

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

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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

38 Introduction

39 Tree death within a forest ecosystem initiates a wide range of responses (Franklin et al. 1987;
40 Gendreau-Berthiaume et al. 2016) and is a key factor shaping forest structure in terms of
41 diameter distribution, stand density and species diversity (Friend et al. 2014). Typically, tree
42 mortality is the result of several interacting factors such as competition, drought, pathogens,
43 snow, fire or frost, all of which decrease tree vitality (Waring 1987). Consequently, tree death can
44 hardly be associated with a single cause, which greatly complicates the mechanistic
45 understanding of mortality (Wang et al. 2012). Robust tree mortality algorithms (Manusch et al.
46 2012) are an important component of Dynamic Vegetation Models (DVMs), which have proven
47 to be useful for simulating forest succession, species range dynamics and the provisioning of
48 ecosystem services in response to environmental changes (Bugmann 2014; Snell et al. 2014)
49 from the local (Bugmann 2001) to the global scale (Bonan et al. 2003).

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

57 Empirical mortality models for European tree species have been developed based on inventory
58 and dendrochronological data. Although inventory data feature a lower temporal resolution, with
59 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 and 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 and 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.

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

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

100 We thus review mortality models based on European inventory data to assess their transferability
101 and suitability for incorporation in DVMs. We rigorously validate the mortality models with
102 extensive inventory data from unmanaged forests in Germany and Switzerland and systematically
103 analyze model performance to address the following questions: (1) Which predictors warrant
104 high accuracy of simulated tree mortality? (2) Are 'regional models', i.e. functions that are
105 calibrated and applied in similar environments, required to account for the variation in mortality?

- 106 (3) Should model applications be restricted to the management intensity in the calibration data?
- 107 (4) Does the size of the calibration and validation datasets influence the accuracy of mortality
- 108 predictions? (5) Are predictions of individual tree mortality models sensitive to the length of
- 109 census intervals?

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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 (Appendix S1, Fig. S1). 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 (Appendix S1, 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 S2. 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.

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 (Appendix S1, 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 (Appendix S3). 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

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

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 S2). In addition, the mortality probability predicted for Δt_j was rescaled to the census interval (Δt) of the respective permanent plot (cf. Appendix S2).

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. 2008a; Wunder et al. 2007). Since we solely used measured crown ratios (CR , cf. Appendix S2), 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 S2). 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 and 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. Appendix S1, 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 (Breiner et al. 2015; Mosteller and Tukey 1977). 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 p_{bias} 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 and Højsgaard 2014). R^2 of the models was determined based on the function `sem.model.fits()` from the package *piecewiseSEM*. Multiple pairwise comparisons were

223 calculated using the package *lsmeans* (Lenth 2016). Bootstrap confidence intervals were derived
224 using the function *boot.ci()* from the package *boot*.

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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 (Appendix S1, 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.

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. Appendix S1, Fig. S12), hump-shaped mortality (*Pinus*, Alenius et al. 2003 1), U-shaped mortality (e.g. *Betula*, Fridman and Ståhl 2001) or no trend of mortality with *DBH* (e.g. *Picea*, Fridman and Ståhl 2001). In most of these cases, the models did not fit well the observed mortality pattern.

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 (Appendix S1, 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 and 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 (Appendix S1, 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* (Appendix S1, Fig. S4). As indicated by

mostly negative p_{bias} values (Appendix S1, 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 Appendix S1, 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 (Appendix S1, Fig. S6+7). However, the improvement of prediction accuracy was largest for covariates of growth (cf. Appendix S1, 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 and Ståhl 2001), *Picea* (Wunder et al. in prep.) and *Pinus* (Alenius et al. 2003 1), and excellent classification, e.g. for *Larix* (Monserud and 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 ($AUC > 0.7$).

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 Appendix S1, 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 (Appendix S1, 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

294 significantly higher classification accuracy (Appendix S1, Fig. S10). Additionally, *AUC*
295 increased with the size of the validation dataset (N_{val} , Appendix S1, Fig. S11). In contrast to
296 prediction accuracy, classification accuracy was not significantly affected by covariates for
297 competition at the tree level, the application within the same ecological zone, nor by the census
298 interval in the validation data.

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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. Appendix S1, 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 (Appendix S1, 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 and 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 (*Pinus*: Alenius et al. 2003; e.g. *Betula*: Fridman and Ståhl 2001). 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 and 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. Appendix S1, 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 (Bircher et al. 2015; Larocque et al. 2011; Radtke et al. 2012; Wernsdörfer et al. 2008).

Second, our results confirm the regional variation of mortality relationships proposed in other studies (e.g. Monserud and 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 and 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 (Lutz 2015; Metcalf et al.

2009). 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. Appendix S1, 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 (Hülsmann et al. 2016; Lutz 2015), 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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Tables

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 S2. For minimum and maximum values of the characteristics refer to Appendix S1, Table S2.

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

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 <i>Quercus pyrenaica</i> 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.

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

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 (***) $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$) 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	***
<i>Alnus</i>	-0.020	0.015			<i>Alnus</i>	0.263	0.038		
<i>Betula</i>	0.038	0.013			<i>Betula</i>	0.156	0.032		
<i>Carpinus</i>	-0.010	0.012			<i>Carpinus</i>	0.182	0.030		
<i>Fagus</i>	-0.015	0.011			<i>Fagus</i>	0.165	0.027		
<i>Fraxinus</i>	-0.007	0.012			<i>Fraxinus</i>	0.210	0.029		
<i>Larix</i>	-0.028	0.027			<i>Larix</i>	0.520	0.069		
<i>Picea</i>	-0.000	0.012			<i>Picea</i>	0.088	0.030		
<i>Pinus</i>	0.001	0.013			<i>Pinus</i>	0.141	0.032		
<i>Quercus</i>	0.004	0.011			<i>Quercus</i>	0.241	0.029		
<i>Tilia</i>	-0.001	0.014			<i>Tilia</i>	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	*

Figure captions

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 Appendix S1, Fig. S12.

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Appendices

Appendix S1. Fig. S1-S12, Tables S1-S3

Appendix S2. Extended material and methods

Appendix S3. Table of coefficients for the validated mortality models (cf. additional .csv-file)

Draft

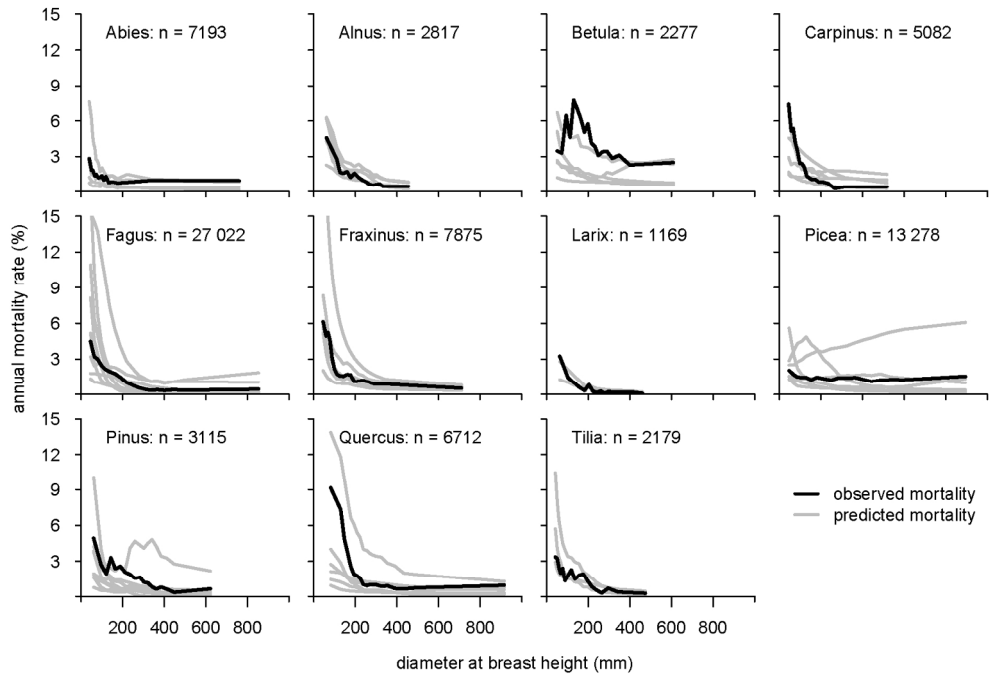


Fig. 1. Observed and predicted annual mortality rates as a function of DBH per tree species. Each grey line represents the predictions of one mortality model. For the sake of simplicity and to focus on overall patterns, we did not differentiate mortality models but show all model predictions in grey. 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 Appendix S1, Fig. S12.

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Supporting information to the paper

Hülsmann, L. et al. How to predict tree death from inventory data – lessons from a systematic assessment of European tree mortality models. *Canadian Journal of Forest Research*.

Supplement S1. Fig. S1-S12, Tables S1-S3

Fig. S1. Map of European tree mortality models and strict forest reserves in Germany and Switzerland.

Fig. S2. Boxplot of p_{bias} at the reserve level for each tree species.

Fig. S3. Fixed effects of the influence of model and data characteristics on the square-root of $|p_{bias}|$.

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 $|p_{bias}|$.

Fig. S5. Boxplot of $|p_{bias}|$ at the reserve level achieved by models with and without a covariate of growth for each tree species.

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.

Fig. S7. $|p_{bias}|$ at the reserve level as a function of the census interval in the validation dataset.

Fig. S8. Fixed effects of the influence of model and data characteristics on arcsine-transformed AUC .

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 .

Fig. S10. Boxplot of AUC at the reserve level achieved by models with and without a covariate of growth for each tree species.

Fig. S11. AUC at the reserve level as a function of the number of records in the validation dataset (N_{val}).

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

Table S1. Number of records per tree species and genus.

Table S2. Minimum and maximum values of the tree, stand and site characteristics that were used as covariates in the mortality models.

Table S3. Mortality models, related species and the model characteristics used to explain achieved model performance.

Supplement S2. Extended material and methods

Tree characteristics

Stand characteristics

Site characteristics

Model application

Prediction bias

Supplement S3. Table of coefficients for the validated mortality models (cf. additional .csv file).

References

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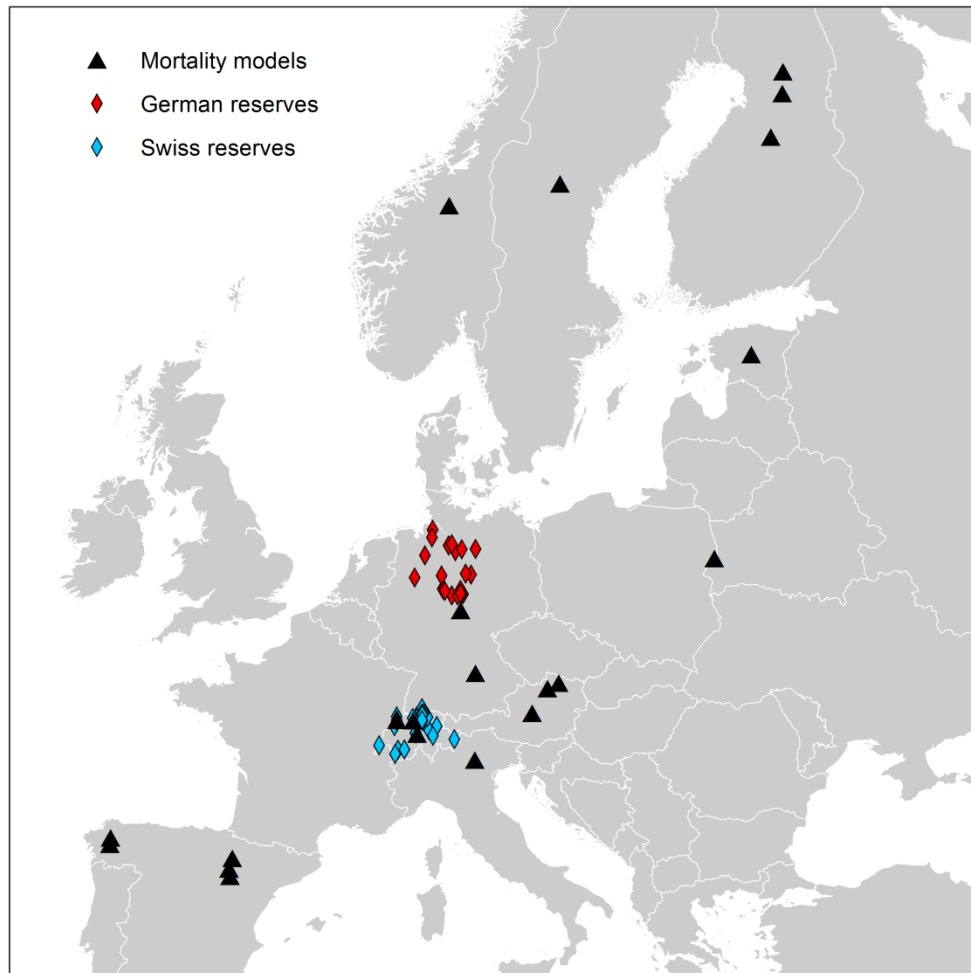
Supplement S1. Fig. S1-S6, Tables S1-S3

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 $n = 32$.

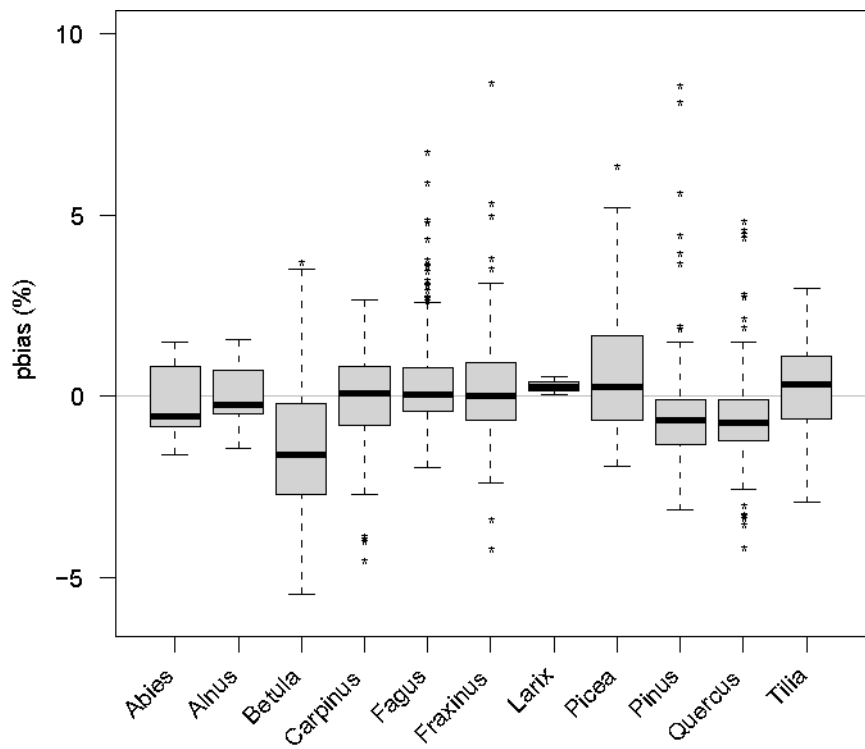


Fig. S2. Boxplot of p_{bias} at the reserve level for each tree species. Prevailing positive or negative p_{bias} values indicate that for the respective species the models used for prediction tend to over- or underestimate tree mortality, respectively.

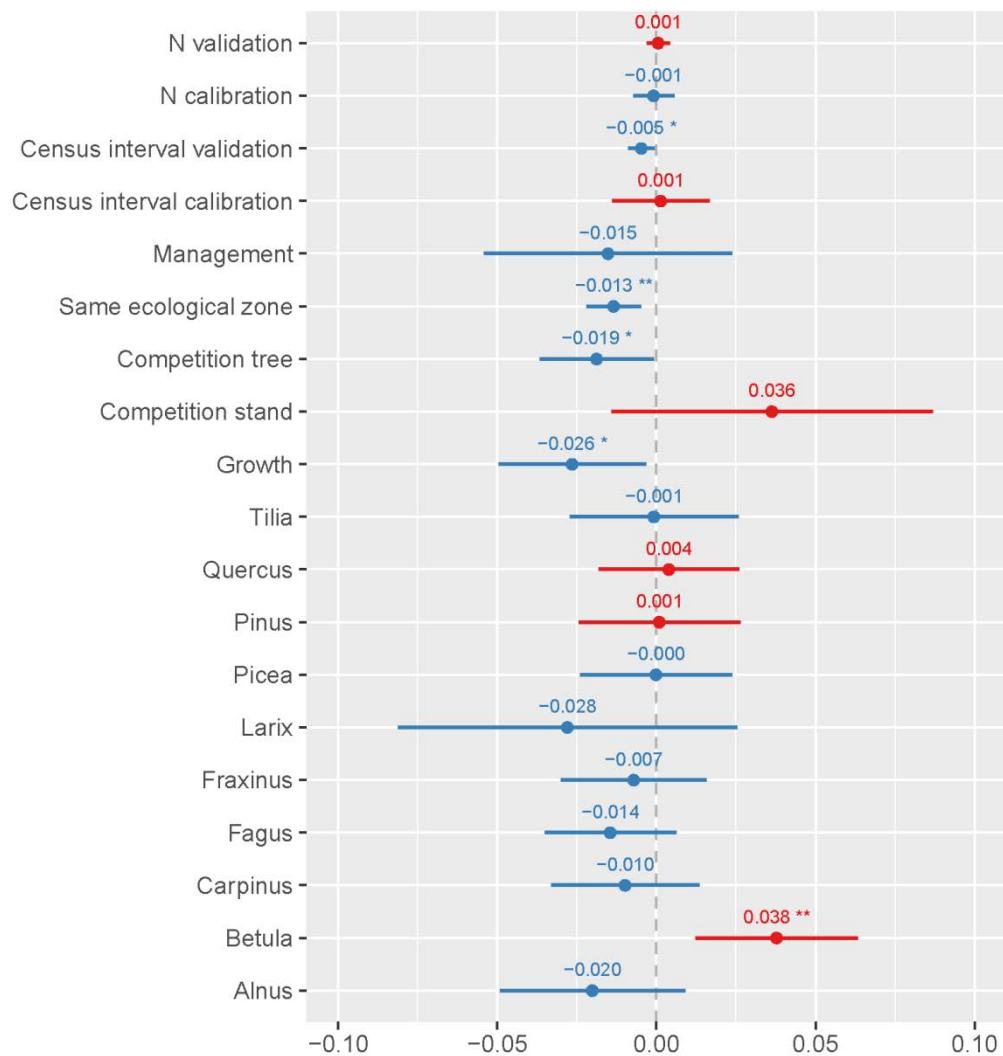


Fig. S3. Fixed effects of the influence of model and data characteristics on the square-root of $|p_{bias}|$. Note that a ‘good’ model features low $|p_{bias}|$. Positive and negative influences on performance are shown in blue and red, respectively. Note that the first level of all factors is the reference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

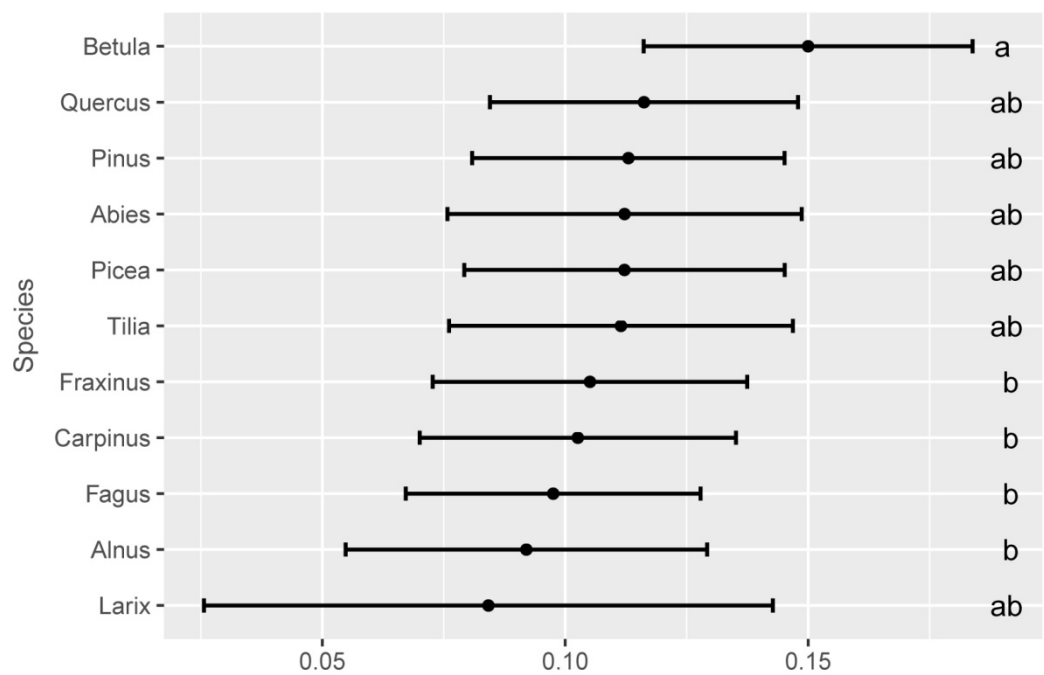


Fig. S4. Multiple pairwise comparison of least-squares means and confidence intervals for different species from the linear mixed-effect model of the square-root of $|p_{bias}|$. Different letters (a-e) indicate significant differences between species ($p < 0.05$).

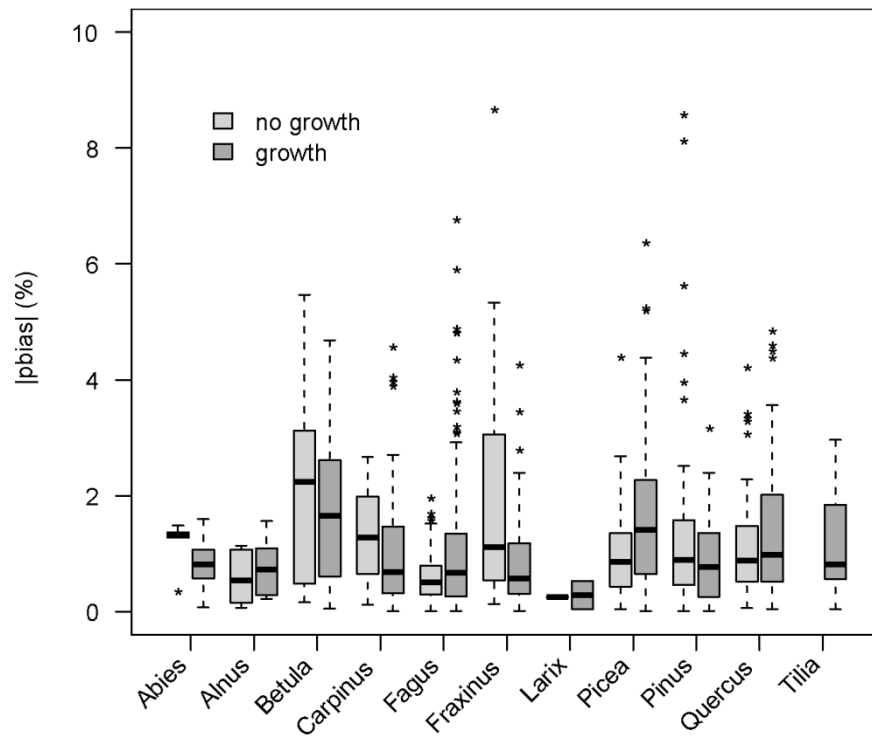


Fig. S5. Boxplot of $|p_{bias}|$ at the reserve level achieved by models with and without a covariate of growth for each tree species. Note that the design regarding the factors 'species' and 'growth' is not balanced.

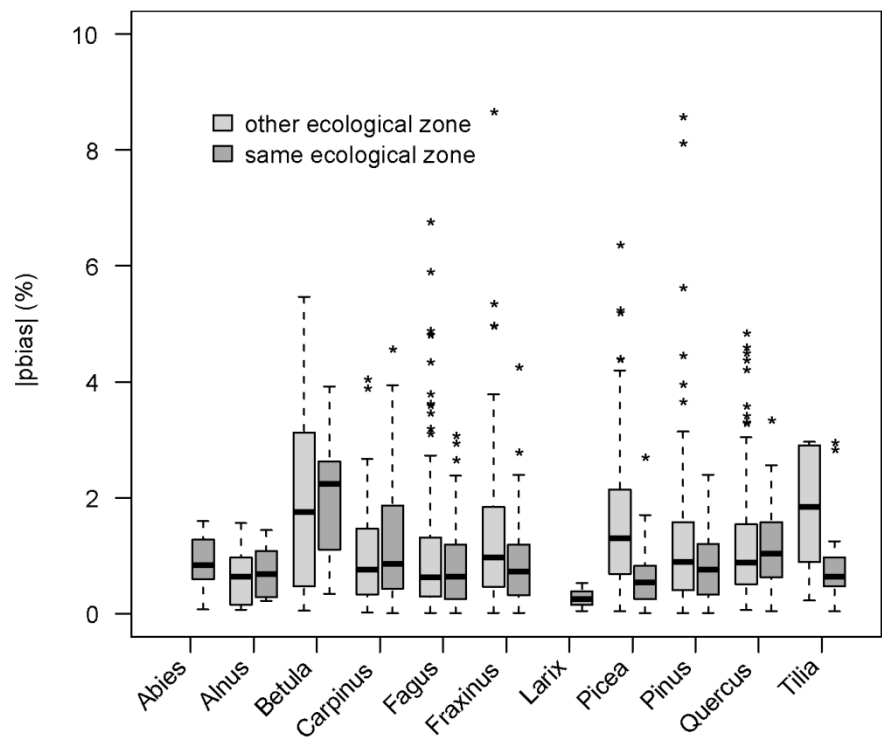


Fig. S6. Boxplot of $|p_{bias}|$ at the reserve level achieved by models that were applied inside or outside the ecological zone in which the models were calibrated for each tree species. Note that the design regarding the factors ‘species’ and ‘ecological zone’ is not balanced.

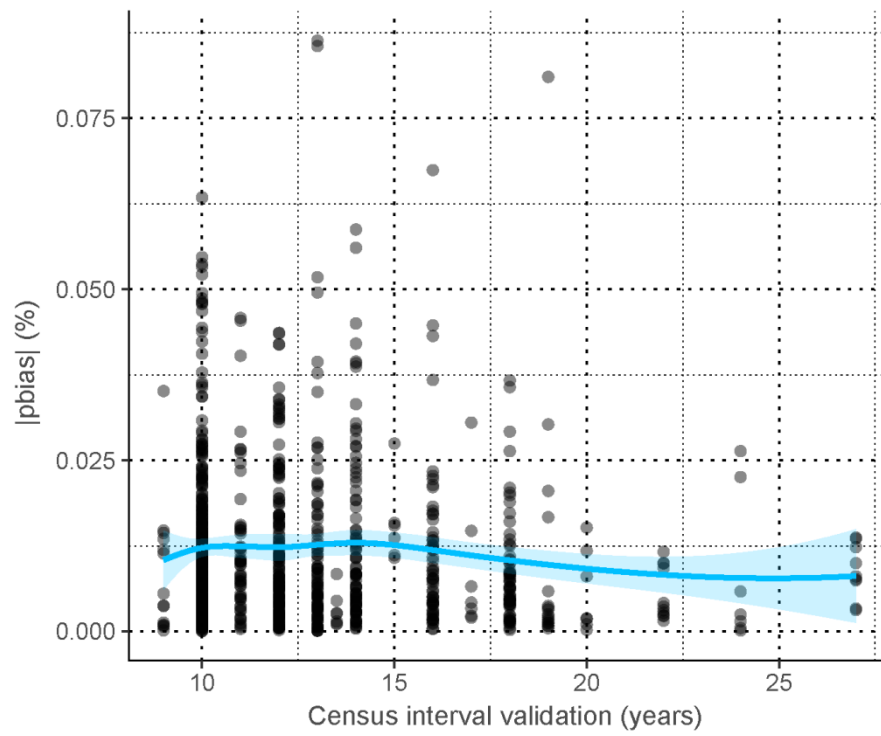


Fig. S7. $|p_{bias}|$ at the reserve level as a function of the census interval in the validation dataset including a loess smoothing (blue).

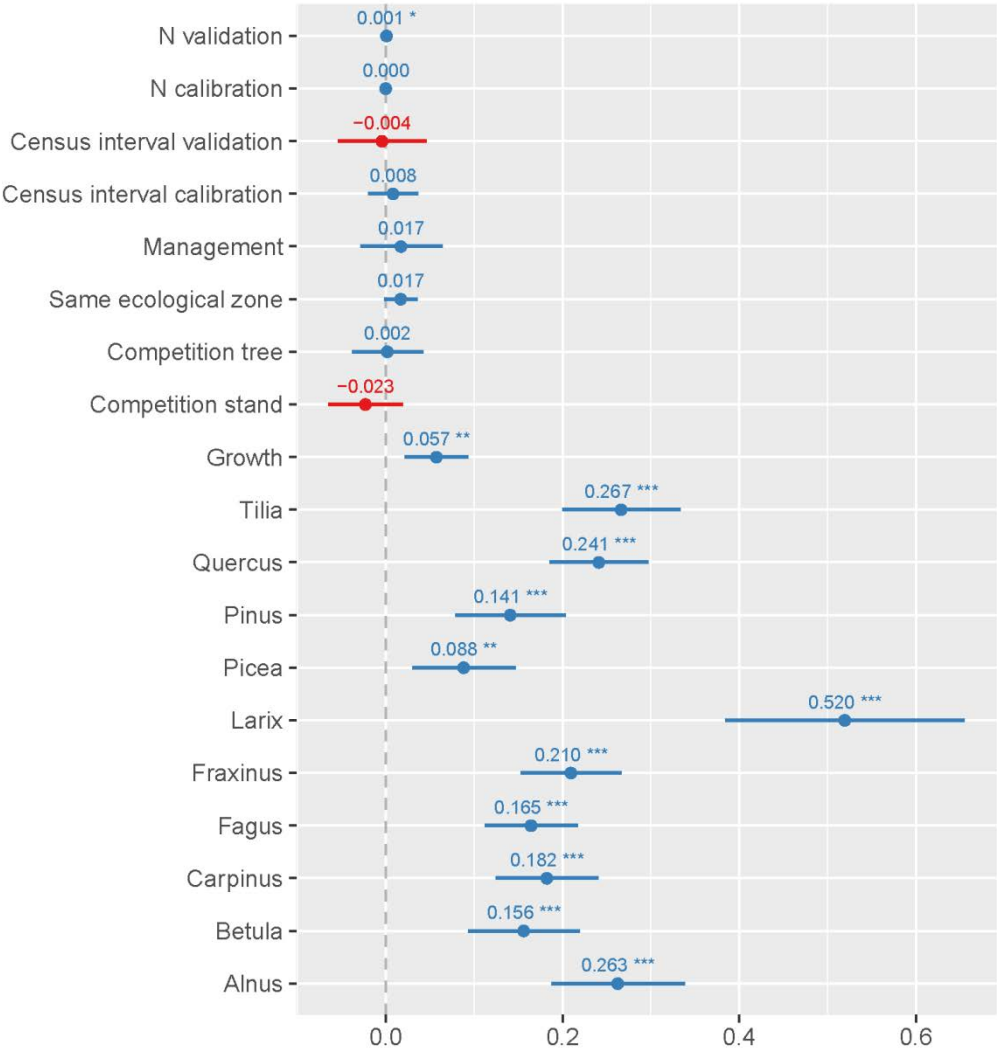


Fig. S8. Fixed effects of the influence of model and data characteristics on arcsine-transformed AUC. Note that a ‘good’ model features high AUC. Positive and negative influences on performance are shown in blue and red, respectively. Note that the first level of all factors is the reference level while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

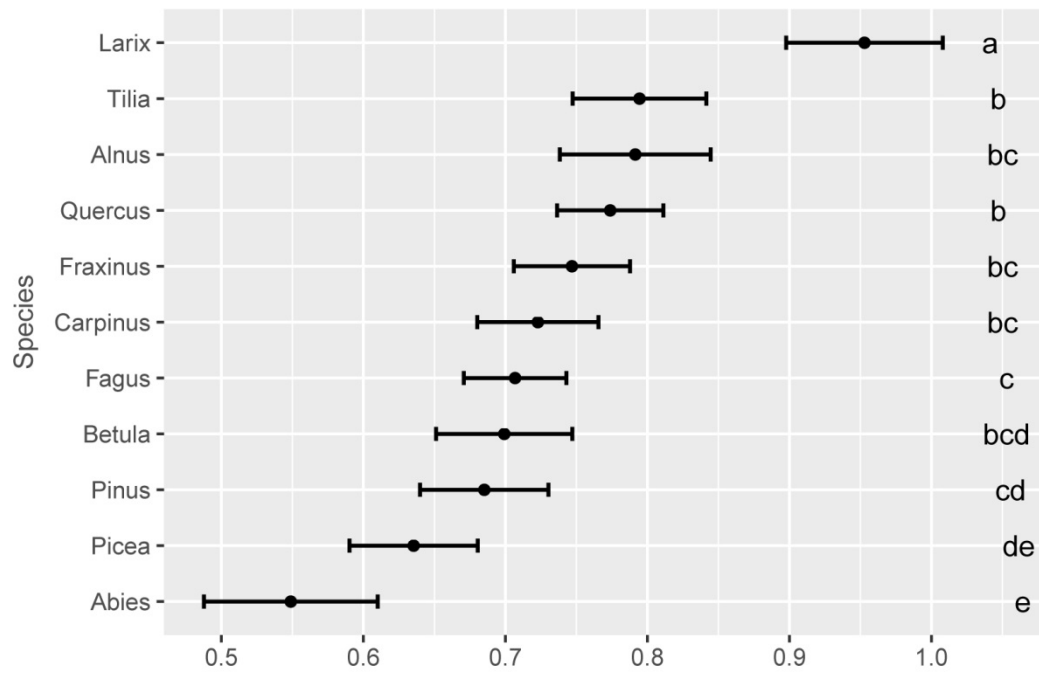


Fig. S9. Multiple pairwise comparison of least-squares means and confidence intervals for different species from the linear mixed-effect model of arcsine-transformed *AUC*. Different letters (a-e) indicate significant differences between species ($p < 0.05$).

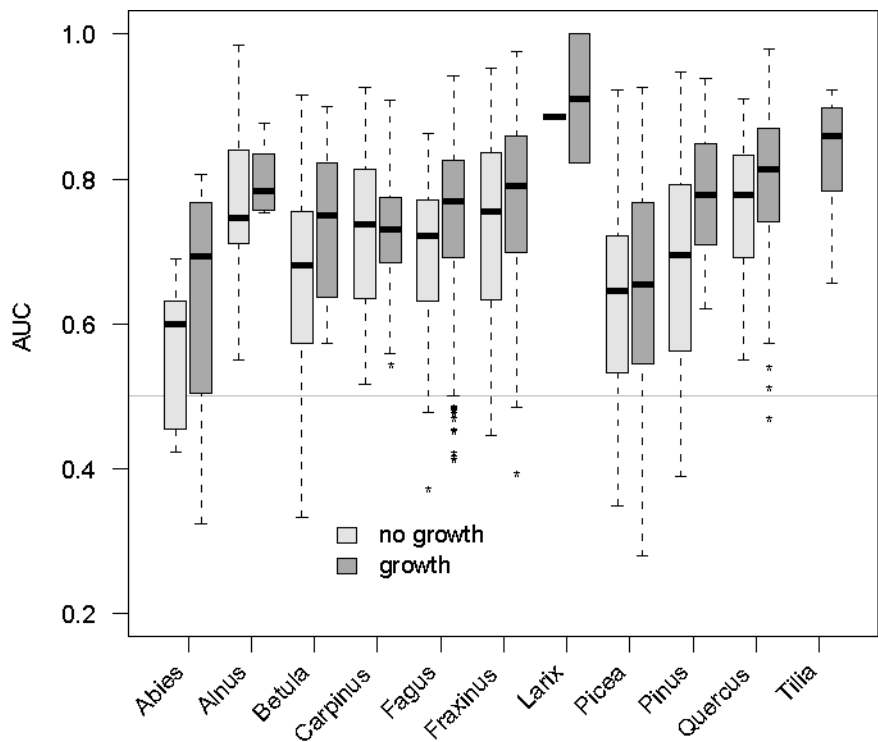


Fig. S10. Boxplot of *AUC* at the reserve level achieved by models with and without a covariate of growth for each tree species. Values larger than 0.5 (grey line) indicate an increasing ability to classify dead and living trees (Hosmer and Lemeshow 2000). Note that the design regarding the factors ‘species’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

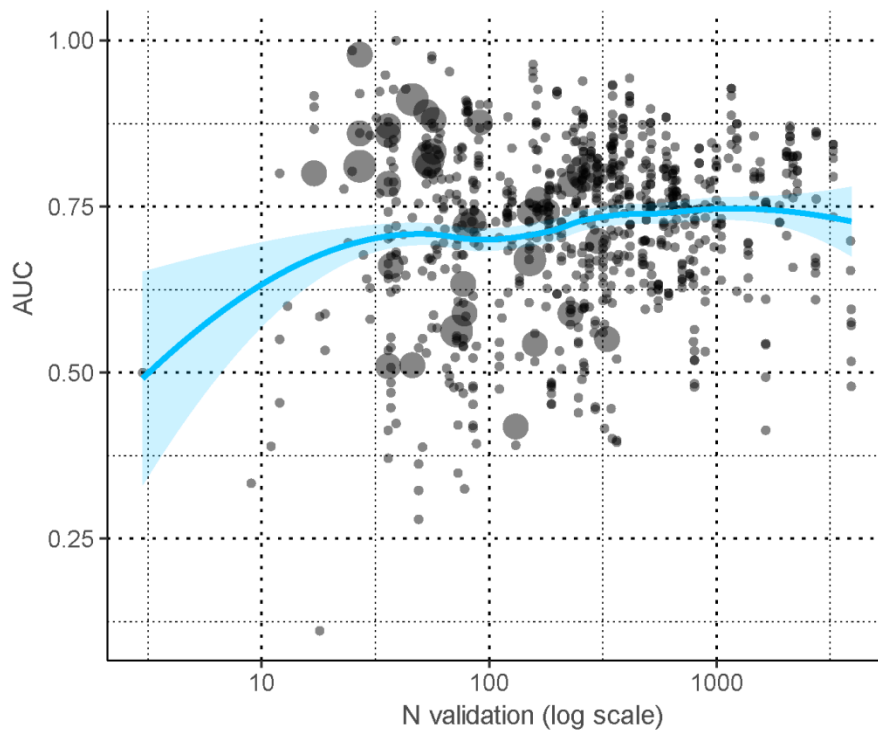


Fig. S11. *AUC* at the reserve level as a function of the number of records in the validation dataset (N_{val}) including a loess smoothing (blue). Note that the size of the points indicates the count of values at the respective location.

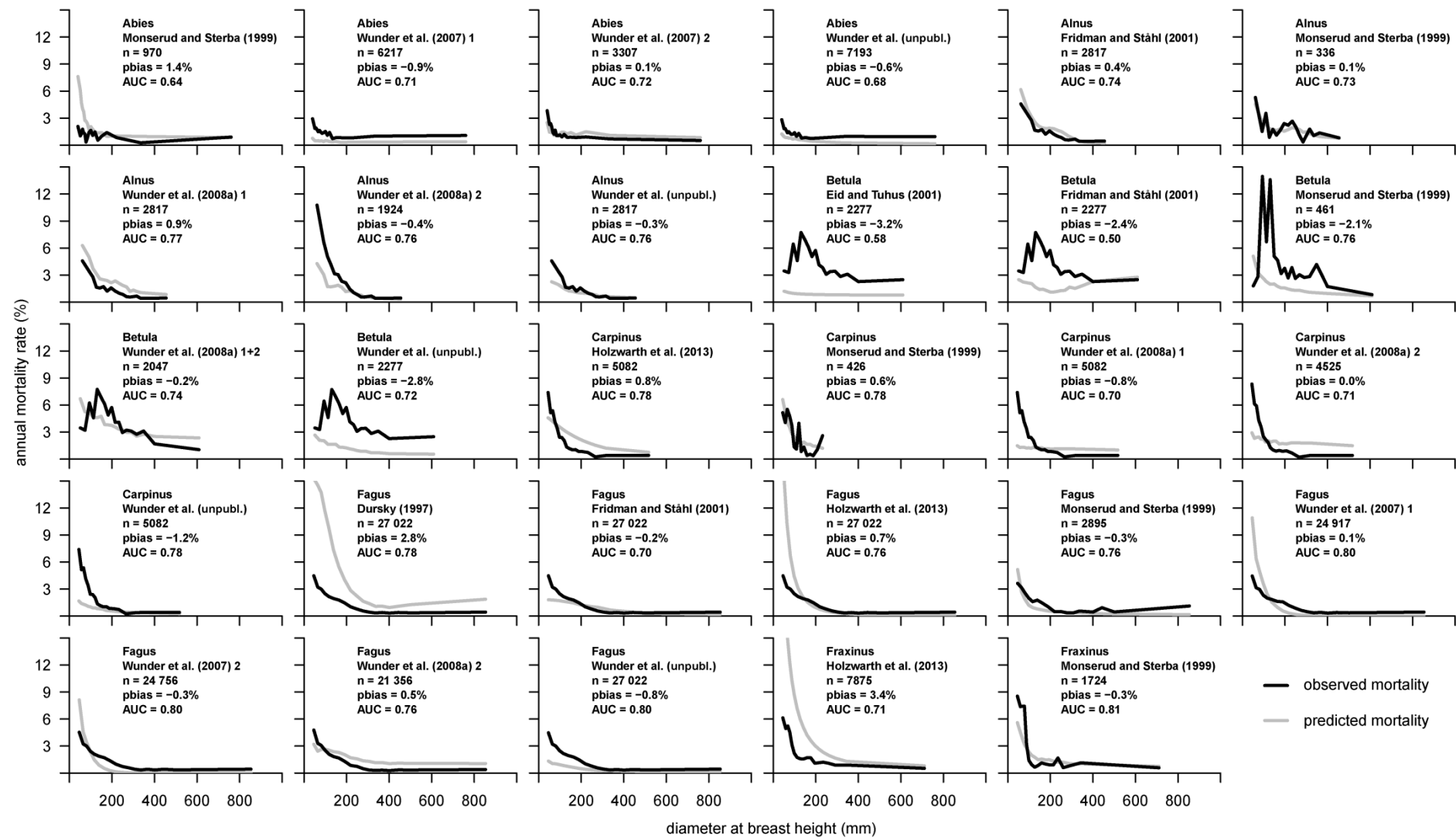


Fig. S12a. Observed and predicted annual mortality rates as a function of DBH separately for each model-species combination.

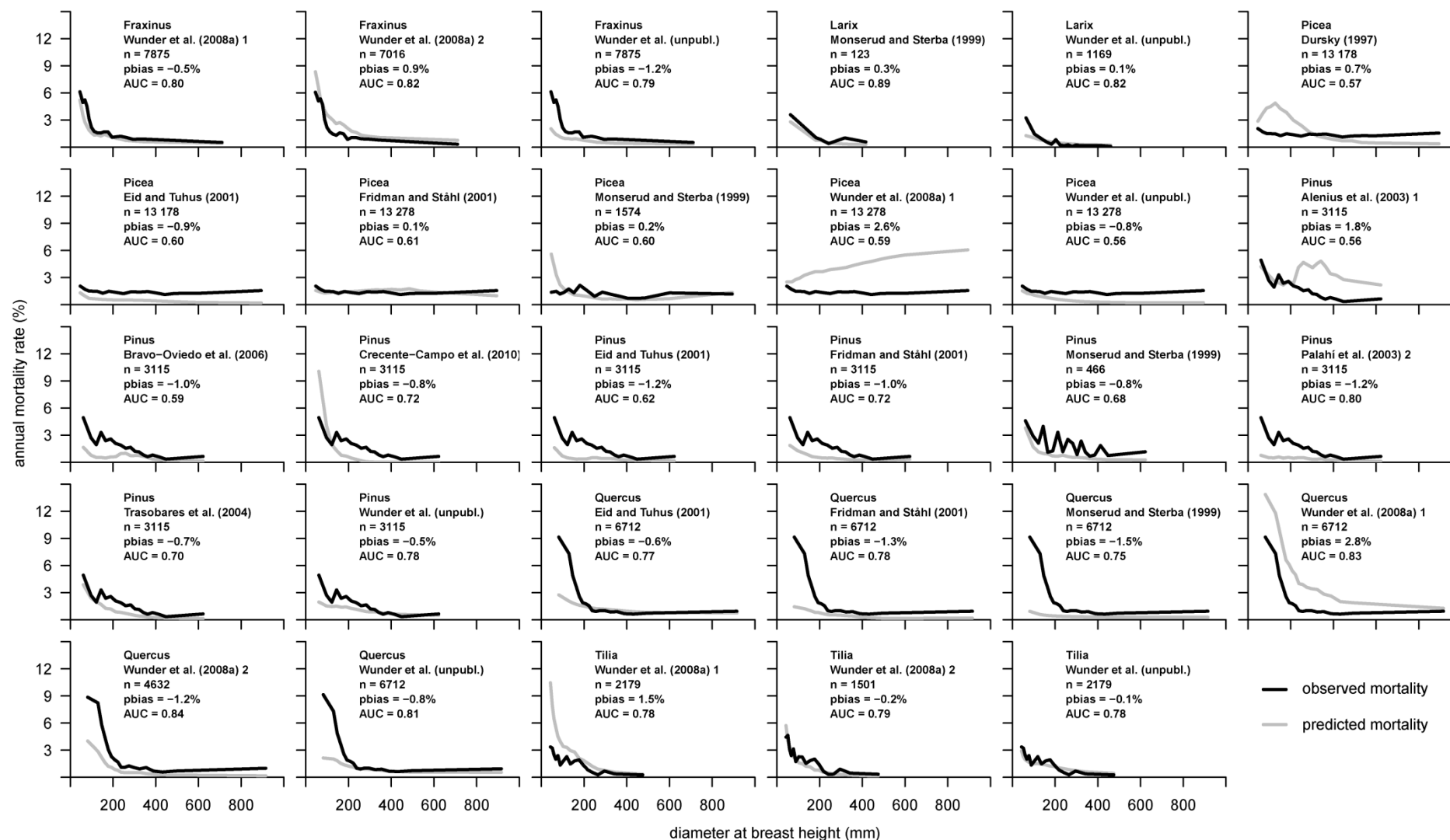


Fig. S12b. Observed and predicted annual mortality rates as a function of *DBH* separately for each model-species combination.

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

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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.

		<i>Abies</i>	<i>Alnus</i>	<i>Betula</i>	<i>Carpinus</i>	<i>Fagus</i>	<i>Fraxinus</i>	<i>Larix</i>	<i>Picea</i>	<i>Pinus</i>	<i>Quercus</i>	<i>Tilia</i>
Tree	<i>DBH</i> (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
	<i>DI</i> (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
	<i>BAI</i> (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
	<i>relBAI</i>	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
	<i>h</i> (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
	<i>CR</i>	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
	<i>BAL</i> (m ² ha ⁻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
	<i>relBAL</i>	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	<i>mDBH</i> (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
	<i>qmDBH</i> (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
	<i>CVd</i>	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
	<i>hdom</i> (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
	<i>BA</i> (m ² ha ⁻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
	<i>N</i> (ha ⁻¹)	367 - 2780	282 - 4000	258 - 2333	204 - 2333	78 - 2780	253 - 3281	482 - 1902	201 - 2780	312 - 2500	244 - 2595	367 - 3281
	<i>PBA</i>			0.00 - 0.86					0.00 - 1.00	0.01 - 1.00		
Site	<i>LAT</i> (°)	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
	<i>ELV</i> (m)	459 - 1560	334 - 564	24 - 599	4 - 632	4 - 1227	54 - 889	1441 - 2094	54 - 2034	83 - 1954	4 - 760	367 - 839
	<i>GDD</i>	903 - 2099	1822 - 2297	1654 - 2243	1443 - 2162	1169 - 2162	1552 - 2302	422 - 1019	465 - 2162	590 - 2243	1613 - 2162	1552 - 2162
	<i>SI50</i> (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. Supplement S2). 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 stand	Competition tree	Ecological zone	Management intensity	Census interval calibration	N_{cal} (N_{dead})
Alenius et al. (2003)	<i>Pinus sylvestris</i>	<i>Pinus sylvestris</i>	mortality	II	5	no	yes	yes	Northern	managed	5	17 293 (372)
Bravo-Oviedo et al. (2006)	<i>Pinus sylvestris</i>	<i>Pinus sylvestris</i>	survival	II	5	no	no	yes	Mediterranean	unmanaged	5	14 197 (360)
Crecente-Campo et al. (2010)	<i>Pinus sylvestris</i>	<i>Pinus sylvestris</i>	survival	I	1	no	no	yes	Mediterranean	managed	7	5447 (475)
Dursky (1997)	<i>Fagus sylvatica</i>	<i>Fagus sylvatica</i>	survival	II	7	yes	no	no	Central	unmanaged	7.5	526 (263)
Dursky (1997)	<i>Picea abies</i>	<i>Picea abies</i>	survival	II	5	yes	no	no	Central	unmanaged	5.5	4764 (2382)
Eid and Tuhus (2001)	<i>Betula spec.</i>	<i>Betula spec.</i>	survival	II	1	no	no	no	Northern	managed	12	15 650 (706)
Eid and Tuhus (2001)	Broadleaf Other	<i>Quercus spec.</i>	survival	II	1	no	no	yes	Northern	managed	12	5405 (565)
Eid and Tuhus (2001)	<i>Picea abies</i>	<i>Picea abies</i>	survival	II	1	no	no	yes	Northern	managed	12	17 250 (461)
Eid and Tuhus (2001)	<i>Pinus sylvestris</i>	<i>Pinus sylvestris</i>	survival	II	1	no	no	yes	Northern	managed	12	7802 (179)
Fridman and Ståhl (2001)	<i>Betula spec.</i>	<i>Betula spec.</i>	mortality	II	5	no	yes	yes	Northern	managed	5	12 196 (935)
Fridman and Ståhl (2001)	Broadleaf Other	<i>Alnus glutinosa</i>	mortality	II	5	no	yes	yes	Northern	managed	5	4226 (464)
Fridman and Ståhl (2001)	Broadleaf Southern	<i>Fagus sylvatica</i> , <i>Quercus spec.</i>	mortality	II	5	no	yes	yes	Northern	managed	5	1183 (54)
Fridman and Ståhl (2001)	<i>Picea abies</i>	<i>Picea abies</i>	mortality	II	5	no	yes	yes	Northern	managed	5	34 403 (1565)
Fridman and Ståhl (2001)	<i>Pinus sylvestris</i>	<i>Pinus sylvestris</i>	mortality	II	5	no	yes	yes	Northern	managed	5	19 812 (1202)
Holzwarth et al. (2013)	<i>Carpinus betulus</i>	<i>Carpinus betulus</i>	mortality	II	1	no	no	no	Central	unmanaged	8	391 (30)
Holzwarth et al. (2013)	<i>Fagus sylvatica</i>	<i>Fagus sylvatica</i>	mortality	II	1	yes	no	no	Central	unmanaged	8	13 297 (1535)
Holzwarth et al. (2013)	<i>Fraxinus excelsior</i>	<i>Fraxinus excelsior</i>	mortality	II	1	no	no	no	Central	unmanaged	8	564 (39)
Monserud and Sterba (1999)	<i>Abies alba</i>	<i>Abies alba</i>	mortality	I	5	no	no	no	Alpine	managed	5	1878 (115)
Monserud and Sterba (1999)	Broadleaf Other	<i>Alnus glutinosa</i> , <i>Betula spec.</i> , <i>Carpinus betulus</i> , <i>Fraxinus excelsior</i>	mortality	I	5	no	no	yes	Alpine	managed	5	2617 (209)
Monserud and Sterba (1999)	<i>Fagus sylvatica</i>	<i>Fagus sylvatica</i>	mortality	I	5	no	no	yes	Alpine	managed	5	4484 (193)
Monserud and Sterba (1999)	<i>Larix decidua</i>	<i>Larix decidua</i>	mortality	I	5	no	no	yes	Alpine	managed	5	3015 (87)
Monserud and Sterba (1999)	<i>Picea abies</i>	<i>Picea abies</i>	mortality	I	5	no	no	yes	Alpine	managed	5	26 699 (1175)
Monserud and Sterba (1999)	<i>Pinus sylvestris</i>	<i>Pinus sylvestris</i>	mortality	I	5	no	no	yes	Alpine	managed	5	4138 (178)
Monserud and Sterba (1999)	<i>Quercus spec.</i>	<i>Quercus spec.</i>	mortality	I	5	no	no	no	Alpine	managed	5	784 (25)
Palahí et al. (2003) 2	<i>Pinus sylvestris</i>	<i>Pinus sylvestris</i>	survival	II	5	yes	no	yes	Mediterranean	managed	5	11 110 (267)
Trasobares et al. (2004)	<i>Pinus sylvestris</i>	<i>Pinus sylvestris</i>	survival	II	10	no	no	yes	Mediterranean	managed	10	7823 (313)
Wunder et al. (2007) 1	<i>Abies alba</i>	<i>Abies alba</i>	survival	II	13	yes	no	no	Alpine	unmanaged	13	251 (14)

Publication	Calibration species	Validation species	Predicted status	Type	Δt	Growth	Competition stand	tree	Ecological zone	Management intensity	Census interval calibration	N_{cal} (N_{dead})
Wunder et al. (2007) 1	<i>Fagus sylvatica</i>	<i>Fagus sylvatica</i>	survival	II	13	yes	no	no	Alpine	unmanaged	13	634 (30)
Wunder et al. (2007) 2	<i>Abies alba</i>	<i>Abies alba</i>	survival	II	12	yes	no	no	Alpine	unmanaged	12.5	527 (50)
Wunder et al. (2007) 2	<i>Fagus sylvatica</i>	<i>Fagus sylvatica</i>	survival	II	12	yes	no	no	Alpine	unmanaged	12.5	654 (7)
Wunder et al. (2008a) 1+2	<i>Betula spec.</i>	<i>Betula spec.</i>	survival	II	10	yes	no	no	Eastern	unmanaged	10	463 (145)
Wunder et al. (2008a) 1	<i>Alnus glutinosa</i>	<i>Alnus glutinosa</i>	survival	II	10	yes	no	no	Eastern	unmanaged	10	227 (26)
Wunder et al. (2008a) 1	<i>Carpinus betulus</i>	<i>Carpinus betulus</i>	survival	II	10	yes	no	no	Eastern	unmanaged	10	802 (74)
Wunder et al. (2008a) 1	<i>Fraxinus excelsior</i>	<i>Fraxinus excelsior</i>	survival	II	10	yes	no	no	Eastern	unmanaged	10	320 (23)
Wunder et al. (2008a) 1	<i>Picea abies</i>	<i>Picea abies</i>	survival	II	10	yes	no	no	Eastern	unmanaged	10	2253 (672)
Wunder et al. (2008a) 1	<i>Quercus robur</i>	<i>Quercus spec.</i>	survival	II	10	yes	no	no	Eastern	unmanaged	10	322 (52)
Wunder et al. (2008a) 1	<i>Tilia cordata</i>	<i>Tilia cordata</i>	survival	II	10	yes	no	no	Eastern	unmanaged	10	1024 (123)
Wunder et al. (2008a) 2	<i>Alnus glutinosa</i>	<i>Alnus glutinosa</i>	survival	II	10	yes	no	no	Alpine	unmanaged	10	278 (24)
Wunder et al. (2008a) 2	<i>Carpinus betulus</i>	<i>Carpinus betulus</i>	survival	II	10	yes	no	no	Alpine	unmanaged	10	219 (52)
Wunder et al. (2008a) 2	<i>Fagus sylvatica</i>	<i>Fagus sylvatica</i>	survival	II	10	yes	no	no	Alpine	unmanaged	10	1999 (243)
Wunder et al. (2008a) 2	<i>Fraxinus excelsior</i>	<i>Fraxinus excelsior</i>	survival	II	10	yes	no	no	Alpine	unmanaged	10	404 (83)
Wunder et al. (2008a) 2	<i>Quercus robur</i>	<i>Quercus spec.</i>	survival	II	10	yes	no	no	Alpine	unmanaged	10	1149 (141)
Wunder et al. (2008a) 2	<i>Tilia cordata</i>	<i>Tilia cordata</i>	survival	II	10	yes	no	no	Alpine	unmanaged	10	321 (24)
Wunder et al. (unpubl.)	high shade tolerance	<i>Abies alba</i> , <i>Carpinus betulus</i> , <i>Fagus sylvatica</i>	survival	II	11	yes	no	no	Alpine	unmanaged	11	902 (33)
Wunder et al. (unpubl.)	intermediate shade tolerance	<i>Alnus glutinosa</i> , <i>Fraxinus excelsior</i> , <i>Picea abies</i> , <i>Tilia cordata</i>	survival	II	11	yes	no	no	Alpine	unmanaged	11	1965 (93)
Wunder et al. (unpubl.)	low shade tolerance	<i>Betula spec.</i> , <i>Larix decidua</i> , <i>Pinus sylvestris</i> , <i>Quercus spec.</i>	survival	II	11	yes	no	no	Alpine	unmanaged	11	1448 (102)

Supplement S2. 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 and Marshall 2000). As a measure of variance of the diameter distribution, the coefficient of variance was calculated using $Cv_d = sdDBH / mDBH$ 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 permanent plots was described by their latitude (*LAT*) and elevation (*ELV*). 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 and Ståhl 2001), which was only required for *Pinus* (cf. Supplement S3), 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 and 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 (Landesforstanstalt Eberswalde 2000 for *Pinus*; Schober 1995 for *Picea*). For all covariates associated with clear cut or other forest interventions (cf. Supplement S3), 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

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

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') $\bar{p}_{\Delta t}$ and the mean mortality rate ('observed mortality') $\bar{y}_{\Delta t}$ over $\Delta t = 1$ year. To this end, the 'simulated mortality' $\bar{p}_{\Delta t} = \sum p_{i,\Delta t}/n$ and the 'observed mortality' $\bar{y}_{\Delta t} = \sum y_i/n$ were averaged for observations and predictions with the same census 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

$$\bar{p}_{\Delta t=1} = 1 - (1 - \bar{p}_{\Delta t})^{\frac{1}{\Delta t}}$$

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Supplement S3. Table of coefficients for the validated mortality models. For an explanation of the covariates refer to Table 1 and Supplement S2. 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	<i>Pinus sylvestris</i>	INTERCEPT	-5.719	-	<i>I-PBA</i> 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	<i>Pinus sylvestris</i>	relBAL	2.091	-	
Alenius et al. (2003) 1	<i>Pinus sylvestris</i>	1-PBA	2.133	-	
Alenius et al. (2003) 1	<i>Pinus sylvestris</i>	qmDBH	-0.128	cm	
Alenius et al. (2003) 1	<i>Pinus sylvestris</i>	BA	0.111	m ² /ha	
Alenius et al. (2003) 1	<i>Pinus sylvestris</i>	1/DBH	30.884	mm	
Bravo-Oviedo et al. (2006)	<i>Pinus sylvestris</i>	INTERCEPT	6.8548	-	<i>SI</i> refers to the dominant height at the age of 100 years
Bravo-Oviedo et al. (2006)	<i>Pinus sylvestris</i>	BAL*CVd	-0.121	m ² /ha	
Bravo-Oviedo et al. (2006)	<i>Pinus sylvestris</i>	SI	-0.037	m	
Bravo-Oviedo et al. (2006)	<i>Pinus sylvestris</i>	1/DBH	-9.792	cm	
Crecente-Campo et al. (2010)	<i>Pinus sylvestris</i>	INTERCEPT	-2.903	-	
Crecente-Campo et al. (2010)	<i>Pinus sylvestris</i>	relBAL* $h_{dom}*\sqrt{N}/100$	0.4687	m/ha	
Crecente-Campo et al. (2010)	<i>Pinus sylvestris</i>	relBAL	-3.214	-	
Crecente-Campo et al. (2010)	<i>Pinus sylvestris</i>	qmDBH	0.3007	cm	
Crecente-Campo et al. (2010)	<i>Pinus sylvestris</i>	DBH	-0.4087	cm	
Dursky (1997)	<i>Fagus sylvatica</i>	INTERCEPT	6.6686	-	<i>BAI</i> was defined as the basal area increment over 5 years
Dursky (1997)	<i>Fagus sylvatica</i>	h/DBH	-7.6495	m/cm	
Dursky (1997)	<i>Fagus sylvatica</i>	DBH	-0.261	cm	
Dursky (1997)	<i>Fagus sylvatica</i>	h	0.2695	m	
Dursky (1997)	<i>Fagus sylvatica</i>	BAI/DBH	3.0796	cm ² /a/cm	
Dursky (1997)	<i>Picea abies</i>	INTERCEPT	5.3908	-	
Dursky (1997)	<i>Picea abies</i>	h/DBH	-5.3998	m/cm	<i>SI</i> refers to the dominant height at the age of 50 years
Dursky (1997)	<i>Picea abies</i>	SI	-0.0406	m	
Dursky (1997)	<i>Picea abies</i>	DBH	-0.0089	cm	<i>BAI</i> was defined as the basal area increment over 5 years
Dursky (1997)	<i>Picea abies</i>	BAI/DBH	1.4802	cm ² /a/cm	
Eid and Tuhus (2001)	<i>Betula spec.</i>	INTERCEPT	4.8923	-	
Eid and Tuhus (2001)	<i>Betula spec.</i>	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	<i>SI</i> refers to the dominant height at the age of 40 years
Eid and Tuhus (2001)	<i>Picea abies</i>	INTERCEPT	8.0599	-	
Eid and Tuhus (2001)	<i>Picea abies</i>	BAL	-0.0281	m ² /ha	
Eid and Tuhus (2001)	<i>Picea abies</i>	PBA	-0.0132	%	
Eid and Tuhus (2001)	<i>Picea abies</i>	SI	-0.0264	m	
Eid and Tuhus (2001)	<i>Picea abies</i>	1/DBH	-6.702	cm	
Eid and Tuhus (2001)	<i>Pinus sylvestris</i>	INTERCEPT	8.4904	-	<i>SI</i> refers to the dominant height at the age of 40 years
Eid and Tuhus (2001)	<i>Pinus sylvestris</i>	BAL	-0.0462	m ² /ha	
Eid and Tuhus (2001)	<i>Pinus sylvestris</i>	SI	-0.0761	m	
Eid and Tuhus (2001)	<i>Pinus sylvestris</i>	1/DBH	-14.266	cm	

Publication	Calibration species	Covariate	Coefficient	Unit	Remarks
Fridman and Ståhl (2001)	<i>Betula spec.</i>	INTERCEPT	-2.83	-	
Fridman and Ståhl (2001)	<i>Betula spec.</i>	BAL	0.0362	m ² /ha	
Fridman and Ståhl (2001)	<i>Betula spec.</i>	mDBH	15.7	m	
Fridman and Ståhl (2001)	<i>Betula spec.</i>	BA	-0.0665	m ² /ha	
Fridman and Ståhl (2001)	<i>Betula spec.</i>	ELV	0.0011	m	
Fridman and Ståhl (2001)	<i>Betula spec.</i>	DBH	-16.5	m	
Fridman and Ståhl (2001)	<i>Betula spec.</i>	DBH ²	27.7	m	
Fridman and Ståhl (2001)	Broadleaf Other	INTERCEPT	-5.4	-	
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	ELV	0.00212	m	
Fridman and Ståhl (2001)	Broadleaf Other	LAT	0.0498	degree	
Fridman and Ståhl (2001)	Broadleaf Other	<20m clearcut	-0.345	-	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	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)	<i>Picea abies</i>	INTERCEPT	-4.58	-	
Fridman and Ståhl (2001)	<i>Picea abies</i>	BAL	0.0282	m ² /ha	
Fridman and Ståhl (2001)	<i>Picea abies</i>	PIDOM	-0.594	-	the categorical variable <i>PIDOM</i> quantifies the domination of <i>Pinus</i> with 1 indicating <i>PBA</i> of <i>Pinus</i> ≥ 0.7.
Fridman and Ståhl (2001)	<i>Picea abies</i>	mDBH	11.2	m	
Fridman and Ståhl (2001)	<i>Picea abies</i>	BA	-0.0545	m ² /ha	
Fridman and Ståhl (2001)	<i>Picea abies</i>	<20m clearcut	0.577	-	the categorical variable '≤20m clearcut' was set to 0 for all observations since no management in the reserves was assumed
Fridman and Ståhl (2001)	<i>Picea abies</i>	management	0.323	-	
Fridman and Ståhl (2001)	<i>Picea abies</i>	1/DBH	0.042	m	
Fridman and Ståhl (2001)	<i>Pinus sylvestris</i>	INTERCEPT	-1.98	-	
Fridman and Ståhl (2001)	<i>Pinus sylvestris</i>	BAL	0.028	m ² /ha	
Fridman and Ståhl (2001)	<i>Pinus sylvestris</i>	PIDOM	-0.456	-	the categorical variable <i>PIDOM</i> quantifies the domination of <i>Pinus</i> with 1 indicating <i>PBA</i> of <i>Pinus</i> ≥ 0.7.
Fridman and Ståhl (2001)	<i>Pinus sylvestris</i>	mDBH	25.6	m	
Fridman and Ståhl (2001)	<i>Pinus sylvestris</i>	mDBH ²	-26.6	m	the mean of the squared DBH (<i>mDBH</i> ²) is approximately equal to (<i>qmDBH</i>) ²
Fridman and Ståhl (2001)	<i>Pinus sylvestris</i>	log(BA)	-0.739	m ² /ha	
Fridman and Ståhl (2001)	<i>Pinus sylvestris</i>	moist	0.327	-	
Fridman and Ståhl (2001)	<i>Pinus sylvestris</i>	DBH	-17.4	m	the categorical variable <i>moist</i> quantifies soil water conditions with 1 indicating moist or wet
Fridman and Ståhl (2001)	<i>Pinus sylvestris</i>	DBH ²	21.5	m	
Holzwarth et al. (2013)	<i>Carpinus betulus</i>	INTERCEPT	-2.8	-	
Holzwarth et al. (2013)	<i>Carpinus betulus</i>	DBH	-0.051	cm	in communication with the authors, both coefficients were corrected and thus are different from the original paper
Holzwarth et al. (2013)	<i>Fagus sylvatica</i>	INTERCEPT	1.8	-	
Holzwarth et al. (2013)	<i>Fagus sylvatica</i>	log(DBH)	-2.1	cm	
Holzwarth et al. (2013)	<i>Fagus sylvatica</i>	DI	-1.4	cm/a	two models for 'early' and 'late' mortality were fitted that add up to the total mortality
Holzwarth et al. (2013)	<i>Fagus sylvatica</i>	INTERCEPT	-8.9	-	
Holzwarth et al. (2013)	<i>Fagus sylvatica</i>	DBH	0.052	cm	
Holzwarth et al. (2013)	<i>Fagus sylvatica</i>	log(DBH)	0	cm	for log-transformed <i>DBH</i> , an additive constant of 8 cm was used
Holzwarth et al. (2013)	<i>Fagus sylvatica</i>	DI	0	cm/a	
Holzwarth et al. (2013)	<i>Fraxinus excelsior</i>	INTERCEPT	1.3	-	
Holzwarth et al. (2013)	<i>Fraxinus excelsior</i>	log(DBH)	-1.6	cm	

Publication	Calibration species	Covariate	Coefficient	Unit	Remarks
Monserud and Sterba (1999)	<i>Abies alba</i>	INTERCEPT	2.0985	-	
Monserud and Sterba (1999)	<i>Abies alba</i>	1/DBH	-10.9085	cm	
Monserud and Sterba (1999)	<i>Abies alba</i>	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)	<i>Fagus sylvatica</i>	INTERCEPT	3.5734	-	
Monserud and Sterba (1999)	<i>Fagus sylvatica</i>	BAL	-0.0161	m ² /ha	
Monserud and Sterba (1999)	<i>Fagus sylvatica</i>	1/DBH	-13.9542	cm	
Monserud and Sterba (1999)	<i>Fagus sylvatica</i>	CR	3.1339	-	
Monserud and Sterba (1999)	<i>Larix decidua</i>	INTERCEPT	4.407	-	
Monserud and Sterba (1999)	<i>Larix decidua</i>	BAL	-0.0326	m ² /ha	
Monserud and Sterba (1999)	<i>Larix decidua</i>	1/DBH	-12.9395	cm	
Monserud and Sterba (1999)	<i>Larix decidua</i>	CR	2.2039	-	
Monserud and Sterba (1999)	<i>Picea abies</i>	INTERCEPT	2.1283	-	
Monserud and Sterba (1999)	<i>Picea abies</i>	BAL	-0.0186	m ² /ha	
Monserud and Sterba (1999)	<i>Picea abies</i>	1/DBH	-10.0745	cm	
Monserud and Sterba (1999)	<i>Picea abies</i>	DBH	0.0425	cm	
Monserud and Sterba (1999)	<i>Picea abies</i>	DBH ²	-0.00081	cm	
Monserud and Sterba (1999)	<i>Picea abies</i>	CR	3.8251	-	
Monserud and Sterba (1999)	<i>Pinus sylvestris</i>	INTERCEPT	4.1076	-	
Monserud and Sterba (1999)	<i>Pinus sylvestris</i>	BAL	-0.0234	m ² /ha	
Monserud and Sterba (1999)	<i>Pinus sylvestris</i>	1/DBH	-18.9714	cm	
Monserud and Sterba (1999)	<i>Pinus sylvestris</i>	CR	2.3267	-	
Monserud and Sterba (1999)	<i>Quercus spec.</i>	INTERCEPT	4.4508	-	
Monserud and Sterba (1999)	<i>Quercus spec.</i>	1/DBH	-12.0041	cm	
Palahí et al. (2003) 2	<i>Pinus sylvestris</i>	INTERCEPT	2.938	-	
Palahí et al. (2003) 2	<i>Pinus sylvestris</i>	BAL	-0.02	m ² /ha	<i>DI</i> was defined as the diameter increment over 5 years
Palahí et al. (2003) 2	<i>Pinus sylvestris</i>	DI	2.719	cm/a	
Trasobares et al. (2004)	<i>Pinus sylvestris</i>	INTERCEPT	2.728	-	
Trasobares et al. (2004)	<i>Pinus sylvestris</i>	BAL/log(DBH)	-0.148	m ² /ha/cm	for log-transformed <i>DBH</i> , an additive constant of 1 cm was used
Trasobares et al. (2004)	<i>Pinus sylvestris</i>	ELV	0.067	100m	
Trasobares et al. (2004)	<i>Pinus sylvestris</i>	CON	-0.006	km	the covariate <i>CON</i> that quantifies continentality was set to the maximum value within the calibration dataset = 186.6 km
Trasobares et al. (2004)	<i>Pinus sylvestris</i>	h	0.107	m	
Wunder et al. (2007) 1	<i>Abies alba</i>	INTERCEPT	1.161	-	
Wunder et al. (2007) 1	<i>Abies alba</i>	relBAI	29.17	1/a	for coefficients and details on the construction of the restricted cubic splines of <i>relBAI</i> refer also to Wunder (2007)
Wunder et al. (2007) 1	<i>Abies alba</i>	relBAI1	-518.37	1/a	
Wunder et al. (2007) 1	<i>Abies alba</i>	relBAI2	1038.53	1/a	
Wunder et al. (2007) 1	<i>Abies alba</i>	relBAI3	-505.01	1/a	<i>relBAI1-4</i> refer to the coefficients, <i>KrelBAI1-4</i> mark the locations of the knots of the restricted cubic splines
Wunder et al. (2007) 1	<i>Abies alba</i>	relBAI4	-15.15	1/a	
Wunder et al. (2007) 1	<i>Abies alba</i>	KrelBAI1	0.02	1/a	
Wunder et al. (2007) 1	<i>Abies alba</i>	KrelBAI2	0.104	1/a	<i>relBAI</i> was defined as the relative basal area increment over 11 years
Wunder et al. (2007) 1	<i>Abies alba</i>	KrelBAI3	0.181	1/a	
Wunder et al. (2007) 1	<i>Abies alba</i>	KrelBAI4	0.395	1/a	

Publication	Calibration species	Covariate	Coefficient	Unit	Remarks
Wunder et al. (2007) 1	<i>Fagus sylvatica</i>	INTERCEPT	-17.63	-	for coefficients and details on the construction of the restricted cubic splines of <i>relBAI</i> refer also to Wunder (2007) <i>relBAI1-4</i> refer to the coefficients, <i>KrelBAI1-4</i> mark the locations of the knots of the restricted cubic splines <i>relBAI</i> was defined as the relative basal area increment over 11 years
Wunder et al. (2007) 1	<i>Fagus sylvatica</i>	log(DBH)	3.57	mm	
Wunder et al. (2007) 1	<i>Fagus sylvatica</i>	relBAI	29.17	1/a	
Wunder et al. (2007) 1	<i>Fagus sylvatica</i>	relBAI1	-518.37	1/a	
Wunder et al. (2007) 1	<i>Fagus sylvatica</i>	relBAI2	1038.53	1/a	
Wunder et al. (2007) 1	<i>Fagus sylvatica</i>	relBAI3	-505.01	1/a	
Wunder et al. (2007) 1	<i>Fagus sylvatica</i>	relBAI4	-15.15	1/a	
Wunder et al. (2007) 1	<i>Fagus sylvatica</i>	KrelBAI1	0.02	1/a	
Wunder et al. (2007) 1	<i>Fagus sylvatica</i>	KrelBAI2	0.104	1/a	
Wunder et al. (2007) 1	<i>Fagus sylvatica</i>	KrelBAI3	0.181	1/a	
Wunder et al. (2007) 1	<i>Fagus sylvatica</i>	KrelBAI4	0.395	1/a	
Wunder et al. (2007) 2	<i>Abies alba</i>	INTERCEPT	-0.4	-	for coefficients and details on the construction of the restricted cubic splines of <i>relBAI</i> refer also to Wunder (2007) <i>relBAI1-4</i> refer to the coefficients, <i>KrelBAI1-4</i> mark the locations of the knots of the restricted cubic splines <i>relBAI</i> was defined as the relative basal area increment over 12.5 years
Wunder et al. (2007) 2	<i>Abies alba</i>	relBAI	29.17	1/a	
Wunder et al. (2007) 2	<i>Abies alba</i>	relBAI1	-518.37	1/a	
Wunder et al. (2007) 2	<i>Abies alba</i>	relBAI2	1038.53	1/a	
Wunder et al. (2007) 2	<i>Abies alba</i>	relBAI3	-505.01	1/a	
Wunder et al. (2007) 2	<i>Abies alba</i>	relBAI4	-15.15	1/a	
Wunder et al. (2007) 2	<i>Abies alba</i>	KrelBAI1	0.02	1/a	
Wunder et al. (2007) 2	<i>Abies alba</i>	KrelBAI2	0.104	1/a	
Wunder et al. (2007) 2	<i>Abies alba</i>	KrelBAI3	0.181	1/a	
Wunder et al. (2007) 2	<i>Abies alba</i>	KrelBAI4	0.395	1/a	
Wunder et al. (2007) 2	<i>Fagus sylvatica</i>	INTERCEPT	-16.86	-	for coefficients and details on the construction of the restricted cubic splines of <i>relBAI</i> refer also to Wunder (2007) <i>relBAI1-4</i> refer to the coefficients, <i>KrelBAI1-4</i> mark the locations of the knots of the restricted cubic splines <i>relBAI</i> was defined as the relative basal area increment over 12.5 years
Wunder et al. (2007) 2	<i>Fagus sylvatica</i>	log(DBH)	3.57	mm	
Wunder et al. (2007) 2	<i>Fagus sylvatica</i>	relBAI	29.17	1/a	
Wunder et al. (2007) 2	<i>Fagus sylvatica</i>	relBAI1	-518.37	1/a	
Wunder et al. (2007) 2	<i>Fagus sylvatica</i>	relBAI2	1038.53	1/a	
Wunder et al. (2007) 2	<i>Fagus sylvatica</i>	relBAI3	-505.01	1/a	
Wunder et al. (2007) 2	<i>Fagus sylvatica</i>	relBAI4	-15.15	1/a	
Wunder et al. (2007) 2	<i>Fagus sylvatica</i>	KrelBAI1	0.02	1/a	
Wunder et al. (2007) 2	<i>Fagus sylvatica</i>	KrelBAI2	0.104	1/a	
Wunder et al. (2007) 2	<i>Fagus sylvatica</i>	KrelBAI3	0.181	1/a	
Wunder et al. (2007) 2	<i>Fagus sylvatica</i>	KrelBAI4	0.395	1/a	
Wunder et al. (2008a) 1	<i>Alnus glutinosa</i>	INTERCEPT	0.958	-	for log-transformed <i>relBAI</i> , an additive constant of 0.002531 was used <i>log(relBAI)1-3</i> refer to the coefficients, <i>KrelBAI1-3</i> 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. (2008a) 1	<i>Alnus glutinosa</i>	log(DBH)	1.105	cm	
Wunder et al. (2008a) 1	<i>Alnus glutinosa</i>	log(relBAI)	1.217	1/a	
Wunder et al. (2008a) 1	<i>Alnus glutinosa</i>	log(relBAI)1	-0.092	1/a	
Wunder et al. (2008a) 1	<i>Alnus glutinosa</i>	log(relBAI)2	0.22	1/a	
Wunder et al. (2008a) 1	<i>Alnus glutinosa</i>	log(relBAI)3	-0.128	1/a	
Wunder et al. (2008a) 1	<i>Alnus glutinosa</i>	KrelBAI1	-4.8459	1/a	
Wunder et al. (2008a) 1	<i>Alnus glutinosa</i>	KrelBAI2	-3.8672	1/a	
Wunder et al. (2008a) 1	<i>Alnus glutinosa</i>	KrelBAI3	-3.16568	1/a	
Wunder et al. (2008a) 1	<i>Alnus glutinosa</i>				

Publication	Calibration species	Covariate	Coefficient	Unit	Remarks
Wunder et al. (2008a) 1	<i>Carpinus betulus</i>	INTERCEPT	5.281	-	for log-transformed <i>relBAI</i> , an additive constant of 0.002531 was used
Wunder et al. (2008a) 1	<i>Carpinus betulus</i>	log(<i>relBAI</i>)	0.643	1/a	
Wunder et al. (2008a) 1	<i>Carpinus betulus</i>	log(<i>relBAI</i>)1	-0.056	1/a	<i>log(relBAI)1-3</i> refer to the coefficients, <i>KrelBAI1-3</i> mark the locations of the knots of the restricted cubic splines
Wunder et al. (2008a) 1	<i>Carpinus betulus</i>	log(<i>relBAI</i>)2	0.123	1/a	
Wunder et al. (2008a) 1	<i>Carpinus betulus</i>	log(<i>relBAI</i>)3	-0.067	1/a	
Wunder et al. (2008a) 1	<i>Carpinus betulus</i>	<i>KrelBAI</i> 1	-5.5368	1/a	in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder et al. (2008a) 1	<i>Carpinus betulus</i>	<i>KrelBAI</i> 2	-4.37017	1/a	
Wunder et al. (2008a) 1	<i>Carpinus betulus</i>	<i>KrelBAI</i> 3	-3.39317	1/a	
Wunder et al. (2008a) 1	<i>Fraxinus excelsior</i>	INTERCEPT	-3.3	-	for log-transformed <i>relBAI</i> , an additive constant of 0.002531 was used
Wunder et al. (2008a) 1	<i>Fraxinus excelsior</i>	log(DBH)	1.171	cm	
Wunder et al. (2008a) 1	<i>Fraxinus excelsior</i>	log(<i>relBAI</i>)	0.333	1/a	<i>log(relBAI)1-3</i> refer to the coefficients, <i>KrelBAI1-3</i> mark the locations of the knots of the restricted cubic splines
Wunder et al. (2008a) 1	<i>Fraxinus excelsior</i>	log(<i>relBAI</i>)1	0.71	1/a	
Wunder et al. (2008a) 1	<i>Fraxinus excelsior</i>	log(<i>relBAI</i>)2	-1.305	1/a	
Wunder et al. (2008a) 1	<i>Fraxinus excelsior</i>	log(<i>relBAI</i>)3	1.911	1/a	in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder et al. (2008a) 1	<i>Fraxinus excelsior</i>	<i>KrelBAI</i> 1	-4.65255	1/a	
Wunder et al. (2008a) 1	<i>Fraxinus excelsior</i>	<i>KrelBAI</i> 2	-3.91917	1/a	
Wunder et al. (2008a) 1	<i>Fraxinus excelsior</i>	<i>KrelBAI</i> 3	-3.04359	1/a	
Wunder et al. (2008a) 1	<i>Picea abies</i>	INTERCEPT	4.647	-	for log-transformed <i>relBAI</i> , an additive constant of 0.002531 was used
Wunder et al. (2008a) 1	<i>Picea abies</i>	log(DBH)	-0.384	cm	
Wunder et al. (2008a) 1	<i>Picea abies</i>	log(<i>relBAI</i>)	0.44	1/a	<i>log(relBAI)1-3</i> refer to the coefficients, <i>KrelBAI1-3</i> mark the locations of the knots of the restricted cubic splines
Wunder et al. (2008a) 1	<i>Picea abies</i>	log(<i>relBAI</i>)1	0.071	1/a	
Wunder et al. (2008a) 1	<i>Picea abies</i>	log(<i>relBAI</i>)2	-0.196	1/a	
Wunder et al. (2008a) 1	<i>Picea abies</i>	log(<i>relBAI</i>)3	0.125	1/a	in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder et al. (2008a) 1	<i>Picea abies</i>	<i>KrelBAI</i> 1	-5.08731	1/a	
Wunder et al. (2008a) 1	<i>Picea abies</i>	<i>KrelBAI</i> 2	-3.93875	1/a	
Wunder et al. (2008a) 1	<i>Picea abies</i>	<i>KrelBAI</i> 3	-3.29096	1/a	
Wunder et al. (2008a) 1	<i>Quercus robur</i>	INTERCEPT	-2.785	-	for log-transformed <i>relBAI</i> , an additive constant of 0.002531 was used
Wunder et al. (2008a) 1	<i>Quercus robur</i>	log(DBH)	2.075	cm	
Wunder et al. (2008a) 1	<i>Quercus robur</i>	log(<i>relBAI</i>)	1.801	1/a	<i>log(relBAI)1-3</i> refer to the coefficients, <i>KrelBAI1-3</i> mark the locations of the knots of the restricted cubic splines
Wunder et al. (2008a) 1	<i>Quercus robur</i>	log(<i>relBAI</i>)1	-0.157	1/a	
Wunder et al. (2008a) 1	<i>Quercus robur</i>	log(<i>relBAI</i>)2	0.382	1/a	
Wunder et al. (2008a) 1	<i>Quercus robur</i>	log(<i>relBAI</i>)3	-0.225	1/a	in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder et al. (2008a) 1	<i>Quercus robur</i>	<i>KrelBAI</i> 1	-5.38701	1/a	
Wunder et al. (2008a) 1	<i>Quercus robur</i>	<i>KrelBAI</i> 2	-4.41242	1/a	
Wunder et al. (2008a) 1	<i>Quercus robur</i>	<i>KrelBAI</i> 3	-3.73213	1/a	
Wunder et al. (2008a) 1	<i>Tilia cordata</i>	INTERCEPT	-1.787	-	for log-transformed <i>relBAI</i> , an additive constant of 0.002531 was used
Wunder et al. (2008a) 1	<i>Tilia cordata</i>	log(DBH)	1.591	cm	
Wunder et al. (2008a) 1	<i>Tilia cordata</i>	log(<i>relBAI</i>)	1.022	1/a	<i>log(relBAI)1-3</i> refer to the coefficients, <i>KrelBAI1-3</i> mark the locations of the knots of the restricted cubic splines
Wunder et al. (2008a) 1	<i>Tilia cordata</i>	log(<i>relBAI</i>)1	-0.095	1/a	
Wunder et al. (2008a) 1	<i>Tilia cordata</i>	log(<i>relBAI</i>)2	0.289	1/a	
Wunder et al. (2008a) 1	<i>Tilia cordata</i>	log(<i>relBAI</i>)3	-0.194	1/a	in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder et al. (2008a) 1	<i>Tilia cordata</i>	<i>KrelBAI</i> 1	-5.2202	1/a	
Wunder et al. (2008a) 1	<i>Tilia cordata</i>	<i>KrelBAI</i> 2	-3.64442	1/a	
Wunder et al. (2008a) 1	<i>Tilia cordata</i>	<i>KrelBAI</i> 3	-2.87098	1/a	

Publication	Calibration species	Covariate	Coefficient	Unit	Remarks
Wunder et al. (2008a) 1+2	<i>Betula spec.</i>	INTERCEPT	1.073	-	for log-transformed <i>relBAI</i> , an additive constant of 0.002531 was used
Wunder et al. (2008a) 1+2	<i>Betula spec.</i>	log(DBH)	0.623	cm	
Wunder et al. (2008a) 1+2	<i>Betula spec.</i>	log(<i>relBAI</i>)	0.813	1/a	<i>log(relBAI)1-3</i> refer to the coefficients, <i>KrelBAI1-3</i> mark the locations of the knots of the restricted cubic splines
Wunder et al. (2008a) 1+2	<i>Betula spec.</i>	log(<i>relBAI</i>)1	-0.031	1/a	
Wunder et al. (2008a) 1+2	<i>Betula spec.</i>	log(<i>relBAI</i>)2	0.073	1/a	
Wunder et al. (2008a) 1+2	<i>Betula spec.</i>	log(<i>relBAI</i>)3	-0.042	1/a	in communication with the authors, the coefficients for <i>log(DBH)</i> and <i>site</i> (PL, CH) and the locations of the knots were corrected and thus are different from the original paper
Wunder et al. (2008a) 1+2	<i>Betula spec.</i>	KrelBAI1	-5.55349	1/a	
Wunder et al. (2008a) 1+2	<i>Betula spec.</i>	KrelBAI2	-4.45592	1/a	
Wunder et al. (2008a) 1+2	<i>Betula spec.</i>	KrelBAI3	-3.64797	1/a	
Wunder et al. (2008a) 2	<i>Alnus glutinosa</i>	INTERCEPT	1.918	-	for log-transformed <i>relBAI</i> , an additive constant of 0.002531 was used
Wunder et al. (2008a) 2	<i>Alnus glutinosa</i>	log(DBH)	1.105	cm	
Wunder et al. (2008a) 2	<i>Alnus glutinosa</i>	log(<i>relBAI</i>)	1.217	1/a	<i>log(relBAI)1-3</i> refer to the coefficients, <i>KrelBAI1-3</i> mark the locations of the knots of the restricted cubic splines
Wunder et al. (2008a) 2	<i>Alnus glutinosa</i>	log(<i>relBAI</i>)1	-0.092	1/a	
Wunder et al. (2008a) 2	<i>Alnus glutinosa</i>	log(<i>relBAI</i>)2	0.22	1/a	
Wunder et al. (2008a) 2	<i>Alnus glutinosa</i>	log(<i>relBAI</i>)3	-0.128	1/a	in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder et al. (2008a) 2	<i>Alnus glutinosa</i>	KrelBAI1	-4.8459	1/a	
Wunder et al. (2008a) 2	<i>Alnus glutinosa</i>	KrelBAI2	-3.8672	1/a	
Wunder et al. (2008a) 2	<i>Alnus glutinosa</i>	KrelBAI3	-3.16568	1/a	
Wunder et al. (2008a) 2	<i>Carpinus betulus</i>	INTERCEPT	1.827	-	for log-transformed <i>relBAI</i> , an additive constant of 0.002531 was used
Wunder et al. (2008a) 2	<i>Carpinus betulus</i>	log(<i>relBAI</i>)	0.207	1/a	
Wunder et al. (2008a) 2	<i>Carpinus betulus</i>	log(<i>relBAI</i>)1	0.626	1/a	<i>log(relBAI)1-3</i> refer to the coefficients, <i>KrelBAI1-3</i> mark the locations of the knots of the restricted cubic splines
Wunder et al. (2008a) 2	<i>Carpinus betulus</i>	log(<i>relBAI</i>)2	-1.373	1/a	
Wunder et al. (2008a) 2	<i>Carpinus betulus</i>	log(<i>relBAI</i>)3	0.747	1/a	
Wunder et al. (2008a) 2	<i>Carpinus betulus</i>	KrelBAI1	-5.5368	1/a	in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder et al. (2008a) 2	<i>Carpinus betulus</i>	KrelBAI2	-4.37017	1/a	
Wunder et al. (2008a) 2	<i>Carpinus betulus</i>	KrelBAI3	-3.39317	1/a	
Wunder et al. (2008a) 2	<i>Fagus sylvatica</i>	INTERCEPT	10.009	-	for log-transformed <i>relBAI</i> , an additive constant of 0.002531 was used
Wunder et al. (2008a) 2	<i>Fagus sylvatica</i>	log(<i>relBAI</i>)	1.743	1/a	
Wunder et al. (2008a) 2	<i>Fagus sylvatica</i>	log(<i>relBAI</i>)1	-0.113	1/a	<i>log(relBAI)1-3</i> refer to the coefficients, <i>KrelBAI1-3</i> mark the locations of the knots of the restricted cubic splines
Wunder et al. (2008a) 2	<i>Fagus sylvatica</i>	log(<i>relBAI</i>)2	0.328	1/a	
Wunder et al. (2008a) 2	<i>Fagus sylvatica</i>	log(<i>relBAI</i>)3	-0.215	1/a	
Wunder et al. (2008a) 2	<i>Fagus sylvatica</i>	KrelBAI1	-5.32948	1/a	in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder et al. (2008a) 2	<i>Fagus sylvatica</i>	KrelBAI2	-4.07211	1/a	
Wunder et al. (2008a) 2	<i>Fagus sylvatica</i>	KrelBAI3	-3.40999	1/a	
Wunder et al. (2008a) 2	<i>Fraxinus excelsior</i>	INTERCEPT	5.413	-	for log-transformed <i>relBAI</i> , an additive constant of 0.002531 was used
Wunder et al. (2008a) 2	<i>Fraxinus excelsior</i>	log(DBH)	1.171	cm	
Wunder et al. (2008a) 2	<i>Fraxinus excelsior</i>	log(<i>relBAI</i>)	2.418	1/a	<i>log(relBAI)1-3</i> refer to the coefficients, <i>KrelBAI1-3</i> mark the locations of the knots of the restricted cubic splines
Wunder et al. (2008a) 2	<i>Fraxinus excelsior</i>	log(<i>relBAI</i>)1	-0.786	1/a	
Wunder et al. (2008a) 2	<i>Fraxinus excelsior</i>	log(<i>relBAI</i>)2	1.444	1/a	
Wunder et al. (2008a) 2	<i>Fraxinus excelsior</i>	log(<i>relBAI</i>)3	0.658	1/a	in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder et al. (2008a) 2	<i>Fraxinus excelsior</i>	KrelBAI1	-4.65255	1/a	
Wunder et al. (2008a) 2	<i>Fraxinus excelsior</i>	KrelBAI2	-3.91917	1/a	
Wunder et al. (2008a) 2	<i>Fraxinus excelsior</i>	KrelBAI3	-3.04359	1/a	

Publication	Calibration species	Covariate	Coefficient	Unit	Remarks
Wunder et al. (2008a) 2	<i>Quercus robur</i>	INTERCEPT	-0.465	-	for log-transformed <i>relBAI</i> , an additive constant of 0.002531 was used
Wunder et al. (2008a) 2	<i>Quercus robur</i>	log(DBH)	2.075	cm	
Wunder et al. (2008a) 2	<i>Quercus robur</i>	log(<i>relBAI</i>)	1.801	1/a	<i>log(relBAI)1-3</i> refer to the coefficients, <i>KrelBAI1-3</i> mark the locations of the knots of the restricted cubic splines
Wunder et al. (2008a) 2	<i>Quercus robur</i>	log(<i>relBAI</i>)1	-0.157	1/a	
Wunder et al. (2008a) 2	<i>Quercus robur</i>	log(<i>relBAI</i>)2	0.382	1/a	
Wunder et al. (2008a) 2	<i>Quercus robur</i>	log(<i>relBAI</i>)3	-0.225	1/a	
Wunder et al. (2008a) 2	<i>Quercus robur</i>	<i>KrelBAI1</i>	-5.38701	1/a	
Wunder et al. (2008a) 2	<i>Quercus robur</i>	<i>KrelBAI2</i>	-4.41242	1/a	in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder et al. (2008a) 2	<i>Quercus robur</i>	<i>KrelBAI3</i>	-3.73213	1/a	
Wunder et al. (2008a) 2	<i>Tilia cordata</i>	INTERCEPT	-0.847	-	for log-transformed <i>relBAI</i> , an additive constant of 0.002531 was used
Wunder et al. (2008a) 2	<i>Tilia cordata</i>	log(DBH)	1.591	cm	
Wunder et al. (2008a) 2	<i>Tilia cordata</i>	log(<i>relBAI</i>)	1.022	1/a	<i>log(relBAI)1-3</i> refer to the coefficients, <i>KrelBAI1-3</i> mark the locations of the knots of the restricted cubic splines
Wunder et al. (2008a) 2	<i>Tilia cordata</i>	log(<i>relBAI</i>)1	-0.095	1/a	
Wunder et al. (2008a) 2	<i>Tilia cordata</i>	log(<i>relBAI</i>)2	0.289	1/a	
Wunder et al. (2008a) 2	<i>Tilia cordata</i>	log(<i>relBAI</i>)3	-0.194	1/a	
Wunder et al. (2008a) 2	<i>Tilia cordata</i>	<i>KrelBAI1</i>	-5.2202	1/a	
Wunder et al. (2008a) 2	<i>Tilia cordata</i>	<i>KrelBAI2</i>	-3.64442	1/a	in communication with the authors, the locations of the knots were corrected and thus are different from the original paper
Wunder et al. (2008a) 2	<i>Tilia cordata</i>	<i>KrelBAI3</i>	-2.87098	1/a	
Wunder et al. (unpubl.)	low shade tolerance	INTERCEPT	7.5825	-	the influence of <i>relBAI</i> was included via four growth categories: Very low growth: <i>relBAI</i> = 0 Low growth: <i>relBAI</i> 0...1.5% Fast growth: <i>relBAI</i> 1.5...3% Very fast growth: <i>relBAI</i> > 3%
Wunder et al. (unpubl.)	low shade tolerance	DBH	0.0672	cm	
Wunder et al. (unpubl.)	low shade tolerance	DBH ²	-0.0005	cm	
Wunder et al. (unpubl.)	low shade tolerance	low <i>relBAI</i>	0.581	-	
Wunder et al. (unpubl.)	low shade tolerance	fast <i>relBAI</i>	1.1968	-	
Wunder et al. (unpubl.)	low shade tolerance	very fast <i>relBAI</i>	2.0417	-	
Wunder et al. (unpubl.)	low shade tolerance	log(GDD)	-1.0107	-	the influence of <i>relBAI</i> was included via four growth categories: Very low growth: <i>relBAI</i> = 0 Low growth: <i>relBAI</i> 0...1.5% Fast growth: <i>relBAI</i> 1.5...3% Very fast growth: <i>relBAI</i> > 3%
Wunder et al. (unpubl.)	intermediate shade tolerance	INTERCEPT	7.7706	-	
Wunder et al. (unpubl.)	intermediate shade tolerance	DBH	0.0672	cm	
Wunder et al. (unpubl.)	intermediate shade tolerance	DBH ²	-0.0005	cm	
Wunder et al. (unpubl.)	intermediate shade tolerance	low <i>relBAI</i>	0.581	-	
Wunder et al. (unpubl.)	intermediate shade tolerance	fast <i>relBAI</i>	1.1968	-	
Wunder et al. (unpubl.)	intermediate shade tolerance	very fast <i>relBAI</i>	2.0417	-	the influence of <i>relBAI</i> was included via four growth categories: Very low growth: <i>relBAI</i> = 0 Low growth: <i>relBAI</i> 0...1.5% Fast growth: <i>relBAI</i> 1.5...3% Very fast growth: <i>relBAI</i> > 3%
Wunder et al. (unpubl.)	intermediate shade tolerance	log(GDD)	-1.0107	-	
Wunder et al. (unpubl.)	high shade tolerance	INTERCEPT	8.59	-	
Wunder et al. (unpubl.)	high shade tolerance	DBH	0.0672	cm	
Wunder et al. (unpubl.)	high shade tolerance	DBH ²	-0.0005	cm	
Wunder et al. (unpubl.)	high shade tolerance	low <i>relBAI</i>	0.581	-	
Wunder et al. (unpubl.)	high shade tolerance	fast <i>relBAI</i>	1.1968	-	the influence of <i>relBAI</i> was included via four growth categories: Very low growth: <i>relBAI</i> = 0 Low growth: <i>relBAI</i> 0...1.5% Fast growth: <i>relBAI</i> 1.5...3% Very fast growth: <i>relBAI</i> > 3%
Wunder et al. (unpubl.)	high shade tolerance	very fast <i>relBAI</i>	2.0417	-	
Wunder et al. (unpubl.)	high shade tolerance	log(GDD)	-1.0107	-	

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Draft

Citation,Calibration_Species,Parameter,Coefficient,Unit
 Alenius et al. (2003) 1,Pinus sylvestris,INTERCEPT,-5.719,-
 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,m²/ha
 Alenius et al. (2003) 1,Pinus sylvestris,1/DBH,30.884,mm
 Bravo-Oviedo et al. (2006),Pinus sylvestris,INTERCEPT,6.8548,-
 Bravo-Oviedo et al. (2006),Pinus sylvestris,BAL*CVD,-0.121,m²/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*hd_{om}*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,-
 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,cm²/a/cm
 Dursky (1997),Picea abies,INTERCEPT,5.3908,-
 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,cm²/a/cm
 Eid and Tuhus (2001),Betula spec.,INTERCEPT,4.8923,-
 Eid and Tuhus (2001),Betula spec.,1/DBH,-2.528,cm
 Eid and Tuhus (2001),Broadleaf Other,INTERCEPT,5.1575,-
 Eid and Tuhus (2001),Broadleaf Other,BAL,-0.0199,m²/ha
 Eid and Tuhus (2001),Broadleaf Other,1/DBH,-7.3544,cm
 Eid and Tuhus (2001),Picea abies,INTERCEPT,8.0599,-
 Eid and Tuhus (2001),Picea abies,BAL,-0.0281,m²/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,-
 Eid and Tuhus (2001),Pinus sylvestris,BAL,-0.0462,m²/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 spec.,INTERCEPT,-2.83,-
 Fridman and Ståhl (2001),Betula spec.,BAL,0.0362,m²/ha
 Fridman and Ståhl (2001),Betula spec.,mDBH,15.7,m
 Fridman and Ståhl (2001),Betula spec.,BA,-0.0665,m²/ha
 Fridman and Ståhl (2001),Betula spec.,ELV,0.0011,m
 Fridman and Ståhl (2001),Betula spec.,DBH,-16.5,m

Fridman and Ståhl (2001), *Betula spec.*, DBH², 27.7, m
 Fridman and Ståhl (2001), Broadleaf Other, INTERCEPT, -5.4, -
 Fridman and Ståhl (2001), Broadleaf Other, BAL, 0.0693, m²/ha
 Fridman and Ståhl (2001), Broadleaf Other, BA, -0.0688, m²/ha
 Fridman and Ståhl (2001), Broadleaf Other, ELV, 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, m²/ha
 Fridman and Ståhl (2001), Broadleaf Southern, BA, -0.14, m²/ha
 Fridman and Ståhl (2001), Broadleaf Southern, DBH, 3.34, m
 Fridman and Ståhl (2001), *Picea abies*, INTERCEPT, -4.58, -
 Fridman and Ståhl (2001), *Picea abies*, BAL, 0.0282, m²/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, m²/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
 Fridman and Ståhl (2001), *Pinus sylvestris*, INTERCEPT, -1.98, -
 Fridman and Ståhl (2001), *Pinus sylvestris*, BAL, 0.028, m²/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*, mDBH², -26.6, m
 Fridman and Ståhl (2001), *Pinus sylvestris*, log(BA), -0.739, m²/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*, DBH², 21.5, m
 Holzwarth et al. (2013), *Carpinus betulus*, INTERCEPT, -2.8, -
 Holzwarth et al. (2013), *Carpinus betulus*, DBH, -0.051, cm
 Holzwarth et al. (2013), *Fagus sylvatica*, INTERCEPT, 1.8, -
 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, m²/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,m²/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,m²/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,m²/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,DBH²,-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,m²/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 spec.,INTERCEPT,4.4508,-
 Monserud and Sterba (1999),Quercus spec.,1/DBH,-12.0041,cm
 Palahí et al. (2003) 2,Pinus sylvestris,INTERCEPT,2.938,-
 Palahí et al. (2003) 2,Pinus sylvestris,BAL,-0.02,m²/ha
 Palahí et al. (2003) 2,Pinus sylvestris,DI,2.719,cm/a
 Trasobares et al. (2004),Pinus sylvestris,INTERCEPT,2.728,-
 Trasobares et al. (2004),Pinus sylvestris,BAL/log(DBH),-0.148,m²/ha/cm
 Trasobares et al. (2004),Pinus sylvestris,ELV,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,-
 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
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 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

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 Wunder et al. (2007) 2, *Abies alba*, KrelBAI1, 0.02, 1/a
 Wunder et al. (2007) 2, *Abies alba*, KrelBAI2, 0.104, 1/a
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 Wunder et al. (2007) 2, *Fagus sylvatica*, relBAI1, -518.37, 1/a
 Wunder et al. (2007) 2, *Fagus sylvatica*, relBAI2, 1038.53, 1/a
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 Wunder et al. (2007) 2, *Fagus sylvatica*, relBAI4, -15.15, 1/a
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 Wunder et al. (2008a) 1, *Alnus glutinosa*, log(relBAI)1, -0.092, 1/a
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 Wunder et al. (2008a) 1, *Alnus glutinosa*, log(relBAI)3, -0.128, 1/a
 Wunder et al. (2008a) 1, *Alnus glutinosa*, KrelBAI1, -4.845897, 1/a
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 Wunder et al. (2008a) 1, *Alnus glutinosa*, KrelBAI3, -3.165683, 1/a
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 Wunder et al. (2008a) 2,*Alnus glutinosa*,KrelBAI3,-3.165683,1/a
 Wunder et al. (2008a) 2,*Carpinus betulus*,INTERCEPT,1.827,-
 Wunder et al. (2008a) 2,*Carpinus betulus*,log(relBAI),0.207,1/a
 Wunder et al. (2008a) 2,*Carpinus betulus*,log(relBAI)1,0.626,1/a
 Wunder et al. (2008a) 2,*Carpinus betulus*,log(relBAI)2,-1.373,1/a
 Wunder et al. (2008a) 2,*Carpinus betulus*,log(relBAI)3,0.747,1/a
 Wunder et al. (2008a) 2,*Carpinus betulus*,KrelBAI1,-5.536796,1/a
 Wunder et al. (2008a) 2,*Carpinus betulus*,KrelBAI2,-4.370165,1/a
 Wunder et al. (2008a) 2,*Carpinus betulus*,KrelBAI3,-3.39317,1/a
 Wunder et al. (2008a) 2,*Fagus sylvatica*,INTERCEPT,10.009,-
 Wunder et al. (2008a) 2,*Fagus sylvatica*,log(relBAI),1.743,1/a
 Wunder et al. (2008a) 2,*Fagus sylvatica*,log(relBAI)1,-0.113,1/a
 Wunder et al. (2008a) 2,*Fagus sylvatica*,log(relBAI)2,0.328,1/a
 Wunder et al. (2008a) 2,*Fagus sylvatica*,log(relBAI)3,-0.215,1/a
 Wunder et al. (2008a) 2,*Fagus sylvatica*,KrelBAI1,-5.32948,1/a
 Wunder et al. (2008a) 2,*Fagus sylvatica*,KrelBAI2,-4.072114,1/a
 Wunder et al. (2008a) 2,*Fagus sylvatica*,KrelBAI3,-3.40999,1/a
 Wunder et al. (2008a) 2,*Fraxinus excelsior*,INTERCEPT,5.413,-
 Wunder et al. (2008a) 2,*Fraxinus excelsior*,log(DBH),1.171,cm
 Wunder et al. (2008a) 2,*Fraxinus excelsior*,log(relBAI),2.418,1/a
 Wunder et al. (2008a) 2,*Fraxinus excelsior*,log(relBAI)1,-0.786,1/a
 Wunder et al. (2008a) 2,*Fraxinus excelsior*,log(relBAI)2,1.444,1/a
 Wunder et al. (2008a) 2,*Fraxinus excelsior*,log(relBAI)3,0.658,1/a
 Wunder et al. (2008a) 2,*Fraxinus excelsior*,KrelBAI1,-4.652545,1/a
 Wunder et al. (2008a) 2,*Fraxinus excelsior*,KrelBAI2,-3.91917,1/a
 Wunder et al. (2008a) 2,*Fraxinus excelsior*,KrelBAI3,-3.04359,1/a
 Wunder et al. (2008a) 2,*Quercus robur*,INTERCEPT,-0.465,-
 Wunder et al. (2008a) 2,*Quercus robur*,log(DBH),2.075,cm
 Wunder et al. (2008a) 2,*Quercus robur*,log(relBAI),1.801,1/a
 Wunder et al. (2008a) 2,*Quercus robur*,log(relBAI)1,-0.157,1/a
 Wunder et al. (2008a) 2,*Quercus robur*,log(relBAI)2,0.382,1/a
 Wunder et al. (2008a) 2,*Quercus robur*,log(relBAI)3,-0.225,1/a
 Wunder et al. (2008a) 2,*Quercus robur*,KrelBAI1,-5.387012,1/a
 Wunder et al. (2008a) 2,*Quercus robur*,KrelBAI2,-4.412423,1/a
 Wunder et al. (2008a) 2,*Quercus robur*,KrelBAI3,-3.732127,1/a
 Wunder et al. (2008a) 2,*Tilia cordata*,INTERCEPT,-0.847,-
 Wunder et al. (2008a) 2,*Tilia cordata*,log(DBH),1.591,cm
 Wunder et al. (2008a) 2,*Tilia cordata*,log(relBAI),1.022,1/a
 Wunder et al. (2008a) 2,*Tilia cordata*,log(relBAI)1,-0.095,1/a
 Wunder et al. (2008a) 2,*Tilia cordata*,log(relBAI)2,0.289,1/a
 Wunder et al. (2008a) 2,*Tilia cordata*,log(relBAI)3,-0.194,1/a
 Wunder et al. (2008a) 2,*Tilia cordata*,KrelBAI1,-5.220199,1/a
 Wunder et al. (2008a) 2,*Tilia cordata*,KrelBAI2,-3.644418,1/a

Wunder et al. (2008a) 2,Tilia cordata,KrelBAI3,-2.870975,1/a
Wunder et al. (unpubl.),low shade tolerance,INTERCEPT,7.5825,-
Wunder et al. (unpubl.),low shade tolerance,DBH,0.0672,cm
Wunder et al. (unpubl.),low shade tolerance,DBH^2,-5.00E-04,cm
Wunder et al. (unpubl.),low shade tolerance,low relBAI,0.581,-
Wunder et al. (unpubl.),low shade tolerance,fast relBAI,1.1968,-
Wunder et al. (unpubl.),low shade tolerance,very fast relBAI,2.0417,-
Wunder et al. (unpubl.),low shade tolerance,log(GDD),-1.0107,-
Wunder et al. (unpubl.),intermediate shade tolerance,INTERCEPT,7.7706,-
Wunder et al. (unpubl.),intermediate shade tolerance,DBH,0.0672,cm
Wunder et al. (unpubl.),intermediate shade tolerance,DBH^2,-5.00E-04,cm
Wunder et al. (unpubl.),intermediate shade tolerance,low relBAI,0.581,-
Wunder et al. (unpubl.),intermediate shade tolerance,fast relBAI,1.1968,-
Wunder et al. (unpubl.),intermediate shade tolerance,very fast relBAI,2.0417,-
Wunder et al. (unpubl.),intermediate shade tolerance,log(GDD),-1.0107,-
Wunder et al. (unpubl.),high shade tolerance,INTERCEPT,8.59,-
Wunder et al. (unpubl.),high shade tolerance,DBH,0.0672,cm
Wunder et al. (unpubl.),high shade tolerance,DBH^2,-5.00E-04,cm
Wunder et al. (unpubl.),high shade tolerance,low relBAI,0.581,-
Wunder et al. (unpubl.),high shade tolerance,fast relBAI,1.1968,-
Wunder et al. (unpubl.),high shade tolerance,very fast relBAI,2.0417,-
Wunder et al. (unpubl.),high shade tolerance,log(GDD),-1.0107,-