence of drought on mortality for all species due to limited data on soil water conditions. In addition, intense drought or bark beetle attacks may lead to sudden tree death (Peterken & Mountford, 1996; Meddens *et al.*, 2012) that cannot be elucidated with multi-annual re-measurements and would require a higher temporal resolution via annual inventories (e.g., Neuner *et al.*, 2015) or dendrochronological data (e.g., Cailleret *et al.*, 2017). Similarly, information on climate and stand properties was available at the level of the permanent plots only rather than for the local tree neighborhood, which may have impeded the identification of such effects on the mortality probability of individual trees.

Species that had additional covariates in the final model belong to different groups with respect to mortality patterns as a function of *DBH* and *relBAI*, and thus feature different life history strategies. In addition, these models included different covariates and effect directions (cf. influence of precipitation). Accordingly, the covariates do not reflect universal but rather species-specific environmental influences that may additionally depend on the available dataset, as discussed in more detail in Appendix C. Finally, none of the covariates interacted with *relBAI*, suggesting that the growth influence on mortality is constant across different environments.

Although we restricted our analysis to species with a minimum data coverage of 20 trees per plot and at least 10 permanent plots, the results indicate that the estimation of environmental effects on mortality critically depends on sufficiently wide and well supported environmental gradients. Otherwise, questionable effects (*Pinus mugo* and *Quercus pubescens*, cf. Appendix C) are likely to occur. In turn, this may have prevented additional covariates to be retained in the models of other species, because many reserves are near the center of a species' range. Thus they do not encompass marginal populations with truly extreme conditions, which however is key for establishing the relationship between environmental effects and ecological processes.

Suitability of empirical mortality models for incorporation in DVMs

Calibration performance

Mortality models for implementation in DVMs need to predict accurate mortality rates (Bircher *et al.*, 2015; Cailleret *et al.*, 2016). We therefore reported the relative variation in prediction accuracy between inventories (*rmad* p_{bias}), revealing considerable differences between species. On the one hand, the high accuracy in predicting mortality rates was often related to homogeneity of the underlying data (few permanent plots from one reserve only, cf. *Cornus mas*). The mortality model for this species is thus not necessarily better than the others, but it was fitted to rather homogeneous stand and site conditions. On the other hand, low *rmad* p_{bias} values were identified for three models that included additional covariates (*Alnus incana*, *Corylus avellana* and *Quercus pubescens*). Thus, the covariates improved the representation of variability in mortality between inventories in these datasets. Nevertheless, prediction accuracy was considerably lower for other species, even if their model included a climate or stand characteristic (e.g., *Picea abies*). This means that observed and predicted mortality rates deviated considerably for several species and that the models under- or overestimated annual mortality by up to 2.7 % (quantified as the absolute value *mad* p_{bias}; cf. Table 3, *Alnus incana*) when applied in the calibration domain.

These findings confirm that the mortality process is highly variable in space and time (cf. Hawkes, 2000; Wunder, 2007), and it remains challenging to explain this variability with climate and/or stand characteristics using inventory data with a low temporal resolution. After all, mortality processes are likely to always be subject to pronounced stochasticity due to the complexity of biological, mechanical and competitive influences on mortality (Allen *et al.*, 2015; Anderegg *et al.*, 2015). Thus, it may be exceedingly hard to include these processes in any mortality functions, even in the most ‘mechanistic’ approaches (Meir *et al.*, 2015). This suggests that more emphasis should be placed on the adequate representation of the uncertainty in parameter estimates of empirical-based mortality functions. Parameter combinations can be sampled within their confidence intervals in a stochastic way as we did here, but we acknowledge that an even more beneficial approach would be to consider the cross-correlations between parameter values, which can be quantified, e.g. using Bayesian methods (Hartig *et al.*, 2012).

The differences in *AUC* between species and trees of different size and the related uncertainty must be considered when empirically-based mortality models are used to simulate forest dynamics in DVMs. Nevertheless, low *AUC* is less crucial for the implementation of mortality functions in DVMs. Poor discriminative ability can be the result of mortality agents that impair the relationship between mortality and the predictors chosen, or it can be due to poor data sources. For example, the unsatisfactory discrimination of *Ulmus glabra* may be caused by the rapid decline in response to infection with *Ophiostoma novo-ulmi* (Dutch elm disease, Brasier, 2000) or by the small sample size used to calibrate its mortality function (cf. Table 1). In turn, the poor discrimination between living and dead trees of *Picea abies* was most likely caused by the impacts of small-scale windthrow, wet snow or insect attacks that often result in sudden death irrespective of tree growth (Svoboda *et al.*, 2010).

In a previous study, *AUC* patterns over *DBH* provided novel insights into the mortality processes of *Fagus sylvatica* that are changing during a tree's lifetime (Hülsmann *et al.*, 2016). Our results for a much extended set of species confirm that the models' discriminative ability is decreasing with tree size also for several other tree species. This supports the conclusion that competition, which disproportionally affects smaller trees (Das *et al.*, 2016), is the dominant mortality process reflected in the models. As competition becomes lower with increasing size and other mortality agents gain importance (cf. Holzwarth *et al.*, 2013), the discriminative ability of the models is reduced. This is supported by the finding that *Cornus mas* and *Corylus avellana*, which reach small *DBH* only, show an increase of *AUC* with size. However, models of other species also retained good discriminative ability for larger *DBH*, and except for *Abies alba*, all these species feature low shade tolerance. This suggests that in shade-intolerant species even large trees may die due to competition, or due to mortality agents affecting the same trees as competition, which confers mortality models a good discrimination also in large individuals.

Considering that the behavior of parsimonious empirical models based on tree size and growth was biologically meaningful for most species, and that their performance was quite high and not impacted by changes in the sampling design (as supported by cross-validation), we propose that the mortality algorithms developed here are suitable for implementation and evaluation in DVMs. Since covariates for climate and stand were only rarely included and partly revealed ecologically questionable relationships, we only implemented models without environmental covariates in ForClim. This appears appropriate since, from the species concerned, only *Picea abies* and *Quercus* spp. are of importance in the simulated permanent plots.

Implementation of the inventory-based mortality models in ForClim

Although the historical predictions of stand basal area and species composition based on the new ForClim versions were generally close to observations, their performance was lower than with ForClim 3.3, especially for two major tree species of Central Europe, *Fagus sylvatica* and *Picea abies*. In addition, PNV could not be simulated adequately and showed a strong overestimation of *Fagus sylvatica* (and *Carpinus betulus* in case of ForClim IM_mean). This was much to the detriment of other species like *Picea abies* or *Tilia spp*., whose growth was excessively reduced by low light availability. For *Picea abies*, the new empirical mortality formulations prevented trees with $DBH > 115$ cm, although *Picea abies* in old-growth, subalpine forests clearly can attain larger size (Hillgarter, 1971). The simulation performance differed considerably among species, and poor results could be attributed to over- and underestimation of mortality rates for different tree sizes. Overall, the calibration performance of the inventory-based models was not necessarily a good predictor for the accuracy of the simulation of species-specific BA and N_{dead} by ForClim.

Since growth is one of the main predictors of tree death, the parameters determining growth and survival are highly correlated (Bircher, 2015). Hence differences between simulated and observed growth rates may partly explain differences between simulated and observed mortality rates. For instance, underestimated mortality rates of *Fagus sylvatica*, especially for trees with $DBH < 20$ cm, can be related to the overestimation of their simulated relative growth rates (see Fig. S4). This systematic bias, which was also observed for *Picea abies* and *Pinus sylvestris* (albeit to a lower extent), can originate from multiple sources such as an inaccurate simulation of the effect of light availability or crown size on tree growth (Mina *et al.*, 2015), difficulties in the growth equation that is used to simulate diameter increment (Moore, 1989), or an unrealistic stand initialization in ForClim. Because of the random and even allocation of trees to an initial set of patches, which are then replicated to obtain 200 patches per simulation, the diversity in stand structure among patches at initialization is much lower than observed in the field. Similarly, as ForClim does not track tree position, the variability in competition intensity among trees may not be represented accurately enough.

Mortality predictions appeared particularly problematic for trees with *DBH* < 10 cm and > 60 cm (cf. Larocque *et al.*, 2011; Bircher *et al.*, 2015). These difficulties are likely to result from extrapolation since the inventory dataset is truncated for small *DBH* (calipering limit of 4 and 7 cm, cf. *Material and methods*), and contains fewer large trees than would occur in true old-growth forests. In addition, different agents affect the mortality of large individuals that may not be reflected well in the empirical mortality models (cf. *AUC* patterns over *DBH*). When implemented in DVMs, U-shaped *DBH*-mortality functions may be preferable over J-shaped ones to avoid the persistence of very large trees in long-term simulations, as observed here with *Fagus sylvatica*. To implement this U-shape in spite of the poor data availability of large trees, semi-empirical models that combine empirically-derived formulations with theoretical adjustments (e.g., assuming a maximum *DBH*; Manusch *et al.*, 2012) may be required. In turn, mortality formulations for small trees should be refined using regeneration surveys, inventories without calipering limit, stem cross-sections or experiments (Wernsdörfer *et al.*, 2008; Canham & Murphy, 2016; Evans & Moustakas, 2016). At the same time, the representation of tree regeneration and establishment that similarly suffer from a poor empirical foundation could be improved by extending mortality models to seedlings (Wehrli *et al.*, 2007).

Due to the non-linearity between the predictors and the mortality probability (cf. logit link function), which is then transposed into a binary variable (tree death or survival) based on a stochastic approach (see Bircher *et al.*, 2015), accounting for uncertainty in model estimates typically increases mortality rates. Although this approach can reduce systematic underestimations of tree mortality rates and thus improve simulation accuracy (Vanoni *et al.*, in prep.), it did not considerably increase mortality rates of *Fagus sylvatica*. This may be related to the large number of records in the calibration dataset of this species, which resulted in low parameter uncertainty. Nevertheless, accounting for uncertainty appears promising for species for which inventory sample size is small and diversity in mortality patterns among sites and individuals is high, and we therefore advocate evaluating this approach further (Cressie *et al.*, 2009).

Conclusion

We identified dominantly J-shaped mortality over tree size and growth across 18 tree species, using inventory data from forest reserves. These patterns reflect the indirect influences of resource availability and tree vitality on mortality but rebut the assumption of a general substantial instability of large trees. Furthermore, the patterns confirmed that size- and growth-dependent mortality relationships are modulated by species-specific attributes such as lifespan, shade and drought tolerance.

If species-specific models are unfeasible due to data limitations, we propose that lifespan and stress tolerance should be used for the classification of tree species into PFTs to predict mortality, but we think that this approach should be tested further (cf. Bircher, 2015). Grouping species according to shade tolerance only disregards the strong impact of lifespan on mortality and bears a high risk of erroneous projections. Since in some species (e.g., *Cornus mas*, *Pinus mugo, Ulmus glabra*) additional attributes modified the mortality patterns, species-specific mortality models should be favoured over parameterizations for PFTs, so as to obtain DVMs with an appropriate representation of demographic diversity.

Based on our analysis of the role of environmental co-variates in mortality models, we conclude that tree size and growth *alone* are well suited to predict tree death of most species. These models consider environmental effects indirectly, i.e. via integrative indicators of tree vitality such as size and growth. Nevertheless, the climatic sensitivity of growth-based mortality functions should be verified using data with higher temporal resolution, followed by an in-depth evaluation in DVMs. Additionally, the predictive ability of tree size and growth is restricted to mortality associated with particular *DBH* classes or growth levels. Thus, processes such as short-term intense drought, mechanical damage or insect attacks may not be fully reflected by these models (Larson & Franklin, 2010; Cailleret *et al.*, 2017). Finally, we emphasize that caution is required when additional covariates are considered in mortality models. Their effects may appear erratically if the environmental gradient underlying the observational data is insufficient. Applying such models means leaving the domain of calibration, which can result in unwarranted extrapolation and misleading inference (Hawkes, 2000; Woolley *et al.*, 2012; Kuhn & Johnson, 2013). Therefore, the selection of environmental covariates in mortality models should be based on the principle of parsimony (Sims *et al.*, 2009; Burkhart & Tomé, 2012).

When incorporated in a DVM, the new inventory-based mortality models successfully simulated short-term dynamics but showed weaknesses in simulating stand structure and species composition in the long term. These difficulties were the result of feedbacks between simulated growth and mortality as well as of extrapolation to small and very large trees. Thus, both, growth and mortality processes and their species-specific differences should be revisited jointly, with a particular focus on small and very large trees, e.g. using a Bayesian calibration approach (Hartig *et al.*, 2012; Bircher, 2015). Yet, we conclude that inventory-based mortality formulations can replace theoretical concepts of mortality in DVMs since they provide species-specific mortality relationships that are not based on single parameters such as maximum age and growth but on empirical relationships over a tree's lifetime.

Considering the need to better simulate forest ecosystems and their response to climate change, implementing accurate mortality functions in DVMs is of utmost importance due to their cascading effects on recruitment, growth and mortality of the remaining trees, and consequently on forest structure and species composition. We strongly recommend inventory-based mortality formulations – in particular those that consider species-specific differences – as a promising element to enhance the robustness and reliability of DVM projections.

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Appendix A – Table S1-6, Fig. S1-6

Table S1 Tree, stand and site characteristics that were considered as covariates in the mortality models. The mean and standard deviation (in brackets) of each characteristic are given per tree species. Abbreviations: *DBH* = diameter at breast height, *relBAI* = annual relative basal area increment, *mDBH* = arithmetic mean *DBH*, *iqrDBH* = interquartile range of *DBH*, *BA* = stand basal area, *N* = number of trees, *P* = mean annual precipitation sum, *mT* = mean annual air temperature.

Species	***DBH*** **(mm)**	***relBAI*** **(-)**	***mDBH*** **(mm)**	***iqrDBH*** **(mm)**	***BA*** **(m^2ha^{-1})**	***N*** **(ha)**	***P*** **(mm)**	***mT*** **(°C)**
Abies alba	139 (132)	0.018 (0.021)	230 (37)	195 (55)	47.9 (8.8)	827 (196)	1360 (222)	7.8 (1.1)
Acer campestre	80 (37)	0.021 (0.021)	161 (28)	113 (55)	31.0 (6.1)	1347 (466)	1100 (208)	9.0 (0.5)
Acer pseudoplatanus	215 (104)	0.014 (0.020)	236 (57)	161 (49)	41.7 (7.1)	854 (353)	1234 (162)	8.2 (1.6)
Alnus incana	163 (64)	0.035 (0.030)	175 (28)	105 (51)	28.4 (3.3)	1035 (341)	1013 (67)	9.0 (0.6)
Betula pendula	218 (113)	0.020 (0.020)	200 (51)	143 (61)	30.7 (9.4)	836 (316)	1011 (192)	9.2 (0.5)
Carpinus betulus	151 (93)	0.011 (0.015)	227 (58)	163 (48)	36.7 (7.5)	824 (398)	985 (200)	9.2 (0.4)
Cornus mas	49 (8)	0.018 (0.016)	151 (16)	100 (38)	26.8 (5.8)	1251 (371)	1017 (42)	8.9 (0.4)
Corylus avellana	62 (19)	0.028 (0.029)	205 (31)	187 (56)	33.2 (6.1)	791 (264)	1082 (130)	9.6 (0.6)
Fagus sylvatica	255 (159)	0.016 (0.015)	269 (82)	170 (58)	39.6 (7.7)	691 (354)	1105 (202)	8.7 (0.9)
Fraxinus excelsior	171 (107)	0.031 (0.026)	187 (48)	131 (62)	32.2 (8.6)	1077 (453)	1134 (177)	8.8 (0.6)
Picea abies	300 (194)	0.015 (0.016)	303 (86)	230 (72)	45.8 (10.0)	596 (314)	1628 (416)	5.0 (2.1)
Pinus mugo	151 (75)	0.015 (0.015)	168 (34)	104 (38)	24.0 (9.1)	925 (334)	1451 (423)	3.5 (1.9)
Pinus sylvestris	264 (124)	0.019 (0.024)	189 (36)	145 (66)	33.9 (13.7)	992 (340)	1000 (246)	8.9 (0.8)
Quercus pubescens	156 (76)	0.019 (0.019)	144 (18)	84 (41)	28.1 (5.9)	1491 (454)	1005 (60)	9.0 (0.5)
Quercus spp.	279 (141)	0.014 (0.012)	221 (48)	161 (51)	37.3 (7.0)	867 (368)	1129 (212)	9.2 (0.6)
Sorbus aria	86 (37)	0.026 (0.024)	172 (28)	120 (44)	35.6 (10.2)	1239 (323)	1256 (160)	8.3 (0.7)
Tilia cordata	169 (106)	0.016 (0.018)	202 (45)	127 (37)	38.7 (5.0)	1110 (399)	1323 (220)	8.9 (0.5)
Ulmus glabra	143 (92)	0.040 (0.038)	182 (29)	123 (25)	29.7 (6.1)	964 (270)	1070 (197)	8.9 (0.4)

Table S2 Site descriptions of the permanent plots used for validation including information on location, plot size, elevation and average climate conditions (mean annual air temperature and precipitation sum). The slope/aspect parameter is an input of ForClim defined as 0 = flat terrain, 1 = steep slope (10 - 30 °), 2 = very steep slope (> 30 °); the sign denote south-facing (+) respectively north-facing (-) slopes. The simulation period is the time between the first and the last inventory, with *n* denoting the number of inventories.

Site	**Acronyms**	**Location (°N / °E)**	**Area (ha)**	**Elevation (m a.s.l.)**	***mT* (°C) / *P* (mm)**	**Slope / aspect**	**Simulation period (*n*)**
Adenberg_01	Ad1	47.6 / 8.6	0.45	~520	9.0 / 1017	+1	1970-2012 (5)
Adenberg_02	Ad2	47.6 / 8.6	0.45	~500	9.0 / 1017	0	1970-2012 (5)
Adenberg_03	Ad3	47.6, 8.6	0.45	~505	9.0 / 1020	0	1970-2012 (5)
Adenberg_04	Ad4	47.6 / 8.6	0.45	~520	9.1 / 1006	+1	1970-2012 (5)
Bois de Chênes_01	BC1	46.4 / 6.2	0.49	~550	9.6 / 1075	0	1970-2007 (4)
Bois de Chênes_02	BC2	46.4, 6.2	0.49	~570	9.5 / 1094	+1	1970-2007 (4)
Bonfol_03	Bf3	47.5 / 7.2	0.53	~440	9.5 / 1003	0	1962-2001 (5)
Fuerstenhalde_01	Fu1	47.6, 8.5	0.53	~460	9.2 / 1065	0	1971-2012 (4)
Fuerstenhalde_02	Fu2	47.6 / 8.5	0.53	~470	9.2 / 1076	0	1971-2012 (4)
Girstel_04	Gi4	47.3, 8.5	0.22	~675	7.9 / 1297	-1	1964-2006 (5)
Girstel_11	Gi11	47.3 / 8.5	0.14	~720	8.1 / 1270	+1	1972-2007 (4)
Leihubelwald_02	Le2	46.9, 8.1	0.25	~1240	6.1 / 1770	-1	1973-2011 (4)
Leihubelwald_03	Le3	46.9 / 8.1	0.24	~1140	6.6 / 1690	+1	1973-2011 (4)
Leihubelwald_04	Le4	46.9 / 8.1	0.25	~1100	6.7 / 1668	0	1973-2011 (4)
Pfynwald_01	Pf1	46.3 / 7.6	0.19	~575	10 / 670	+1	1956-2003 (6)
Scatlè_01	Sc1	46.8 / 9.0	3.47	~1650	3.7 / 1582	+1	1965-2006 (4)
St.Jean_01	SJ1	47.1, 7.0	0.28	~1375	4.7 / 1520	0	1961-2006 (5)
St.Jean_02	SJ2	47.1 / 7.0	0.44	~1370	4.8 / 1510	0	1961-2006 (5)
Tariche Haute Côte_03	Ta3	47.3 / 7.2	0.91	~735	8.1 / 1228	-1	1974-2012 (4)
Tariche Haute Côte_04	Ta4	47.3, 7.2	0.56	~740	7.9 / 1250	+1	1974-2012 (4)
Tariche Haute Côte_06	Ta6	47.3 / 7.2	0.54	~720	8.1 / 1228	0	1976-2012 (4)
Tutschgenhalden_13	Tu13	47.5 / 8.8	0.25	~600	9.1 / 1151	0	1971-2013 (4)
Tutschgenhalden_14	Tu14	47.5 / 8.8	0.58	~580	9.1 / 1151	0	1971-2013 (4)
Vorm Stein_01	Vo1	47.5 / 8.5	0.25	~545	8.9 / 1144	+2	1972-2012 (4)
Vorm Stein_02	Vo2	47.6, 8.5	0.24	~540	9.2 / 1067	+2	1972-2012 (4)
Weidwald_02	We2	47.4 / 8.0	0.76	~635	8.7 / 1163	0	1976-2011 (4)
Weidwald_03	We3	47.4 / 8.0	0.25	~660	8.6 / 1180	0	1976-2011 (4)
Weidwald_04	We4	47.4 / 8.0	0.53	~640	8.6 / 1180	+1	1976-2011 (4)

Table S3 Parameter estimates, standard errors, significance levels (*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$) and confidence intervals of the calibrated models. *DBH* = diameter at breast height (mm), *relBAI* = annual relative basal area increment, *mDBH* = arithmetic mean *DBH* (mm), *BA* = stand basal area (m^2ha^{-1}), *P* = mean annual precipitation sum (mm), *mT* = mean annual air temperature (°C). The transformation threshold *c* for the logst-transformation of *relBAI* was calibrated to the combined *relBAI* values of all tree species (*c* = 0.002183).

Species	Formula	Coefficient	*β*	*se*	*p*	Significance	*CI*
Abies alba	A7	Intercept	-8.102	0.608	0.000	***	[-9.29, -6.91]
Abies alba	A7	log(*DBH*)	-0.456	0.052	0.000	***	[-0.56, -0.35]
Abies alba	A7	logst(*relBAI*)	-4.250	0.513	0.000	***	[-5.26, -3.24]
Abies alba	A7	(logst(*relBAI*))^2	-0.679	0.109	0.000	***	[-0.89, -0.47]
Acer campestre	A7	Intercept	-7.231	1.389	0.000	***	[-9.95, -4.51]
Acer campestre	A7	log(*DBH*)	-0.913	0.171	0.000	***	[-1.25, -0.58]
Acer campestre	A7	logst(*relBAI*)	-5.362	1.062	0.000	***	[-7.44, -3.28]
Acer campestre	A7	(logst(*relBAI*))^2	-0.858	0.224	0.000	***	[-1.30, -0.42]
Acer pseudoplatanus	A5	Intercept	-0.125	0.661	0.850		[-1.42, 1.17]
Acer pseudoplatanus	A5	log(*DBH*)	-1.426	0.115	0.000	***	[-1.65, -1.20]
Acer pseudoplatanus	A5	logst(*relBAI*)	-1.390	0.123	0.000	***	[-1.63, -1.15]
Alnus incana	B7	Intercept	-10.228	1.539	0.000	***	[-13.24, -7.21]
Alnus incana	B7	log(*DBH*)	-0.615	0.108	0.000	***	[-0.83, -0.40]
Alnus incana	B7	logst(*relBAI*)	-4.007	0.562	0.000	***	[-5.11, -2.91]
Alnus incana	B7	(logst(*relBAI*))^2	-0.743	0.142	0.000	***	[-1.02, -0.46]
Alnus incana	B7	log(*BA*)	1.913	0.404	0.000	***	[1.12, 2.70]
Betula pendula	A7	Intercept	-7.997	0.760	0.000	***	[-9.49, -6.51]
Betula pendula	A7	log(*DBH*)	-0.279	0.069	0.000	***	[-0.41, -0.14]
Betula pendula	A7	logst(*relBAI*)	-4.896	0.672	0.000	***	[-6.21, -3.58]
Betula pendula	A7	(logst(*relBAI*))^2	-0.803	0.147	0.000	***	[-1.09, -0.52]
Carpinus betulus	A7	Intercept	-2.685	0.786	0.001	***	[-4.22, -1.14]
Carpinus betulus	A7	log(*DBH*)	-1.536	0.058	0.000	***	[-1.65, -1.42]
Carpinus betulus	A7	logst(*relBAI*)	-4.401	0.612	0.000	***	[-5.60, -3.20]
Carpinus betulus	A7	(logst(*relBAI*))^2	-0.754	0.124	0.000	***	[-1.00, -0.51]
Cornus mas	A4	Intercept	-14.030	1.581	0.000	***	[-17.13, -10.93]
Cornus mas	A4	logst(*relBAI*)	-7.594	1.355	0.000	***	[-10.25, -4.94]
Cornus mas	A4	(logst(*relBAI*))^2	-1.286	0.279	0.000	***	[-1.83, -0.74]
Corylus avellana	B7	Intercept	-22.132	2.823	0.000	***	[-27.67, -16.60]
Corylus avellana	B7	log(*DBH*)	-1.025	0.186	0.000	***	[-1.39, -0.66]
Corylus avellana	B7	logst(*relBAI*)	-3.067	0.498	0.000	***	[-4.04, -2.09]
Corylus avellana	B7	(logst(*relBAI*))^2	-0.563	0.111	0.000	***	[-0.78, -0.34]
Corylus avellana	B7	log(*P*)	2.862	0.367	0.000	***	[2.14, 3.58]
Fagus sylvatica	A7	Intercept	-6.317	0.387	0.000	***	[-7.08, -5.56]
Fagus sylvatica	A7	log(*DBH*)	-0.926	0.024	0.000	***	[-0.97, -0.88]
Fagus sylvatica	A7	logst(*relBAI*)	-4.739	0.316	0.000	***	[-5.36, -4.12]
Fagus sylvatica	A7	(logst(*relBAI*))^2	-0.741	0.065	0.000	***	[-0.87, -0.61]
Fraxinus excelsior	A11	Intercept	2.901	0.928	0.002	**	[1.08, 4.72]
Fraxinus excelsior	A11	log(*DBH*)	-2.719	0.183	0.000	***	[-3.08, -2.36]
Fraxinus excelsior	A11	logst(*relBAI*)	-1.053	0.574	0.067		[-2.18, 0.07]
Fraxinus excelsior	A11	(logst(*relBAI*))^2	-0.816	0.084	0.000	***	[-0.98, -0.65]
Fraxinus excelsior	A11	log(*DBH*):logst(*relBAI*)	-0.842	0.091	0.000	***	[-1.02, -0.66]

Species	**Formula**	**Coefficient**	***ß***	***se***	***p***	**Significance**	***CI***
Picea abies	B5	Intercept	-11.248	0.466	0.000	***	[-12.16, -10.34]
Picea abies	B5	log(*DBH*)	-0.375	0.032	0.000	***	[-0.44, -0.31]
Picea abies	B5	logst(*relBAI*)	-0.763	0.043	0.000	***	[-0.85, -0.68]
Picea abies	B5	log(*mDBH*)	1.294	0.090	0.000	***	[1.12, 1.47]
Pinus mugo	B3	Intercept	-3.449	0.237	0.000	***	[-3.91, -2.98]
Pinus mugo	B3	logst(*relBAI*)	-1.137	0.054	0.000	***	[-1.24, -1.03]
Pinus mugo	B3	sqrt(*P*)	-0.095	0.006	0.000	***	[-0.11, -0.08]
Pinus sylvestris	A5	Intercept	-0.237	0.421	0.573		[-1.06, 0.59]
Pinus sylvestris	A5	log(*DBH*)	-1.280	0.078	0.000	***	[-1.43, -1.13]
Pinus sylvestris	A5	logst(*relBAI*)	-1.411	0.076	0.000	***	[-1.56, -1.26]
Quercus pubescens	B7	Intercept	-19.001	2.558	0.000	***	[-24.02, -13.99]
Quercus pubescens	B7	log(*DBH*)	-2.563	0.127	0.000	***	[-2.81, -2.31]
Quercus pubescens	B7	logst(*relBAI*)	-8.032	0.976	0.000	***	[-9.94, -6.12]
Quercus pubescens	B7	$(\text{logst}(relBAI))^2$	-1.358	0.209	0.000	***	[-1.77, -0.95]
Quercus pubescens	B7	log(*mT*)	7.500	1.028	0.000	***	[5.49, 9.52]
Quercus spp.	B7	Intercept	-9.354	0.909	0.000	***	[-11.14, -7.57]
Quercus spp.	B7	log(*DBH*)	-1.828	0.064	0.000	***	[-1.95, -1.70]
Quercus spp.	B7	logst(*relBAI*)	-7.352	0.591	0.000	***	[-8.51, -6.19]
Quercus spp.	B7	$(\text{logst}(relBAI))^2$	-1.220	0.125	0.000	***	[-1.46, -0.98]
Quercus spp.	B7	log(*BA*)	1.496	0.150	0.000	***	[1.20, 1.79]
Sorbus aria	A7	Intercept	-9.305	0.873	0.000	***	[-11.02, -7.59]
Sorbus aria	A7	log(*DBH*)	-0.712	0.121	0.000	***	[-0.95, -0.48]
Sorbus aria	A7	logst(*relBAI*)	-7.328	0.711	0.000	***	[-8.72, -5.93]
Sorbus aria	A7	$(\text{logst}(relBAI))^2$	-1.330	0.157	0.000	***	[-1.64, -1.02]
Tilia cordata	A9	Intercept	6.545	1.903	0.001	***	[2.81, 10.28]
Tilia cordata	A9	log(*DBH*)	-2.891	0.424	0.000	***	[-3.72, -2.06]
Tilia cordata	A9	logst(*relBAI*)	2.680	0.774	0.001	***	[1.16, 4.20]
Tilia cordata	A9	log(*DBH*):logst(*relBAI*)	-0.846	0.171	0.000	***	[-1.18, -0.51]
Ulmus glabra	A3	Intercept	-4.893	0.263	0.000	***	[-5.41, -4.38]
Ulmus glabra	A3	logst(*relBAI*)	-0.495	0.136	0.000	***	[-0.76, -0.23]

Table S4 Most promising additional climate and stand characteristic and its most suitable transformation (log, square root or none) per tree species. Those additional covariates were selected that resulted in the lowest *BS* when included in the most flexible model (cf. Table 3, Formula C12 with different transformations of the additional characteristics).

Species	**Additional characteristic**
Abies alba	log(*iqrDBH*)
Acer campestre	log(*P*)
Acer pseudoplatanus	*mT*
Alnus incana	log(*BA*)
Betula pendula	log(*P*)
Carpinus betulus	sqrt(*iqrDBH*)
Cornus mas	log(*N*)
Corylus avellana	log(*P*)
Fagus sylvatica	log(*N*)
Fraxinus excelsior	log(*P*)
Picea abies	log(*mDBH*)
Pinus mugo	sqrt(*P*)
Pinus sylvestris	sqrt(*mDBH*)
Quercus pubescens	log(*mT*)
Quercus spp.	log(*BA*)
Sorbus aria	log(*P*)
Tilia cordata	sqrt(*BA*)
Ulmus glabra	log(*P*)

Table S5 Parameter estimates, standard errors, significance levels (*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$) and confidence intervals of the alternatively calibrated models without additional climate or stand characteristics. *DBH* = diameter at breast height (mm), *relBAI* = annual relative basal area increment. The transformation threshold *c* for the logst-transformation of *relBAI* was calibrated to the combined *relBAI* values of all tree species ($c = 0.002183$).

Species	**Formula**	**Coefficient**	**β**	**se**	**p**	**Significance**	**CI**
Alnus incana	A7	Intercept	-3.889	0.717	0.000	***	[-5.29, -2.48]
Alnus incana	A7	log(*DBH*)	-0.603	0.107	0.000	***	[-0.81, -0.39]
Alnus incana	A7	logst(*relBAI*)	-4.041	0.556	0.000	***	[-5.13, -2.95]
Alnus incana	A7	$(\text{logst}(relBAI))^2$	-0.769	0.140	0.000	***	[-1.04, -0.50]
Corylus avellana	A5	Intercept	1.008	0.793	0.204		[-0.55, 2.56]
Corylus avellana	A5	log(*DBH*)	-1.173	0.181	0.000	***	[-1.53, -0.82]
Corylus avellana	A5	logst(*relBAI*)	-0.544	0.066	0.000	***	[-0.67, -0.42]
Picea abies	A3	Intercept	-6.011	0.098	0.000	***	[-6.20, -5.82]
Picea abies	A3	logst(*relBAI*)	-0.821	0.044	0.000	***	[-0.91, -0.74]
Pinus mugo	A3	Intercept	-6.819	0.128	0.000	***	[-7.07, -6.57]
Pinus mugo	A3	logst(*relBAI*)	-1.133	0.055	0.000	***	[-1.24, -1.03]
Quercus pubescens	A5	Intercept	3.553	0.587	0.000	***	[2.40, 4.70]
Quercus pubescens	A5	log(*DBH*)	-2.375	0.121	0.000	***	[-2.61, -2.14]
Quercus pubescens	A5	logst(*relBAI*)	-1.714	0.094	0.000	***	[-1.90, -1.53]
Quercus spp.	A7	Intercept	-4.088	0.728	0.000	***	[-5.51, -2.66]
Quercus spp.	A7	log(*DBH*)	-1.848	0.063	0.000	***	[-1.97, -1.73]
Quercus spp.	A7	logst(*relBAI*)	-7.651	0.588	0.000	***	[-8.80, -6.50]
Quercus spp.	A7	$(\text{logst}(relBAI))^2$	-1.301	0.124	0.000	***	[-1.54, -1.06]

Table S6 Site-specific *RMSE* and *rbias* (%) of *BA* and N_{dead} simulated by the three ForClim version 3.3, IM_mean and IM_sd at the last inventory of every permanent plot. For each permanent plot and variable of interest, the lowest *RMSE* and the *rbias* closest to zero were highlighted in bold. Trees with *DBH* < 4 cm were not considered.

	Species basal area (*BA*)						**Number of dead stems per ha (N_{dead})**					
Permanent plot	**3.3**		**IM_mean**		**IM_sd**		**3.3**		**IM_mean**		**IM_sd**	
	RMSE	*rbias*	*RMSE*	*rbias*	*RMSE*	*rbias*	*RMSE*	*rbias*	*RMSE*	*rbias*	*RMSE*	*rbias*
Adenberg_01	**1.5**	**1.4**	3.4	16.3	3.1	6.7	**2.9**	**-44.8**	4.7	-64.2	4.4	-55.3
Adenberg_02	**1.6**	**-0.5**	3.0	11.8	3.4	4.6	**1.5**	**-40.7**	2.5	-63.6	2.4	-50.8
Adenberg_03	**1.3**	**6.0**	2.9	21.9	2.8	13.7	**2.9**	**-50.4**	4.2	-72.2	4.0	-63.6
Adenberg_04	**1.2**	**5.3**	3.9	18.7	4.1	10.2	**3.1**	**-51.8**	4.4	-66.9	4.2	-57.0
BoisdeChenes_01	4.4	-21.1	**2.9**	**-12.2**	3.4	-21.3	0.5	14.1	**0.2**	-28.0	0.3	**2.9**
BoisdeChenes_02	1.3	-1.2	**0.3**	**-0.5**	2.9	-26.6	1.7	-17.5	**1.4**	-39.5	1.4	**12.0**
Bonfol_03	4.0	-6.4	**1.8**	**1.9**	2.9	-26.4	1.1	**3.0**	0.8	-39.5	**0.7**	8.5
Fuerstenhalde_01	**2.2**	**11.6**	6.4	30.9	7.2	20.9	**1.4**	**-43.5**	2.2	-64.6	2.3	-46.6
Fuerstenhalde_02	**6.2**	**46.7**	10.9	79.0	10.2	73.2	**3.8**	**-58.8**	5.1	-77.4	4.8	-73.4
Girstel_04	**2.4**	-12.0	2.8	**-6.8**	3.4	-13.8	2.0	-43.6	1.8	-42.5	**1.5**	**-26.9**
Girstel_11	3.6	10.0	5.2	18.8	**6.5**	**8.3**	**1.8**	-29.9	2.3	-34.8	2.6	**-13.7**
Leihubelwald_02	3.8	-15.1	**3.8**	**-10.0**	5.7	-17.0	1.7	-39.1	1.8	-52.8	**1.4**	**-40.5**
Leihubelwald_03	**4.8**	**3.4**	7.1	15.4	9.6	6.5	**0.9**	**-5.7**	5.4	-37.0	4.2	-24.9
Leihubelwald_04	**2.7**	**-1.7**	4.4	-10.1	6.0	-16.8	**3.1**	**-35.4**	4.7	-58.1	3.5	-45.6
Pfynwald_01	3.6	-70.0	**1.7**	**-41.7**	2.2	-49.6	**1.7**	**-18.2**	1.8	-23.2	1.7	-21.0
Scatle_01	6.6	21.3	**1.5**	**-4.9**	1.5	-4.9	4.4	-70.7	**3.2**	**-50.4**	3.2	-50.9
St.Jean_01	7.6	-36.7	**4.6**	**-26.0**	5.0	-32.3	1.0	46.4	**1.2**	**-0.3**	1.0	30.6
St.Jean_02	**1.5**	**2.2**	4.3	-21.7	4.1	-22.0	**0.3**	-17.9	0.6	**-0.2**	0.5	13.0
TaricheHauteCote_03	**1.8**	**10.5**	4.1	27.4	3.5	20.1	2.7	-37.3	2.8	-49.8	**1.5**	**-27.6**
TaricheHauteCote_04	**3.0**	-8.5	3.7	**-2.9**	3.8	-16.5	2.5	-55.5	2.8	-61.4	**2.4**	**-44.4**
TaricheHauteCote_06	**2.9**	**18.9**	7.3	37.4	6.5	30.5	3.8	-32.5	3.8	-41.6	**1.4**	**-16.7**
Tutschgenhalden_13	5.5	**4.5**	3.9	18.2	**3.2**	11.0	1.1	**-26.0**	1.1	-43.1	**0.9**	-27.8
Tutschgenhalden_14	1.9	**-2.2**	**1.8**	10.8	2.0	4.8	**0.6**	**-40.4**	0.9	-61.3	0.8	-48.9
VormStein_01	**3.3**	-7.4	4.1	12.7	3.8	**4.9**	1.3	**-16.9**	1.6	-33.1	**1.1**	-17.5
VormStein_02	**1.6**	-14.0	1.4	**-8.2**	2.2	-16.8	0.9	-22.0	0.8	-37.7	**0.6**	**-16.3**
Weidwald_02	**1.9**	**18.2**	5.0	36.0	4.8	29.4	**0.9**	**-41.4**	1.7	-57.6	1.6	-43.5
Weidwald_03	**5.4**	**34.7**	9.8	58.1	8.9	50.2	**2.0**	**-51.6**	3.0	-68.7	2.7	-59.8
Weidwald_04	**3.2**	35.3	4.9	47.5	5.1	**23.8**	**1.0**	-35.6	1.5	-40.8	1.9	**3.1**
Number of plots with best performance	**18**	**15**	8	10	2	3	**15**	**15**	4	3	9	10

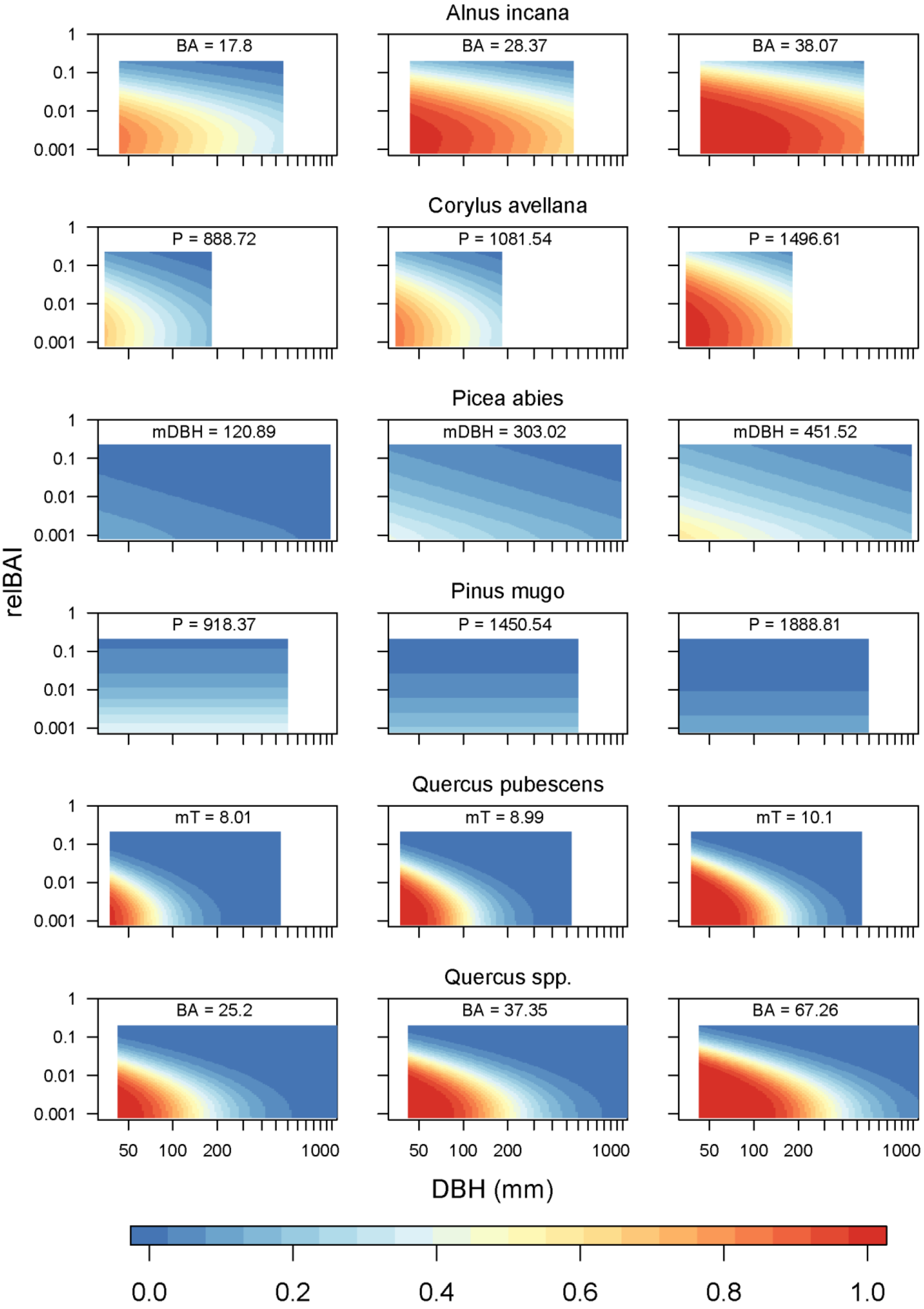


Fig. S1 Prediction maps of ten-year mortality probability as a function of *DBH* and *relBAI* for minimum, medium and maximum conditions of the additional covariate included in the model. Only species for which the final model included an additional climate or stand characteristic are shown. The respective level of the covariate, i.e., *mDBH*, *BA*, *P* and *mT*, is indicated in each sub-plot. Axes have the same scales as in Fig. 1.

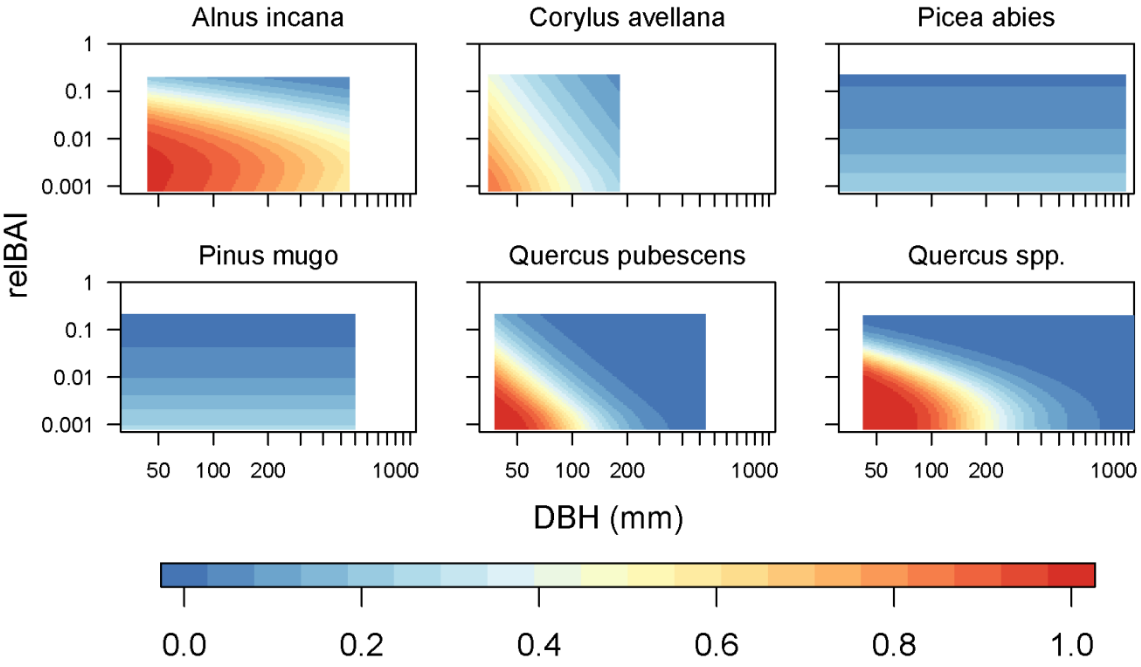


Fig. S2 Prediction maps of ten-year mortality probability as a function of *DBH* and *relBAI* for the alternative models without the additional climate or stand characteristic. Axes have the same scales as in Fig. 1.

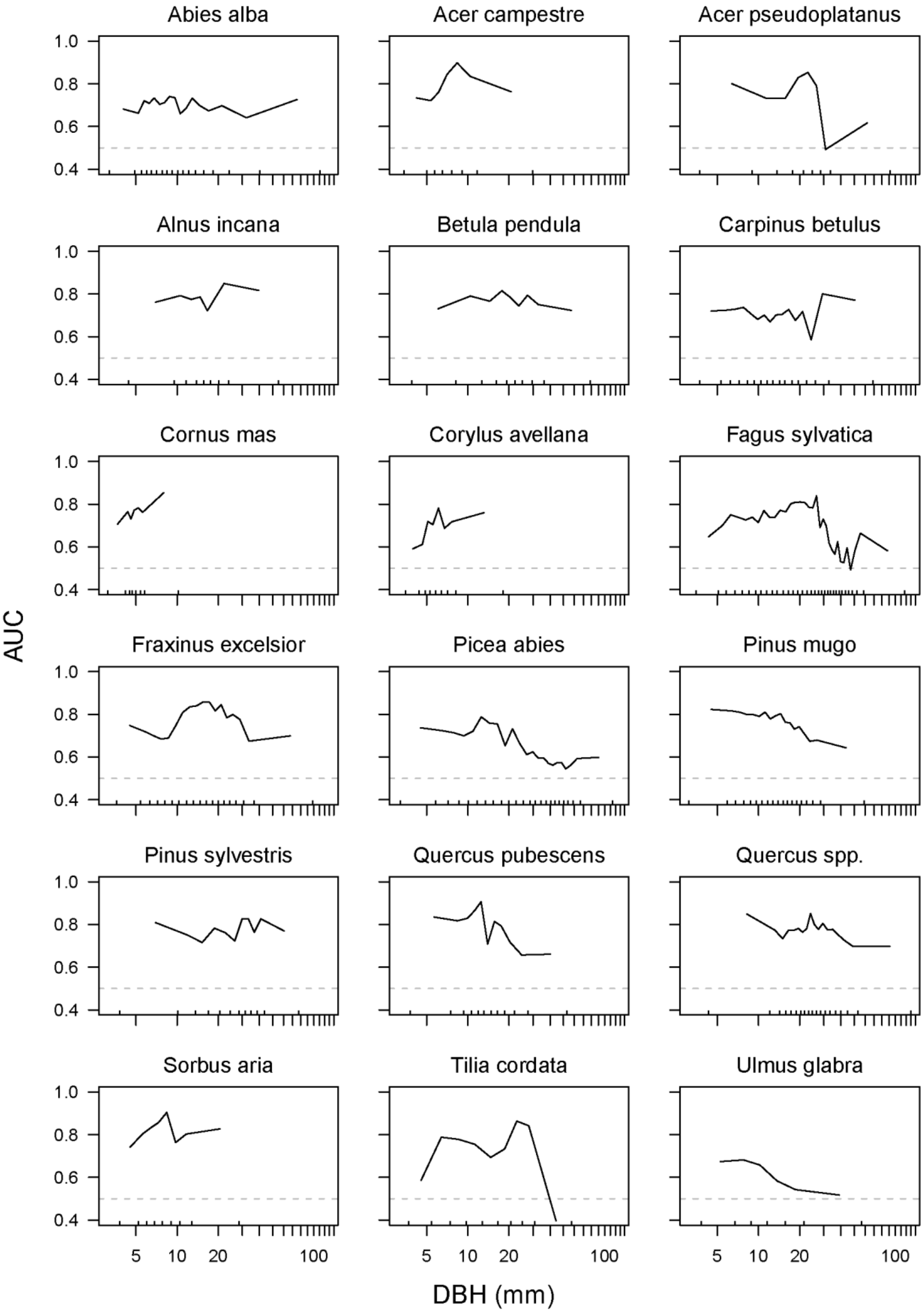


Fig. S3 *AUC* values calculated separately for *DBH* classes to assess the influence of tree size on the discriminative power. *DBH* classes are approximately equally-sized with the number of classes adjusted to the number of records available per species. The limits of the classes are indicated as rugs. The grey dashed line at *AUC* = 0.5 indicates discrimination as good as random mortality assignment.

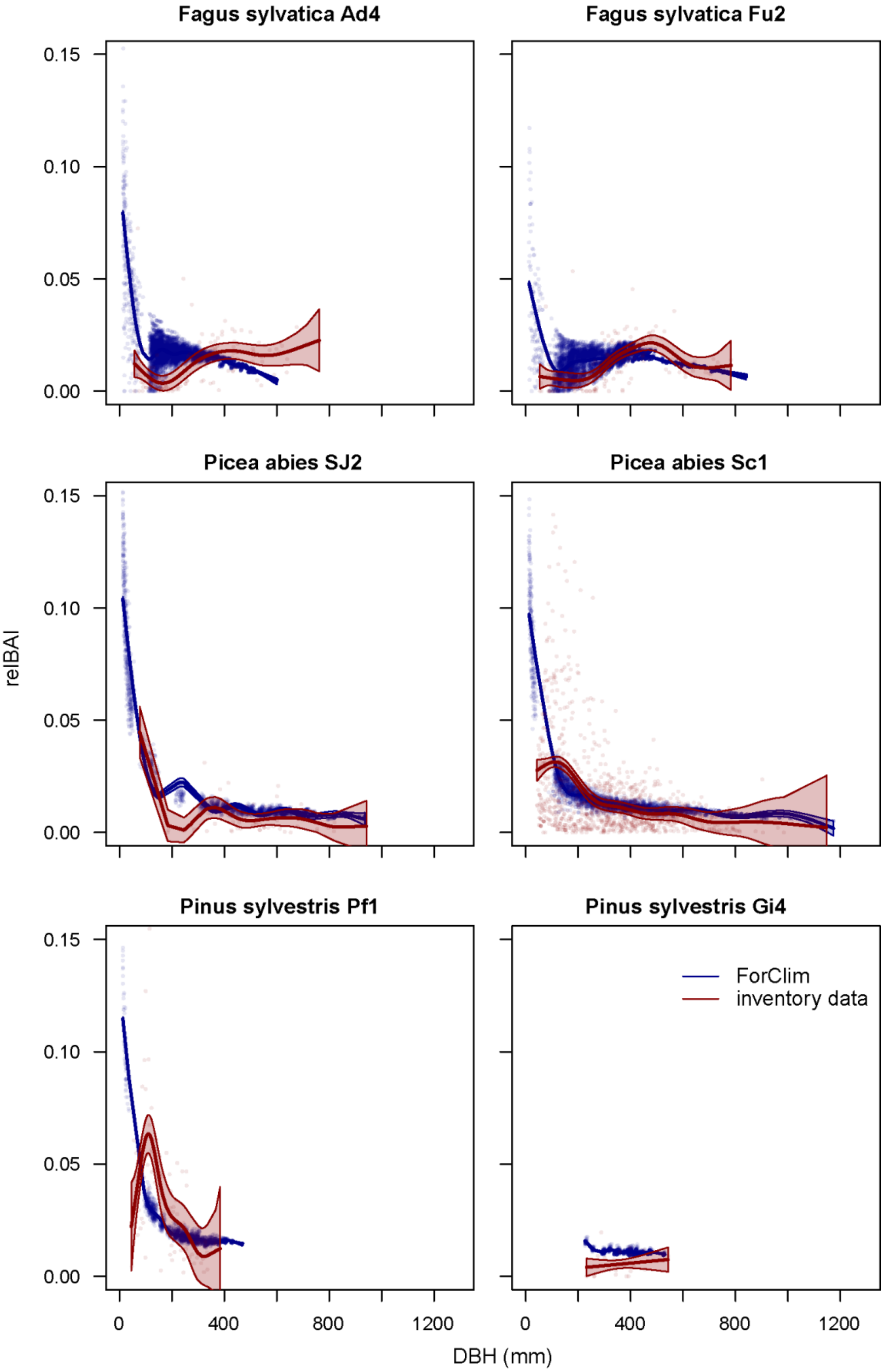


Fig. S4 Growth (*relBAI*) simulated by ForClim (blue) in comparison with observed growth from the inventory data (red) as a function of *DBH* for the species *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*. Data is shown for the last inventory used for model calibration at two example permanent plots per species. Dots indicate observed or simulated values. Lines and polygons show the fit of Generalized Additive Models (GAM) with 95% confidence bands.

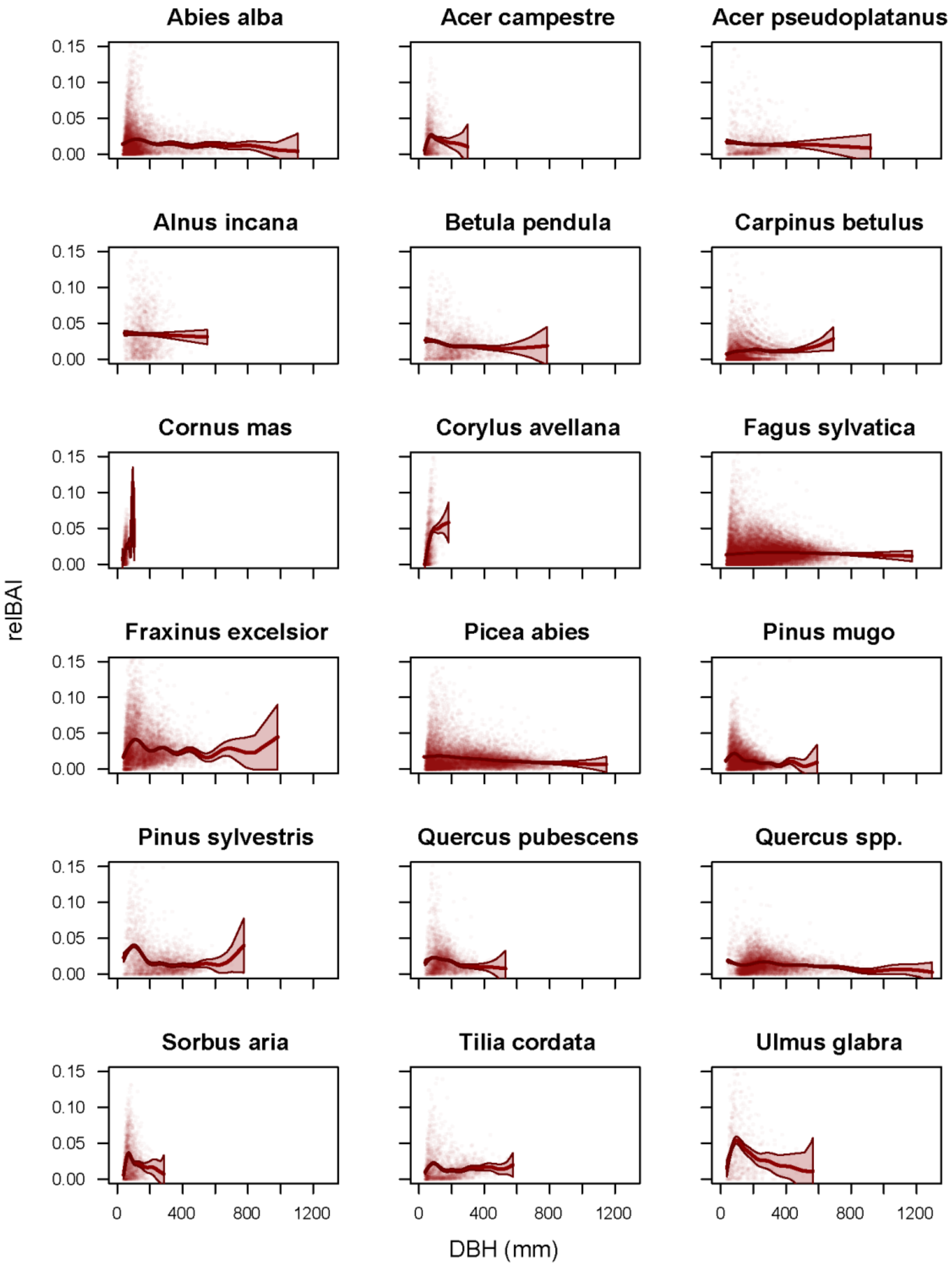


Fig. S5 Observed growth (*relBAI*) from inventory data as a function of *DBH*. Dots indicate observed values. Lines and polygons show the fit of Generalized Additive Models (GAM) with 95% confidence bands.

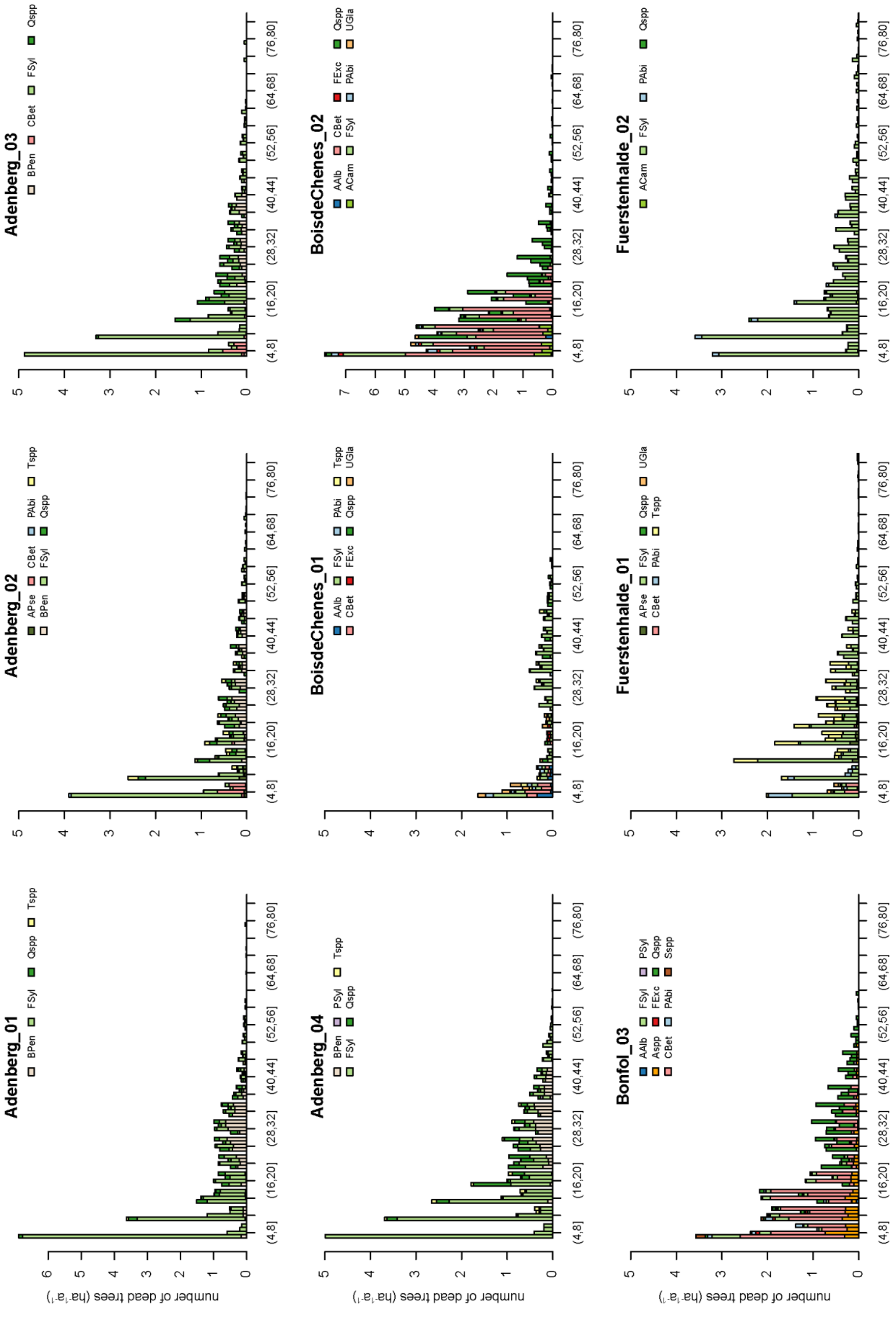


Fig. S6a Species-specific N_{dead} separately per *DBH* class (cm) observed (leftmost bar; from inventory data) and simulated by the three model versions of ForClim (from left to right: ForClim 3.3, IM_mean; IM_sd).

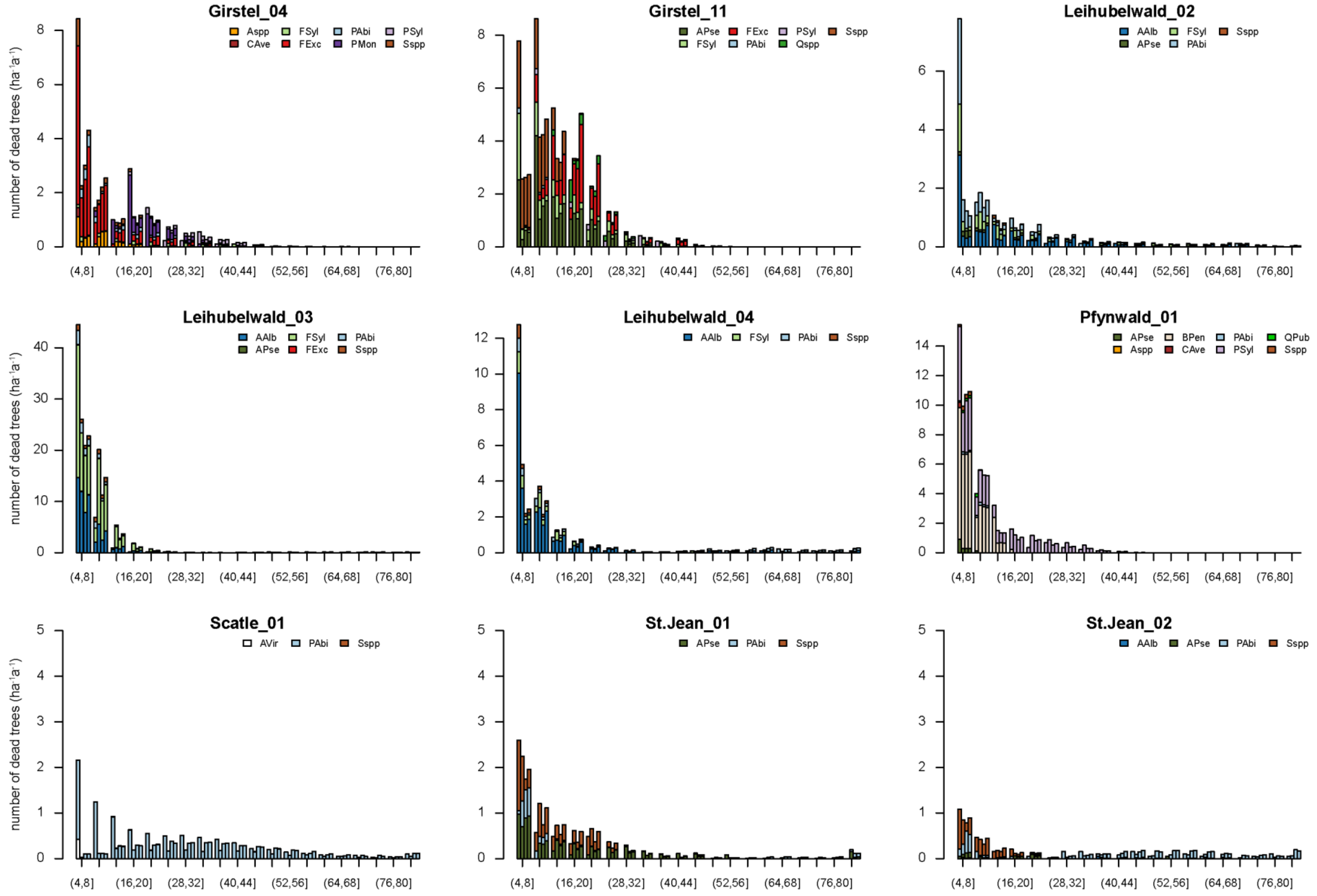


Fig. S6b Species-specific N_{dead} separately per *DBH* class (cm) observed (leftmost bar; from inventory data) and simulated by the three model versions of ForClim (from left to right: ForClim 3.3, IM_mean; IM_sd).

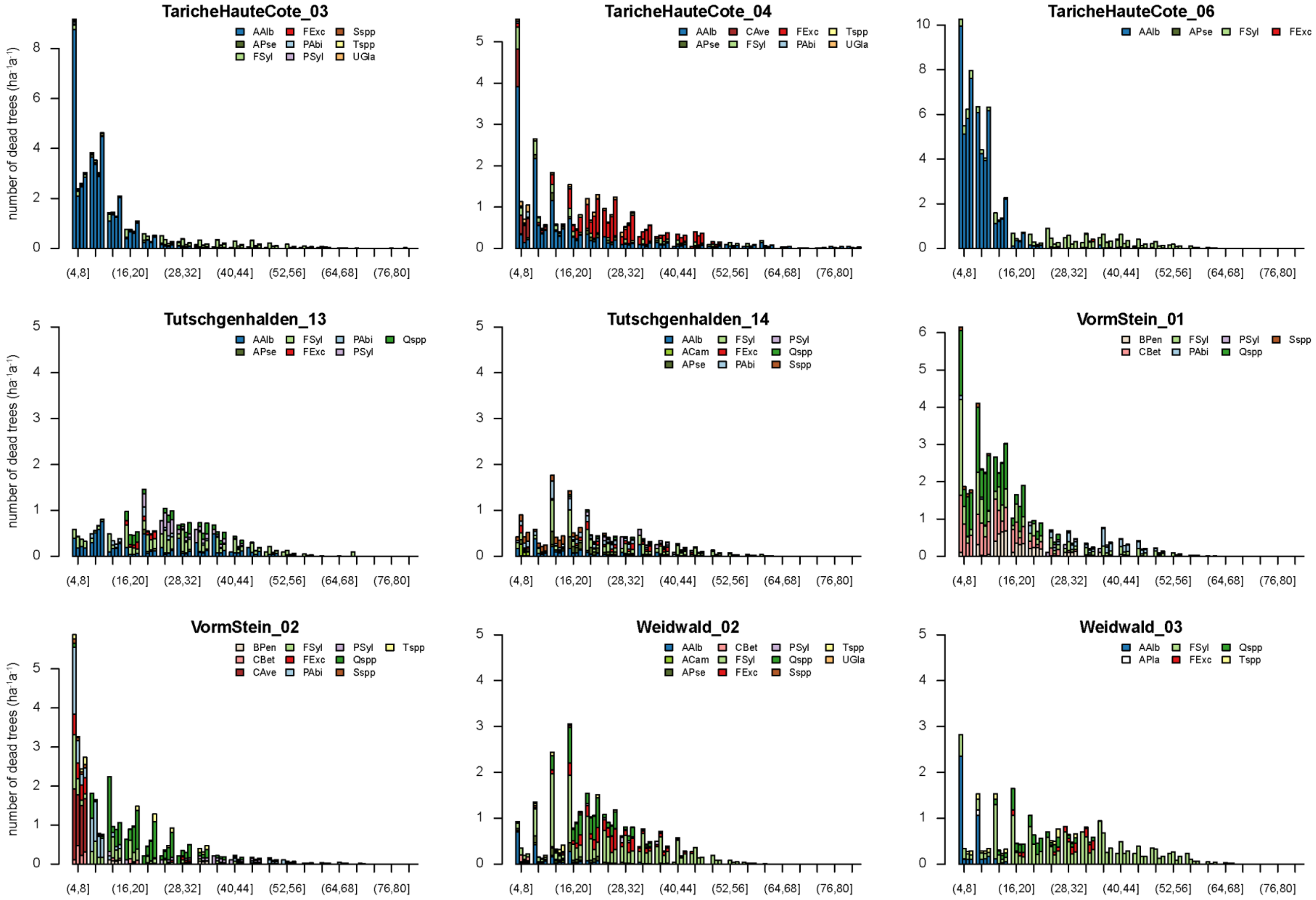


Fig. S6c Species-specific N_{dead} separately per *DBH* class (cm) observed (leftmost bar; from inventory data) and simulated by the three model versions of ForClim (from left to right: ForClim 3.3, IM_mean; IM_sd).

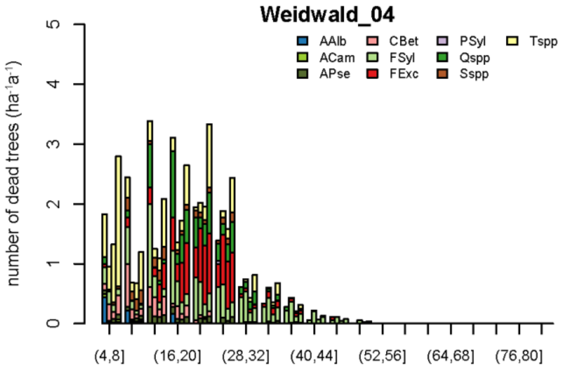
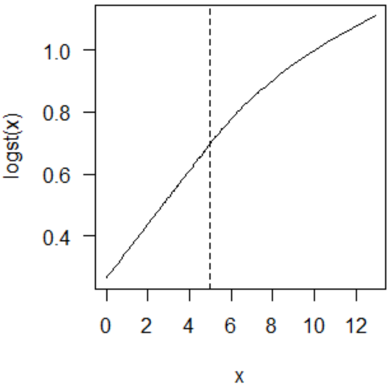


Fig. S6d Species-specific N_{dead} separately per *DBH* class (cm) observed (leftmost bar; from inventory data) and simulated by the three model versions of ForClim (from left to right: ForClim 3.3, IM_mean; IM_sd).

Appendix B – Extended material and methods

Logst-transformation



The logst-transformation is based on the common logarithm and modifies small and zero observations such that the transformation yields finite values (Stahel, 2015; cf. http://stat.ethz.ch/~stahel/regression/regr0.pdf). Below threshold *c*, the transformation continues linearly with the derivative of the log curve at this point (cf. Figure on the right, *c* = 5). The transformation threshold *c* is calibrated based on the data, following the rationale that for lognormal data 2 % of the values are identified as small. In this study, *c* was calibrated for the combined *relBAI* values of all species (*c* = 0.002183).

Climate data

Temperature and precipitation data were derived using the DAYMET model (Thornton *et al.*, 1997; available from Landscape Dynamics, WSL), interpolating MeteoSwiss station data to a grid of 1 ha cell size. Daily minimum and maximum temperatures as well as daily precipitation sums were derived for each permanent plot by calculating the average of the DAYMET cell that included the center of the permanent plot and the eight surrounding cells, following Rasche *et al.* (2012). In the mortality models, we considered mean annual air temperature (*mT*) and mean annual precipitation sums (*P*). The same data were used for short-term ForClim simulations.

Model selection

In a first step, the most promising climate or stand characteristic and its most suitable transformation (log, square root or none) were identified for each species. To this end, covariates were included in highly flexible models, i.e., model formulae that can capture even complex influences of *DBH* and *relBAI* on mortality (cf. Table 2, Formula C12 with different transformations of the climate and stand characteristics) and the covariate was selected that resulted in the smallest mean Brier Score (*BS*). *BS* corresponds to the mean squared error of the model defined as

$$BS = \frac{1}{n}\sum_{i=1}^{n}\left(p_{i,\Delta t} - y_i\right)^2$$

and ranges between 0 and 1 with low values indicating good calibration (i.e., correct mortality rates) and good discrimination (i.e., correct attribution of dead/alive status; cf. Harrell, 2015). *BS* does, however, not allow for the comparison of models based on different datasets since it depends on the overall outcome incidence, i.e., the overall mortality rate, which differs between species (Steyerberg *et al.*, 2010).

In a second step, the final model was selected from a large set of model formulas (cf. Table 2) with varying complexity and flexibility considering the terms log(*DBH*), logst(*relBAI*), their interaction and the respective quadratic terms (Formulas 1-12). These were analyzed without an additional covariate (A1-12), with the most promising climate or stand characteristic (B1-12) and with this characteristic and its interaction with logst(*relBAI*) (C3-12). A 10-fold cross-validation scheme and the 'one standard error rule' (Breiman *et al.*, 1984; Hastie *et al.*, 2001) were applied to select the most parsimonious mortality model. A stratified sampling scheme was employed in each fold to achieve roughly the original proportion of dead vs. living trees. Brier score (*BS*) values per fold were used to estimate the respective mean (*meanBS*) and standard error (*seBS*). To achieve robust estimates, the 10-fold cross-validation was repeated 20 times and *meanBS* and *seBS* were averaged, as suggested by De'ath and Fabricius (2000).

Model performance was considered as equal where the *BS* distribution fulfilled the condition $meanBS_{equal} < (meanBS_{best} + seBS_{best})$ with BS_{equal} and BS_{best} denoting the *BS* of the optional and the best model, respecitively (Breiman *et al.*, 1984). From all models with equal performance, the simplest formula was selected based on Table 2.

For models that included an additional climate or stand characteristic, also an alternative model without that covariate was derived to compare its performance with the respective full model. These were selected by applying the 'one standard error rule' only to the formulae A1-12.

AUC from cross-validation

Following Airola *et al.* (2009), cross-validation *AUC* was derived by first calculating *AUC* separately for each cross-validation fold, which were then averaged. Again, cross-valiation was repeated 20 times and the mean of all *AUC* values was reported (De'ath and Fabricius 2000).

Performance criterion p_{bias}

p_{bias}, which indicates calibration accuracy, is defined here as the difference of the mean predicted annual mortality probability ('simulated mortality') $\overline{p}_{\Delta t=1}$ and the mean annual mortality rate ('observed mortality') $\overline{y}_{\Delta t=1}$. To this end, the 'simulated mortality' $\overline{p}_{\Delta t} = \sum p_{i,\Delta t}/n$ and the 'observed mortality' $\overline{y}_{\Delta t} = \sum y_i/n$ were averaged for observations and predictions with the same mortality period length Δt. To render the values comparable, mean simulated and observed mortality rates were re-scaled to one year before calculating the overall mean. Taking the example of the 'simulated mortality', this can be formulated as

$$\overline{p}_{\Delta t=1} = 1 - \left(1 - \overline{p}_{\Delta t}\right)^{\frac{1}{\Delta t}}$$

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Appendix C – Extended discussion

U-shaped mortality

In addition to the discussion in the main document, we like to point out that the identification of mortality patterns strongly relies on the approach used. Thus, multivariate models, i.e., models including several tree characteristics such as size and growth, may elucidate a different picture than when observed mortality rates are analyzed as a function of *DBH* only. This is because a joint analysis of the influence of tree size and growth on mortality may implicitly result in U-shaped mortality over *DBH* since most of the relevant mortality agents do not result in abrupt death but may also decrease the tree's vitality and thus its growth. Although we aimed to minimize the correlation of tree size and growth by using a relative measure of growth, i.e., *relBAI*, a slight growth trend was identified for several species (cf. Fig. S5). Reduced growth at large *DBH* can lead to higher mortality probabilities of large trees in predictions for the calibration data, even though no quadratic *DBH* term is included in the formula. Bearing these interdependencies in mind, the shape of mortality over *DBH* identified by a model strongly depends on its explanatory variables and on the degree of their correlation. In our models, dependencies were most evident for *Ulmus glabra*, where *relBAI* first increased and again decreased with *DBH*. This resulted in higher mortality probabilities of large trees when the model was applied to the calibration data, although *DBH* was not explicitly included in the model.

All models revealed that only slow-growing trees have a higher mortality risk and fast growth was not associate with lethal stress. This is contrasting with the growth-differentiation balance hypothesis, which suggests a U-shaped mortality over *relBAI* (Herms & Mattson, 1992; e.g., supported by Wunder *et al.*, 2008). Instead, quadratic *relBAI* terms were always negative and thus resulted in a hump-shaped mortality pattern, which caused lower risk for very slow-growing trees and may be the result of *relBAI* = 0, and thus the logst-transformation. Finally, growth patterns before death strongly change according to the source of mortality (Cailleret *et al.*, 2017).

Climate and stand influences on mortality

When interpreting the effect direction of additional covariates, it must be taken into account that the distribution of the explanatory variables *DBH* and *relBAI* may not be independent of the environment, i.e., trees may be small and grow slowly under unfavorable conditions without being exposed to stress. Consequently, a tree with the same size and growth may have a higher chance to survive at a dry site since it is more vigorous compared to a tree having the same attributes at a moist site. Such adaptive strategies (cf. Rose *et al.*, 2009; Aranda *et al.*, 2015) are indicated by effect directions that are opposite to those expected by stress theory, i.e., lower instead of higher mortality probability, e.g., under dry conditions.

The mortality probability of *Picea abies* increased with *mDBH*, i.e., a tree of the same size and growth experiences a higher probability to die in older stands with a greater proportion of large trees. This can be attributed to the high susceptibility of this species to infestation by the bark beetle *Ips typographus* L., which preferentially attacks large host trees (Mezei *et al.*, 2014; Sproull *et al.*, 2015). In addition, stands including many large and thus tall trees may also experience a higher risk of windthrow (Mayer *et al.*, 2005).

Similarly, *Alnus incana* and *Quercus* spp. exhibited a greater mortality risk in stands with higher basal area (*BA*), which corresponds to their low shade tolerance that seems not fully reflected by small size and slow growth. Thus, trees of these species die more often when exposed to high competition (cf. Rohner *et al.*, 2012).

Mortality of *Pinus mugo* was lower at sites with greater precipitation. However, most of the observations originated from two reserves with strongly differing stand dynamics, history and site conditions. E.g., mortality of *Pinus mugo* is enhanced by fungi and bark beetles in the dry Swiss National Park, while these mortality agents are less relevant at the other site (Dobbertin *et al.*, 2001; Brang *et al.*, 2014). Therefore, we argue that the environmental gradient of this species was not sufficient to robustly estimate the effect of additional covariates and identify the drivers of the observed differences.

In contrast, mortality of *Corylus avellana* increased with precipitation. This may be the result of adaptation such that a tree with equal size and growth experiences a higher mortality probability at a site with higher precipitation because here, trees typically grow faster and have a larger size. In addition, interspecific competition may be larger under more moist conditions since competing tree species, e.g., *Fagus sylvatica*, reach larger dimensions, and thus the mortality probability of less competitive species increases.

Bearing in mind the thermophilous character of *Quercus pubescens*, its higher mortality probability at higher mean temperature suggests a similar adaptive process, especially considering that the Swiss stands are close to its northern distribution limit (San-Miguel-Ayanz *et al.*, 2016). However, the number of permanent plots available for this species was rather low, and thus the results should be interpreted with caution.

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Synthesis

In this thesis, I aimed to analyze patterns of tree death and to advance empirically-based mortality formulations. To this end, I assessed the predictive behavior and the transferability of available models to new environmental conditions, developed and evaluated new species-specific mortality formulations and implemented these in the dynamic forest model ForClim. In the following, I aim to synthesize the results of the four chapters. In particular, I comment on (1) the state of the art in empirical mortality modeling, (2) the suitability of different calibration datasets, (3) the patterns of tree death with respect to tree size and growth, (4) the climatic sensitivity of mortality predictions and (5) the performance of empirical mortality formulations in Dynamic Vegetation Models (DVMs). I conclude by outlining what I believe to be fruitful strategies to further improve the understanding and prediction of mortality using empirical models.

State of the art in empirical tree mortality modeling

In Chapters 1 and 2, I systematically analyzed empirical mortality models that have been published in the last decades with respect to their general structure, predictive behavior and suitability for simulating tree mortality, with a particular focus on their structural suitability for implementation in DVMs. Literature search revealed an increasing number of studies since the turn of the millennium that used inventory and dendrochronological datasets to develop mortality models of individual trees. These intensified efforts can be considered as a response to previous calls asking for more emphasis on tree mortality as a key process of large-scale vegetation dynamics (Allen & Breshears, 1998) and an improved, empirically-based quantification of tree death in models of forest dynamics (Hawkes, 2000; Bugmann, 2001; Keane *et al.*, 2001). However, the studies differ considerably in the approaches used for model development (cf. Cailleret *et al.*, 2016). In addition, mortality models were typically calibrated using datasets that are restricted with respect to site, species and time, thus complicating and limiting their application and comparison.

Therefore, it seemed beneficial to synthesize the various models, e.g., by carrying out a multivariate meta-analysis (Jackson *et al.*, 2011). By doing so, the effect sizes of the individual mortality predictors could have been systematically combined to obtain more general estimates of the effects, e.g., of tree size and growth. However, it was impossible to separate the effect of single variables due to the nonlinear link between the mortality probability and its predictors, i.e., the logit link function (Bagos & Adam, 2015), and the different period lengths of the mortality probability. In addition, covariance matrices that would have been necessary for multivariate meta-analysis were typically not reported.

Instead, I compared the available mortality models at the level of their predictions by applying them to inventory and tree-ring datasets. In Chapter 1 (cf. Hülsmann *et al.*, 2017), I used inventory-based mortality models from all over Europe to predict the probability of tree death for inventory data in Swiss and German forest reserves and compared the predictions with the observed tree status. This model validation using independent datasets constitutes a rigorous examination of model transferability and, for the first time, allowed for the comparison of mortality patterns at the European scale. The results indicate that many mortality models can be applied successfully beyond their calibration domain. However, others failed to match observed mortality patterns or achieved low prediction or classification accuracy. In addition, it was possible to identify particularly suitable modeling strategies. Specifically, mortality rates were predicted with higher accuracy by models that included covariates for growth or competition at the level of individual trees and that were applied in a similar ecological context. Furthermore, the results emphasize the pivotal importance of tree growth to achieve a good discrimination between dead and living trees.

The approach that I applied to obtain these findings has two main restrictions: (1) the mortality models that were calibrated with data from all over Europe could only be validated with data from Central European forests, and (2) the validation data were collected in unmanaged stands only, i.e., managed forests were not used as a reference. Since different mortality rates and patterns are assumed to prevail in managed vs. unmanaged stands (Bravo-Oviedo *et al.*, 2006), I assessed if the predictive accuracy of mortality models from unmanaged forests was superior to that from managed forests when validated with the reserve data. Although no clear effect was found, this issue may require additional verification, e.g., using validation data from forests with different management intensities, such as data from National Forest Inventories (NFI).

In Chapter 2, I analyzed the large variability of mortality predictions more closely. To this end, I also considered tree-ring-based mortality models that were applied to dendrochronological data. The predictive behavior of the models was compared using a hierarchical cluster analysis, which, however, revealed no distinct patterns with respect to model characteristics or the calibration species. These results reflect the diversity of approaches in mortality modeling and emphasize that these differences do not modify mortality predictions in a systematic manner. The predictions from tree-ring-based mortality models were characterized by even larger diversity than those from inventory-based models, in particular due to different sampling schemes (cf. *Calibration datasets*).

The mortality studies analyzed in Chapters 1 and 2 differed considerably concerning calibration data, methodology and covariates considered. As these characteristics influence the suitability of a model for being applied in a new context, a comprehensive model documentation, covering the data and their processing, the model development and the covariate selection would be essential, but unfortunately was often not provided. This strongly complicated the analyses that were carried out in Chapters 1 and 2. Among others, it was necessary to get in contact with several authors in order to adequately reconstruct their models, e.g., because of unreported units or erroneous model specifications (cf. Chapter 1, Table S4). Finally, the diameter range that is covered in the calibration data was not reported in several publications, which may result in accidental extrapolation of the models.

In conclusion, the review of mortality studies revealed that the availability of empirical mortality models has increased strongly in the last decades. Their incorporation in DVMs, however, still lags behind (Bircher, 2015). Developers of such models may benefit from the systematic presentation of model characteristics, parameterization and expected mortality predictions of inventory and tree-ring-based mortality models (cf. Chapter 1, Fig. S12 and Chapter 2, Fig. 2). This would stimulate the evaluation of currently available mortality algorithms and finally may lead to more empirical mortality formulations being incorporated in DVMs.

Calibration datasets

In this thesis, a wide range of inventory and tree-ring-based mortality models were developed and/or evaluated in calibration, validation and simulation, revealing different assets and drawbacks of the two data sources. During the last decades, inventory datasets have been explored extensively for the development of mortality models; already 46 European models were independently validated in Chapter 1 alone. The analysis of the drivers of validation performance of these models revealed no effect of data amount on prediction or discrimination accuracy, and even models based on a few hundred observations only resulted in reliable mortality patterns. This suggests that the models were not restricted by the amount of calibration data. Other factors, however, are likely to have dominated the transferability of the mortality formulations to our reserve data, i.e., the predictors considered and the degree of similarity between calibration and validation sites and stands. I conclude that datasets for the development of mortality models do not necessarily need to be large to obtain high validity within their calibration domain. Yet, the risk that the mortality patterns and rates are unreliable increases if models are calibrated using very small datasets with few death events only. If models of higher generality are sought, datasets covering a larger number of stands along sufficiently wide and well-replicated environmental gradients are of great importance for detecting environmental effects on the mortality probability. This was shown in Chapter 4 (cf. Hülsmann *et al.*, in prep.), where poorly supported gradients resulted in questionable environmental effects in the models (cf. *Climatic sensitivity of mortality models*).

Using inventory data for the development of tree mortality models that include growth variables requires a set of three inventories per tree and thus results in a strong aggregation of growth and mortality information over multiple years. This may have complicated the identification of environmental effects to explain spatial and temporal variability in mortality in Chapters 3 (cf. Hülsmann *et al.*, 2016) and 4. The low temporal resolution can be regarded as the major disadvantage of inventory data for the calibration of mortality models.

As shown in Chapter 2, mortality predictions of tree-ring-based models are highly sensitive to the sampling scheme (cf. Cailleret *et al.*, 2016). In turn, it is clear that none of the possible schemes based on dendrochronological data alone can provide reliable mortality rates at the stand scale. The paired sampling forces mortality probabilities to vary around an average value of 50 % (cf. Chapter 2, Fig. 2). Yet, the ‘all-years-approach’ considering all available observations mimics mortality probabilities at a similar level to that of stand-scale mortality rates, at least for small trees, and has been successfully incorporated in a DVM (Bircher *et al.*, 2015). Nevertheless, this sampling involves a bias towards dead trees at larger diameter (Wunder *et al.*, 2008b; Cailleret *et al.*, 2016). Therefore, we fitted mortality models to observations from tree-ring data that were re-sampled with respect to inventory-based mortality rates (Vanoni *et al.*, in prep.). This approach allowed for combining the annual resolution of growth observations in dendrochronological data with stand-scale mortality rates (cf. Das *et al.*, 2007). Although the calibration performance of these models was considerably high, the re-sampling of limited tree-ring data introduced a bias since single trees were highly influential if only few trees were available in a diameter class. Consequently, we observed a high uncertainty of model estimates, in particular for small and large trees. Accounting for these uncertainties when implementing the tree-ring-based mortality formulations in ForClim improved the simulations because it reasonably increased mortality. We conclude that the approach appears promising in theory but the re-sampling strategy is crucial, in particular for small tree-ring datasets. This suggests that, in contrast to findings of Wunder *et al.* (2008b), models based on tree-ring datasets suffer more from restricted data amounts than those based on inventory data.

Assessing data on tree populations in the field nearly always involves a sampling bias (Morrison & Marcot, 1995). The following issues should be considered if long-term datasets are used for the calibration of mortality models based on tree size and growth. In forest inventories, trees are measured only if their diameter at breast height (*DBH*) exceeds the calipering limit (i.e., ingrowth). The aggregation of three re-measurements per tree to obtain one mortality record may result in a systematic bias for ingrowth for two reasons: (1) trees with a *DBH* close to 4 or 7 cm in the second inventory must have grown slowly between the first and second measurement (cf. Fig. 1), and (2) using tree-ring data from dead trees only and aggregating all available observations (i.e., sampling scheme *T*; cf. Cailleret *et al.*, 2016) may create a bias towards fast growth for small trees since many small and slow-growing trees died but decayed before they could be sampled. In addition, a bias towards slow growth for larger trees may occur since these are expected to show reduced vitality prior to death (cf. Bigler & Bugmann, 2003; Nehrbass-Ahles *et al.*, 2014; Vanoni *et al.*, 2016). Thus, the size-specific growth patterns from the two data sources are distinctly different. I suggest that the bias involved in inventory-based approaches is rather small, whereas it may be inappropriate to estimate the relationship between tree size, growth and mortality from tree-ring data including dead trees only. In any case, the sampling of the underlying data must be considered for interpreting patterns of mortality.

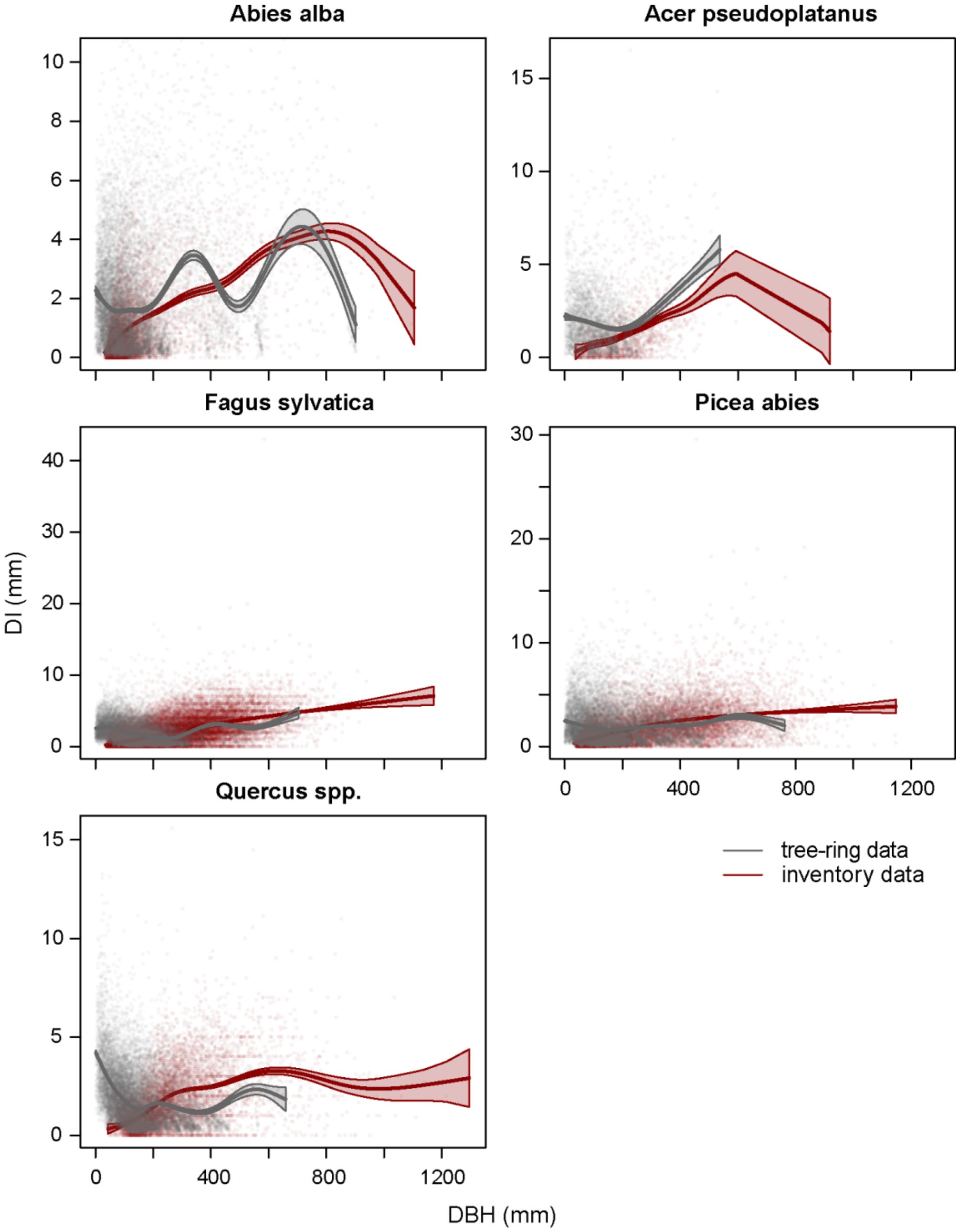

Fig. 1 Absolute growth (annual diameter increment, *DI*) from inventory data (red) in comparison with growth from tree-ring data (gray) as a function of *DBH* for the species *Abies alba*, *Acer pseudoplatanus*, *Fagus sylvatica*, *Picea abies* and *Quercus* spp.. Note that the data do not allow for assessing the sampling bias and its consequences for the mortality models due to different patterns of death observations. Dots indicate the observed growth values. Lines and polygons show the fit of Generalized Additive Models (GAM) with 95% confidence bands.

This thesis provides multiple evidence that the prediction of mortality is particularly crucial for very small and very large trees. Inventory-based models revealed highly variable predictions for the mortality probability of small trees (cf. Chapters 1 and 2), whereas the discrimination ability was usually lowest for large trees (cf. *AUC* patterns over *DBH*, Chapters 3 and 4). Similar uncertainties in mortality predictions were found when inventory and tree-ring-based models were incorporated in ForClim, i.e., the prediction of tree death was particularly problematic for *DBH* < 10 cm and > 60 cm (cf. Chapter 4 and Vanoni *et al.*, in prep.). First, this can be attributed to the limited amount of data supporting mortality predictions for small and large trees. Inventory data are typically truncated at a specific *DBH*, wich is often higher than in the forest reserves investigated here (e.g., 10 cm; cf. Eid & Tuhus, 2001). In dendrochronological samples, small (dead) trees are underrepresented since they may decay faster and it is more difficult to crossdate their short ring width series (Nehrbass-Ahles *et al.*, 2014). Large trees are underrepresented in most European forests in general. Thus, mortality predictions for small and large trees are prone to extrapolation when such models are incorporated in DVMs. Often, this can not be avoided since little empirical evidence is available for mortality patterns of smaller trees. In addition, DVMs are particularly sensitive to biased mortality predictions for trees with small and large *DBH*, i.e., survival of small trees strongly shapes the species composition and, in the long term, the simulated stand structure (Wernsdörfer *et al.*, 2008), whereas survival of large trees defines light availability for all other trees on a patch as well as key stand attributes such as carbon storage (cf. Chapter 4). Second, the nature of mortality varies during the lifetime of a tree (Harcombe, 1987). With increasing tree size, competition becomes less relevant, and more complex mortality agents gain importance (Franklin *et al.*, 1987). Mortality models may thus be less accurate in predicting the correct tree status at large *DBH* (cf. *AUC* patterns over *DBH*, Chapters 3 and 4).

Patterns of tree mortality with respect to tree size and growth

In this thesis, mortality models were developed based on two main predictors, which were identified as highly suitable to accurately predict tree mortality: tree size and radial stem growth. This is supported by the assumption that the dimensions of a tree represent its access to resources and constraints on the hydraulic system (Grote *et al.*, 2016) but also its susceptibility to mechanical damage. In turn, radial growth provides an indication of tree vitality (Harcombe, 1987; Dobbertin, 2005). With a few exceptions only, mortality over tree size and growth (assessed as relative basal area increment, *relBAI*) was reverse J-shaped in the inventory-based models (cf. Chapters 3 and 4). The predictions of most previously published mortality models based on inventory and tree-ring data confirmed this patterns (cf. Chapters 1 and 2). I conclude that this provides strong evidence for considering the reverse J-shaped form as a general pattern of mortality in managed and unmanaged forests of Central Europe.

In turn, this suggests that most trees die because of competition. There is only little evidence for pronounced instability of large trees (Holzwarth *et al.*, 2013), which would have resulted in U-shaped mortality that has often been proposed as a reasonable relationship of tree size and mortality (Buchman *et al.*, 1983; Lorimer & Frelich, 1984). In my case, only the data from a primeval beech forest in Western Ukraine revealed a higher mortality risk for large trees. This suggests that the processes that may act to amplify the mortality of large trees such as stem rot or wind breakage develop only in stands that have not been managed for much longer than the Swiss and German reserves. For the application in DVMs, a U-shaped form of mortality over tree size may be desirable from a mathematical perspective since it confines tree age more strongly than a reverse J-shaped relationship. This may be necessary in ForClim (and other DVMs) since large trees, mostly of *Fagus sylvatica*, showed a very high persistence and strongly controlled the structure of unmanaged stands in long-term simulations (cf. Chapter 4). Models that feature U-shaped mortality may perform more similarly to the maximum age approach that is currently incorporated in ForClim (Bircher *et al.*, 2015; Mina *et al.*, 2015), and that was superior in simulating stand dynamics, in particular for *Fagus sylvatica*.

In contrast, the tree-ring-based models indicated a clear U-shape of mortality over *DBH*, most pronounced for slow growing trees (Vanoni *et al.*, in prep.). This is surprising since the models were developed based on dendrochronological data re-sampled using the same inventory data as for the inventory-based models. These distinct mortality patterns likely result from differences in the model selection approach (more robust formulae were favored in selecting inventory-based models, cf. Chapter 4) and in the sampling characterizing the underlying data sources (different patterns of tree size and growth, cf. Fig. 1). In addition, the mortality predictors in the tree-ring-based models were not log-transformed. It is therefore difficult to compare the patterns obtained from the two model types. I suggest that mortality relationships found using inventory data are more reliable since they feature a lower sampling bias. In addition, the re-sampling procedure should be revisited to address the sampling bias.

It must also be taken into account that the type of the growth variable influences not only the growth-mortality relationship but also the shape of mortality with respect to tree size, if the covariates for size and growth are correlated. This is more likely true for absolute growth variables, e.g., diameter increment (*DI*) or ring width (*RW*, used in the tree-ring-based models). In contrast, relative measures of growth, e.g., *relBAI*, are less correlated with tree size (compare Fig. 1 and Chapter 4, Fig. S5 for absolute and relative growth, respectively). For identifying mortality patterns with respect to tree size and growth, the predictors should be correlated only weakly (Dormann *et al.*, 2013), and thus relative growth measures are more suitable.

The relationships between mortality and its main predictors, tree size and growth, that were considered in this thesis are relatively simple, i.e., only a linear and a quadratic term were tested. Other authors suggested that more flexibility is required to capture the relationship between tree size, growth and death, and thus they applied restricted cubic splines or non-parametric Bayesian methods (e.g., Wunder *et al.*, 2007; Metcalf *et al.*, 2009). In contrast, the model selection used in Chapters 3 and 4 avoids complex models that are not well supported by the data but favors parsimonious models that are suitable for the robust prediction of mortality, in particular outside their calibration domain (Hawkins, 2004). Since the newly developed models achieved similarly high performance as more flexible approaches (cf. Wunder *et al.*, 2008a), I recommend these simpler models as promising alternatives that require fewer parameters and are much easier to be reconstructed (cf. model coefficients of restricted cubic splines, Chapter 1, Table S4). Correspondingly, the relationships between log-transformed growth and mortality that were identified using restricted cubic splines may be approximated well using a linear and a quadratic term (cf. Wunder *et al.*, 2008a, Fig. 5). However, suitable transformations should be considered for the explanatory variables (Mosteller & Tukey, 1977). Finally, more flexible relationships may be considered with the focus on a detailed analysis of mortality patterns. In this case, higher flexibility should not be restricted to growth but should also be applied to tree size (cf. Chapter 1, Fig. 1 and Chapter 2, Fig. 1+2).

Based on the mortality patterns that were identified for a wide range of species in Chapter 4, I identified lifespan and stress tolerance as the most important attributes for characterizing the species-specific relationship of tree size, growth and mortality (cf. Wunder, 2007). Thus, I suggest these characteristics to be used jointly for the classification of tree species into ‘Plant Functional Types’ (PFTs) if species-specific models are not feasible due to data limitations. However, this approach should be further verified (cf. Bircher, 2015). In European temperate forests, where disturbance-related mortality and large dieback are rare, species may exhibit rather similar mortality rates and patterns (Allen *et al.*, 2010). In ecosystems that are more strongly shaped by insect- or drought-related, large-scale mortality events, species should probably be grouped more cautiously due to differences in their susceptibility to biotic attacks (Clancy *et al.*, 2013). Unfortunately, the large differences in model approaches and the pronounced variability in predicted mortality probabilities made it impossible to verify the need for species-specific models or the suitability of the grouping that was proposed in Chapter 4 based on the genealogy constructed in Chapter 2.

Despite their high performance as predictors of tree mortality, the predictive power of size and growth is restricted to mortality agents that are associated with particular *DBH* classes or growth levels. Since tree death is a complex process, the unexplained variability of the model remains typically high (*AUC* are rarely > 0.9; cf. Boeck *et al.*, 2014). This 'stochastic' part of mortality, which in the reserve dataset probably is mostly associated with mechanical damage or insect attacks (Larson & Franklin, 2010), may constrain the performance of empirical mortality models at a certain, probably species-specific limit that cannot be exceeded (cf. Chapter 3 and 4). These small-scale disturbances are reflected in the intercept of the mortality models and ensure correct mortality rates at least for the calibration data, but do not improve the discrimination accuracy of a model, i.e., *AUC*. The low ability of the mortality models that I developed to simulate the highly variable mortality rates (cf. $rmad\, p_{bias}$, Chapter 4) suggests that it is rather difficult to explain the spatial variability of mortality with tree characteristics. As also environmental covariates only weakly improved the mortality models (cf. Chapter 3 and 4), improved concepts for integrating the stochasticity in mortality simulations should be considered and evaluated, e.g., by accounting for the uncertainty in parameter estimates (cf. Chapter 4 and Vanoni *et al.*, in prep.).

Climatic sensitivity of mortality models

Tree mortality studies are often justified by the need for understanding and predicting the reactions of ecosystems to future environmental change (Adams *et al.*, 2013), in particular to drought (McDowell *et al.*, 2013b). Inherently, this implies that mortality formulations need to be sensitive to climatic conditions. Three main pathways to achieve this may be distinguished: (1) empirical models that explicitly include environmental covariates (e.g., Dietze & Moorcroft, 2011; Neuner *et al.*, 2015), (2) empirical models that are based on predictors that themselves respond to environmental conditions, and (3) truly mechanistic models that explicitly incorporate the physical and biological processes involved (e.g., McDowell *et al.*, 2013a). The advantages as well as the restrictions of empirical and mechanistic approaches have been discussed comprehensively in Adams *et al.* (2013). I believe that mechanistic models are excellent to test hypotheses, disentangle the underlying processes and, in general, improve our understanding of the highly complex process of tree death. As long as this knowledge remains restricted, empirical modeling may serve as a relatively simple and adequate solution to simulate tree mortality.

Environmental covariates are considered in empirical models with two distinct goals: (1) to account for the spatial and temporal variability in the relationship of tree characteristics and mortality, i.e., to improve model applicability and generality, and (2) to allow for mortality simulations that respond to environmental conditions and respective changes. Thus, today’s spatial differences are used as a proxy for future climate change, i.e., space is considered as a surrogate for time (Pickett, 1989; Pearson & Dawson, 2003). This approach was comprehensively evaluated in Chapter 3 and 4. To this end, I studied the mortality of 18 European tree species along environmental gradients and explicitly considered a wide range of environmental covariates in models that predict tree mortality based on size and growth. In contrast to expectations, additional climate and stand characteristics only weakly improved the prediction and discrimination accuracy and were therefore retained in the model for a few species only. The following factors may explain this finding: tree size and growth implicitly reflect environmental influences on mortality (e.g., stand density is well reflected by tree growth, with the advantage of growth being assessed at the level of single trees and density only at the plot level); inventory data provide growth and mortality information aggregated over several years and thus only poorly reflect short-term processes; environmental covariates were available at the level of permanent plots and thus may have lower explanatory power for the mortality probability of a single tree; and detailed drought effects could only be analyzed for *Fagus sylvatica* (cf. Chapter 3) since data on soil water conditions for other species were limited.

Moreover, the environmental effects retained in the models were not always ecologically plausible (cf. Chapter 4), suggesting that the data requirements for deriving climate-sensitive mortality models are particularly high. Suitable datasets should encompass broad environmental gradients including marginal populations with a considerable replication of the site conditions. In my opinion, it is therefore necessary to constrain the variable selection and aim for model robustness and parsimony in order to avoid questionable and insecure effects. Therefore, a future increase of mortality due to climate change may not be directly assessable from such parsimonious mortality models. This is in contrast to current trends of high impact journals that strive for raising great attention in and beyond the scientific community. I believe that such trends may bias the outcome of current mortality studies. Due to a robust model selection, the models that I developed remained simple and thus agree with the concept of parsimony that is especially helpful when mortality functions are to be implemented in DVMs (Hawkins, 2004).

As tree growth is a surrogate indicator for the carbon balance of an entire tree (Kobe & Coates, 1997), models may implicitly account for the effects of climate and stand characteristics on mortality. Under stress, radial stem growth has lower priority than photosynthetic tissue and root growth and well reflects the factors that impair the vitality of a tree, e.g., drought, frost, competition and pests (Dobbertin, 2005). Hawkes (2000) thus proposed growth as a biologically reasonable mortality predictor and even as a ‘resolution to the mechanistic-empirical divide’. Mortality models that respond to the environment via tree growth are appealing since radial stem growth is already simulated in many DVMs, and thus the approach retains simplicity and parsimony. Nevertheless, the adequacy of this assumption cannot be verified with the data at hand, and the combined response of tree growth and mortality to environmental drivers should be investigated further, e.g., using data with higher temporal resolution and better coverage of environmental gradients. In addition, the propagation of climatic signals via growth to mortality should be studied in a simulation environment, e.g., by applying ForClim and evaluating the effects of drought on simulated tree growth and subsequently on mortality. Finally, experiments and mechanistic models may assist in disentangling the relationships between environment, tree characteristics and mortality (Adams *et al.*, 2013). Although intra-specific genetic variation may additionally affect the relationship between mortality and its predictors (Anderegg, 2015), I consider environmental effects as more substantial and suggest that their estimation should have priority. Finally, the identification of genetic influences on mortality and their interaction with the environment may require excessively large datasets and thus may not be feasible with observational data.

Both empirical approaches, however, are restricted to today's climate gradients while future conditions may be beyond current extremes (Bugmann, 2014). Thus, the relationships between mortality and its predictors are extrapolated when applied under future climate scenarios. To be implemented in DVMs, growth-based mortality formulations additionally require that tree growth is simulated adequately in response to future climates. However, it is impossible to test if the relationships between climate, growth and mortality will remain stable in a changing environment, in particular since plasticity and local adaptation may alter current mortality patterns (Morin & Thuiller, 2009). This emphasizes that mortality algorithms will require ongoing refinement and verification based on experiments and observations of tree reaction, particularly during extreme drought events.

Empirical mortality models in DVMs

The mortality models derived in Chapter 4 were incorporated in the DVM ForClim and evaluated based on short- and long-term simulations. Similar to an earlier attempt (cf. Bircher, 2015), the simulations obtained with the new mortality models were inferior to the current version of ForClim, although to a lower extent. This lower performance has been attributed to the growth model in ForClim, since both processes are strongly intertwined (Bugmann, 2014). Since the mortality models were developed based on the same data that were used for the historical (short-term) simulations with ForClim, i.e., within the domain of forest reserves in Central Europe, the interdependencies of growth and mortality could be analyzed more closely. To this end, simulated growth and mortality were compared with the respective observations to detect discrepancies in the process representation in ForClim. While the overall level of simulated tree growth appeared promising, its variability was underestimated (cf. Chapter 4, Fig. S4), among others due to the insufficient spatial heterogeneity in the ForClim simulations. Since the trees were allocated randomly and evenly to the initial set of patches, both the more open and the denser parts of the stands are not represented. Patches with high competition may develop during the simulation, but this ‘diversification’ appeared rather slow. In addition, the simulation of size-specific growth revealed shortcomings, in particular for small trees and for *Fagus sylvatica*.

Two consequences arise for the simulation of mortality: (1) the lack of growth extrema, in particular of low growth values, results in an underestimation of mortality due to the nonlinear link between growth and mortality, and (2) under- or overestimated growth for specific size classes produces incorrect patterns of mortality over tree size and distorts the simulated stand structure. Thus, the influences of tree size and growth on mortality cannot be analyzed independently. For enhancing the performance of inventory-based mortality models in DVMs, I suggest that a more realistic representation of growth variability could improve the mortality predictions for several species. For *Fagus sylvatica*, however (and possibly also for some species of minor importance), the growth calculation for small trees should be reconsidered. The growth module in DVMs typically simulates no biotic and mechanical damage nor reduces tree growth in response to such factors, which however are of great importance for forest dynamics. For that reason, simulated growth has a lower ability than observed growth to accurately predict mortality, albeit biotic and mechanical damage are probably less relevant for reduced growth than competition and environmental stress (Dobbertin, 2005).

Finally, the strong effect of tree growth on mortality may explain why the calibration performance of inventory-based models and their performance in ForClim were related only weakly (cf. Chapter 4). More precisely, the variation of the prediction accuracy between sites and inventory periods for the developed models ($rmad\ p_{bias}$) was not correlated with the root mean square error (*RMSE*) of stand characteristics simulated by ForClim. Also, high discrimination accuracy (*AUC*) did not necessarily guarantee a high performance of the species' model in the DVM simulation. This does not disprove the advantage and suitability of the measures that I used to assess calibration performance, but rather emphasizes that the differences between observed and simulated growth dominated the behavior of the mortality formulations. Addressing these differences may allow for further conclusions with respect to the calibration performance and the performance levels that can be considered as being 'good enough'. In my thesis, such judgments were made subjectively, e.g., in Chapter 1, since objective thresholds to identify 'good performance' are missing. Nevertheless, I would like to emphasize the need for reporting the prediction accuracy of mortality models (i.e., p_{bias} or estimates describing its variability) since the correct prediction of mortality rates is a fundamental requirement for simulations of forest dynamics using DVMs (cf. Bircher *et al.*, 2015; Cailleret *et al.*, 2016). Until now, this aspect has often been neglected in the development of tree mortality models, as only *AUC* was reported.

As indicated above, an improved representation of the variability of growth and mortality may be essential to achieve more realistic mortality predictions in DVMs. Accounting for parameter uncertainty strongly improved the ForClim simulations based on the tree-ring-based mortality models, most likely due to the small sample size and the large uncertainty in the estimated parameters. Higher mortality probabilities were also the consequence of using this approach for the inventory-based models. Species that were underestimated already were affected positively, but not so the very important species *Fagus sylvatica*. Since the interactions of growth and mortality may have dominated the simulation results, I suggest that accounting for parameter uncertainty should be further evaluated and may result in more realistic and – as emphasized especially in Chapter 4 – more variable mortality rates. In this context, Bayesian methods constitute a promising solution to account for uncertainty and correlation among the parameters (Van Oijen *et al.*, 2005).

Strategies for improved mortality predictions

In this thesis, the potential of empirically-based mortality models was determined and mortality formulations for a wide range of European tree species were provided. Nevertheless, also shortcomings of current mortality models were identified, suggesting the following strategies for further advancements.

Representation of the sapling stage

To improve the mortality prediction for small trees, mortality in the *DBH* classes < 10 cm should be analyzed in detail, e.g., using existing or newly installed regeneration surveys, inventories without calipering limit, stem cross-sections or experiments (Wernsdörfer *et al.*, 2008; Evans & Moustakas, 2016). Following Kobe and Coates (1997) and Caspersen and Kobe (2001), species-specific mortality models for individual saplings may be built based on growth and site conditions, possibly complemented by a measure of size. To ensure their predictive ability in a simulation environment, the simulation of growth for small trees should be evaluated thoroughly using observational data. In contrast to mortality probabilities for individuals, mortality algorithms for DVMs may be based on models that predict mortality rates of particular *DBH*-cohorts depending on stand density and site conditions only. I expect that the development of such models may provide robust estimates while requiring fewer data (Lichstein *et al.*, 2010). Finally, it must be considered that sapling mortality may be strongly affected by ungulate browsing, the degree of which has a great potential for explaining the recruitment potential of different tree species and its regional variability (Didion *et al.*, 2011; Clasen *et al.*, 2015).

Environmental influences on mortality

To explicitly address the temporal and spatial variability in mortality patterns and to verify the climate sensitivity of mortality models via tree growth, the relationship between tree size, growth, mortality and environmental conditions should be consolidated using data with high temporal resolution such as annual inventories (e.g., Neuner *et al.*, 2015) or dendrochronological data (e.g., Gillner *et al.*, 2013) along sufficiently wide and well-replicated environmental gradients, preferentially at larger, e.g., European, scale. Provided that such extensive datasets are available, environmental variables should be tested not only as an additional term but also assuming nonlinear relationships (i.e., quadratic terms) and in interaction with tree size and growth since the environment, e.g. drought, may act differently on small vs. large or slow vs. fast growing trees (Grote *et al.*, 2016).

Disturbance-related mortality

Future efforts should also address an improved representation of disturbance-related mortality, both non-catastrophic, small-scale mortality and larger events of forest dieback, which are likely to gain in importance under future climates (Seidl *et al.*, 2011). The results of Chapter 3 revealed that mortality models from primeval forests, e.g. the Ukrainian beech forest, may help to improve long-term predictions of Potential Natural Vegetation (PNV) since they provide improved estimates of the mortality risk of very large trees. Such old-growth forests have an extraordinary value to investigate and understand natural mortality and its patterns including instability of large trees and disturbances. Nevertheless, other datasets and tools than those proposed in this thesis are needed for incorporating disturbance-related mortality more explicitly in a simulation context. To this end, the separation of mortality agents is required, which is difficult because of strong interdependencies. Thus, mortality data are needed that allow for assigning the reason of tree death – or a combination of several mortality agents – to death events, which requires at least annual mortality assessments including a detailed visual inspection of the dead trees (Holzwarth *et al.*, 2013; Lutz, 2015). In this context it would be particularly interesting to differentiate competition-induced mortality and build a respective mortality model, most likely with a very high accuracy, and to address other mortality agents, e.g., wind or insects, using process-oriented sub-modules.

Empirical mortality models in DVMs

When incorporated in DVMs, the spatial and temporal variability in mortality should be considered better, e.g., by accounting for uncertainty in the model parameters, and by making sure that the spatial heterogeneity of the forest stand is adequately represented in the initialization procedure of the model. The approach tested here could be further advanced using Bayesian approaches that explicitly consider the correlation among parameters (Van Oijen *et al.*, 2005). Variability was also identified as an important feature of the simulation of tree growth, emphasizing that the sub-modules of DVMs should have a good representation of uncertainty (cf. Bircher *et al.*, 2015).

The mortality models developed here were implemented in one particular DVM, taking ForClim as a case study. To assess their suitability in a more general context, their performance should be further evaluated in other models, e.g., SORTIE (Pacala *et al.*, 1996), FORMIND (Huth & Ditzer, 2000) or iLand (Seidl *et al.*, 2012). In addition, I suggest to evaluate previously published mortality models in DVMs, which is facilitated by the systematic representation of their model coefficients (cf. Chapters 1 and 2).

Data requirements

Although several data sources have been used for modeling tree mortality, I am convinced that more robust models and more reliable conclusions are possible if existing data are explored more effectively and combined to larger datasets, and if new data are gathered with the clear objective to address particular features of mortality. In summary, datasets should

(1) provide size, growth and mortality of saplings and trees at an annual resolution with a representative sampling to allow for the derivation of stand-scale mortality rates,
(2) cover full environmental gradients that are quantified by meaningful and reliable climate and stand characteristics including drought conditions and soil water availability,
(3) specify the mode of death or reason for mortality, and
(4) be gathered in managed and unmanaged stands as well as in primeval forests to include large tree sizes and old-growth stages, such that disturbance patterns become evident.

In spite of the large number of empirical mortality models and recent efforts towards improved mortality formulations in DVMs, I believe that the empirically-based modeling of tree mortality still holds a great potential. The strategies towards an improved understanding and quantification of mortality that were developed based on the extensive analyses in this thesis hopefully will facilitate such advancements.

This thesis allows one to systematically assess previous strategies for tree mortality modeling for the first time and provides robust mortality models for a wide range of tree species. Their mortality patterns could be related to species-specific life history strategies. Finally, the analyses indicated the most important mortality factors and their importance in managed and unmanaged forests in Europe. Due to the unique spatial extent and the extensive database in combination with cautious, systematic analyses and modelling, the conclusions can be transferred to a wider European context.

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Curriculum vitae

Lisa Hülsmann
May 31, 1985
Bielefeld, Germany

Education

10/2012 - 09/2016	**Doctoral studies at WSL and ETH Zurich** Title: ‘Tree mortality in Central Europe: Empirically-based modeling using long-term datasets’
01/2013 - 05/2015	**Diploma of advanced studies ‘Applied Statistics’ at ETH Zurich**
10/2008 - 03/2012	**Master ‘Hydrogeology’ at University of Göttingen** Title: ‘Process-based hydrological modeling using SWAT: Estimation of groundwater recharge in the large-scale river catchment Kharaa / Mongolia’
10/2005 - 09/2008	**Bachelor ‘Forest Science and Ecology’ at University of Göttingen** Title: ‘Infestation of mistletoe on Scotch pine in the region Hessian Ried in correlation with groundwater lowering’

Work experience

03/2014 - 04/2016	**Assistance in R courses at WSL** Introduction to R, advanced data management and manipulation using R
12/2007 - 09/2012	**Scientific assistant at NW-FVA** plausibility checks and processing of soil and forest monitoring data
10/2010 - 02/2011	**Student assistant at University of Göttingen**
06/2011 - 03/2012	supervision of international students, coordination
02/2009 - 06/2009	**Student assistant at University of Göttingen**
10/2010 - 03/2011	analysis of hydrological data, assistance in hydrogeological courses