

# Predicting tree mortality from growth data: how virtual ecologists can help real ecologists

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## Summary

1. Tree growth and mortality are key elements of forest dynamics, and thus are of great concern for forest managers. It is widely accepted that tree mortality can be predicted using tree growth data. Several approaches have been proposed for modelling the growth-mortality relationship, differing in terms of data sources and model flexibility. However, little is known about their ability to reliably reconstruct the shape of the real growth-mortality relationship due to a lack of long-term data.
2. We adopted a ‘virtual ecology’ approach to this problem, simulating forests with either of two *a priori* specified growth-mortality relationships. Different sampling regimes in these virtual forests resulted in virtual tree-ring data, forest inventory data, or a combination of both. We used eight existing or newly developed models of different structural flexibility to analyse the growth-mortality relationship. The accuracy of the different model outputs, i.e. the deviation from the *a priori* specified growth-mortality relationships, was quantified with the Kullback-Leibler distance.
3. For all data sources, reliable growth-mortality models could be identified. The highest accuracies were found for tree-ring based models, which require only a small sample size (60 dead trees). High model accuracies were also found for forest inventory based models, starting at sample sizes of 500 trees.
4. Flexible statistical approaches turned out to be superior to less flexible models only for large sample sizes (totally 2000 trees). The additional use of Bayesian statistics, specifically designed for small sample sizes, led to high model accuracies only when model flexibility was constrained.
5. *Synthesis.* Our study shows that simulated experiments are a powerful tool for selecting reliable approaches to analyse ecological processes such as tree mortality. Reliable models are fundamental for gaining novel ecological insights into the growth-mortality relationship of tree species. The use of more accurate growth-mortality relationships in forest succession models would allow for strongly improved projections of past and future forest dynamics. Our study provides the theoretical basis for a sound estimation of such growth-mortality models, and it also provides guidelines for efficient sampling schemes in real forests.

**Key-words:** Bayesian statistics, forest dynamics, forest inventory, Kullback-Leibler distance, *Picea abies*, succession models, tree growth, tree mortality, tree rings, virtual ecology

## Introduction

Forest dynamics comprise three major processes: growth, mortality and regeneration of trees. Together, they are regarded as the key elements of succession shaping forest structure and composition (Aubréville 1938; Watt 1947; Remmert 1991). The link between growth and mortality of trees gives rise to so-called ‘slow-growth’ mortality (cf. Keane *et al.* 2001), reflecting the inability of trees to cope with severe environmental stress that leads to unfavourable growing

conditions, e.g. low light availability in the shade of adult trees (Kobe *et al.* 1995), prolonged drought (Villalba & Veblen 1998) or mechanical damage (Schweingruber 1996). Reduced radial growth is often linked to increased mortality rates (Pedersen 1998; Suarez *et al.* 2004; Dobbertin 2005), which can be explained by the carbon allocation rules of trees: under environmental stress, a tree invests its carbohydrates with highest priority into new foliage or new roots and only with a lower priority into radial growth (Waring & Pitman 1985). A better knowledge of the growth-mortality relationship would also be highly useful in sustainable forest management, which tries to emulate natural processes rather than working against them. However, a quantitative understanding of the growth-mortality relationship is required to achieve this end.

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The quantitative analysis of the species-specific behaviour of trees under stressed conditions must be based on a functional relation between growth rates and survival probabilities. Many statistical models have been proposed to fulfil this aim, though they are based on different data sources and are characterized by widely differing flexibility. In practice, data sources comprise tree-ring series with annual growth information (Bigler & Bugmann 2004; Wunder *et al.* 2006; Das *et al.* 2007) or forest inventory data with multi-annual growth information (Bravo-Oviedo *et al.* 2006; Fridman & Ståhl 2001; Wunder *et al.* 2007). Mortality models based on either of these data sources, or their combinations, are characterized by structures of strongly different flexibility, ranging from rigid ‘classical’ threshold models (e.g. Botkin *et al.* 1972) to highly flexible nonparametric models (e.g. Wyckoff & Clark 2000) or models that are based on flexible variable transformations such as restricted cubic splines (Wunder *et al.* 2007). Yet, the statistical analysis of the growth–mortality relationship is often difficult for two reasons. First, the available data rarely reflect the highly variable nature of mortality over space and time in a satisfactory manner, as they represent small samples only (Hawkes 2000; Keane *et al.* 2001). Secondly, even in the case of comparatively large data sets, the underlying real growth–mortality relationship is obviously unknown. Thus, it remains impossible to evaluate the accuracy of growth–mortality models directly against the underlying real growth–mortality relationship.

The objective of our study was to evaluate the accuracy of growth–mortality models that rely on different data sources (e.g. tree rings vs. forest inventory data) and that are characterized by a varying flexibility in their model structure (e.g. logistic regression vs. nonparametric methods). Because analyses of processes with a low signal-to-noise-ratio usually require large (and costly) data sets, many ecologists are highly interested in the level of accuracy that can be achieved with a certain sampling design (data source and model structure). Given that information, it is possible to select the most efficient sampling design with an accuracy that is appropriate for a given application.

We conducted a simulated experiment based on virtual ecology, an approach that is increasingly used to test system behaviour (Grimm *et al.* 1999; Hirzel *et al.* 2001; Tyre *et al.* 2001). Using a ‘virtual ecology’ approach, we simulated forests that have two key advantages compared with the existing, restricted data sources: (i) their size and temporal extent, which is, at least theoretically, unlimited, in our case covering several thousand trees simulated over many centuries; and (ii) the *a priori* specification of the underlying growth–mortality relationships, so that a direct comparison of the estimated and the underlying ‘virtual’ relationships is possible. These virtual forests contain submodels describing growth, mortality, snag standing time and regeneration of trees and, as such, their features closely mimic those of real forests. Samples selected from these virtual forests were used to fit a range of growth–mortality models and to assess their ability to recover the underlying *a priori* growth–mortality relationship. In this context, the success or failure of a certain method depends on

three factors, i.e. the data source, the model structure, and the structure of the virtual forest itself. First, data sources included tree-ring data, forest inventory data, and a combination of both. Secondly, model structure comprised an inflexible linear and two more flexible nonlinear relationships between the logit of mortality probability and tree growth. We also reduced the sample size to evaluate a Bayesian approach that had been developed specifically for handling the problem of small sample sizes (Wyckoff & Clark 2000). Thirdly, to address the effect of the structure of the virtual forest, we created two forests of differing complexity and applied all methods to both of them.

Our analyses focused on two main questions.

1. How does the accuracy of models based on tree-ring data compare with models based on forest inventory data or a combination of both? We hypothesize a higher accuracy of models based on tree rings, or a combination of tree rings and inventory data, compared with models based solely on inventory data, because of the higher temporal resolution of the tree-ring data.
2. Does a higher flexibility of the growth–mortality models result in a higher accuracy? Prior research suggested that for flexibly structured models, substantial sample sizes might be required to exceed the performance of less flexible models (Reineking & Schröder 2006).

Answering these questions implies the development of statistical tools that can be used to evaluate the efficiency of certain sampling designs before conducting an actual field campaign. More specifically, reliable tree growth–mortality relationships, derived with efficient sampling designs, pave the way towards new insights into the life-history strategies of trees and improved projections of forest dynamics in changing environments.

## Methods

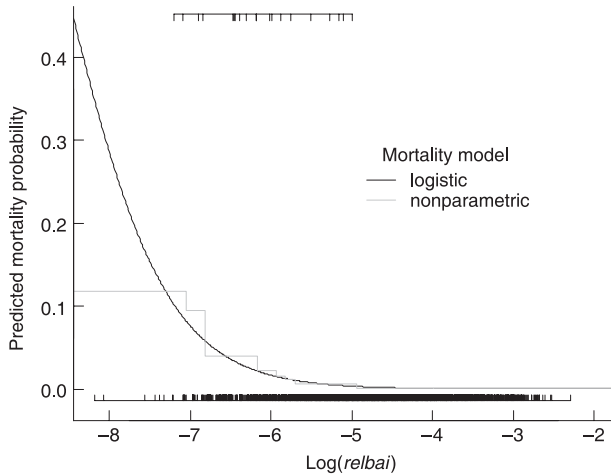
We shall first introduce the virtual forests that were used to simulate growth, mortality and regeneration of trees using an *a priori* specified growth–mortality relationship. Next, we present different sampling procedures that were applied to the virtual forest, resulting in various types of survey data. We then describe the statistical growth–mortality models that were evaluated for their ability to capture the underlying virtual growth–mortality relationship. Subsequently, we present the Kullback–Leibler distance, an accuracy measure that we used to quantify the distance between the underlying and the estimated growth–mortality relationships. Finally, we describe the simulation experiment.

### VIRTUAL FORESTS

The virtual forests were individual-based and consisted of four submodels that describe growth, mortality, the standing time of snags (standing dead trees) and regeneration (Table 1). We defined two forest types, a simple and a complex forest, which differed in the flexibility of the underlying virtual growth–mortality relationship.

Generally, each virtual forest consisted of a constant number of sites in which a single tree can grow. At each site, a newly established tree grew according to the growth submodel, it died according to the mortality submodel and turned into a snag whose standing time was defined by the snag standing time model. After the end of the snag





**Fig. 2.** Submodel for tree mortality. Two predefined underlying growth–mortality relationships were used in the virtual forest: a logistic mortality model (black line) for the simple forest and a nonparametric mortality model (grey line) for the complex forest. Original (annual) growth values are shown as rug plot for 20 dead trees: growth in the year of death (top) and all other years (bottom). For details of the parameterization, see Appendix S2.

For each tree and time step, we calculated the logarithm of the relative basal area increment [=  $\log(\text{relbai})$ ], which relates individual basal area increment to current basal area (Table 1, eqn 2). This variable can be regarded as a proxy for tree vigour and has been successfully applied to predict tree mortality using tree rings (Bigler & Bugmann 2004; Bigler *et al.* 2004).

#### Submodel for tree mortality

Annual tree mortality was modelled as a monotonously increasing function of the growth performance in the previous year, expressed as  $\log(\text{relbai})$ . In order to test how the underlying relationship affects the performance of the different model approaches, we used two relationships (Fig. 2): a simple one, where the logit of the annual mortality probability was a linear function of the growth variable (Table 1, eqn 3), and a complex one, where the logit of the annual mortality probability was a nonparametric function of the growth variable (Table 1, eqn 4, cf. Wyckoff & Clark 2000). No other sources of mortality were included.

#### Submodel for snag standing time

Snag standing time defines how long a dead tree will stand as a snag (and therefore can still be sampled in a survey by the virtual ecologist) before it topples down due to decay processes. Snag standing times were stochastic and followed a Weibull probability density function (Table 1, eqn 5).

#### Submodel for tree regeneration

Tree regeneration was modelled simply by deterministically replacing each fallen snag immediately with one young sapling with an initial basal area equal to the initial value of the Richards equations (see above). Thus, the number of trees in the regeneration phase has an upper bound set by the total number of sites in the virtual forest.

#### Limitations inherent in the virtual forests

The deliberately simplified model structure leads to several model limitations. First, cumulative basal area data simulated with the Richards equation (eqn 1, Fig. 1) are likely to reflect slow-growth periods in the early and in the end phase of every tree's life, but they cannot portray suppression periods that may alternate with periods of higher growth. This may lead to some deviations of our virtual forests from the diameter at breast height (d.b.h.) and age distributions of real forests. Also, our model is likely to overestimate the speed of regeneration, because the virtual trees in our model started to grow at breast height (1.3 m), i.e. smaller trees were not modelled. Each snag that disappeared was immediately replaced by exactly one new tree, and this strongly reduced the abundance of young trees (results not shown).

With respect to the growth–mortality relationship, two aspects warrant discussion: First, the two underlying virtual relationships differ most prominently in the region of very low growth, where empirical data are sparse, i.e. at values for  $\log(\text{relbai}) < -7.5$  (Fig. 2): whereas the mortality probability increases steadily with reduced growth in the logistic mortality model, it reaches a plateau in the nonparametric model. The strong increase of mortality probability in the logistic model may be less realistic, though little can be said about the shape of the growth–mortality relationship underlying the real forests from which we derived the two virtual growth–mortality relationships. However, we neither claim that any of the two virtual relationships is identical to the real-world situation, nor is this crucial for our study. The two virtual relationships cover two rather extreme situations. Thus, estimation procedures that can recover both of these relationships with little error are likely to be successful also in real world situations. Conversely, procedures with large deviations in both cases can be expected to have limited accuracy also in real world situations.

Secondly, the models used assume a constant growth–mortality relationship, without large-scale disturbances. In reality, mortality rates are probably changing both in time and in space, and they are characterized by episodic pulses that can bias estimates considerably. The performance estimates from virtual forests should therefore be interpreted as upper bounds of what can be achieved.

#### SAMPLING PROCEDURE

In the virtual forest, we used a 'virtual ecologist' to collect tree growth and survival information of different quality. We distinguish between three data types with different structure and sampling effort: tree-ring data, forest inventory data, and a combination of both types of data. Tree-ring data from dead trees provided growth information nested within the trees, i.e. there were repeated growth values for each tree, and each growth value is linked to tree survival information, i.e. all growth values except the one of the death year are related to the status 'alive'. In contrast, the forest inventory data comprised aggregated growth information, i.e. only one growth and survival observation was available for each living and dead tree. For all data types, we analysed only trees with a d.b.h. > 4 cm.

The first data type, tree-ring data, comprised the entire growth history of all snags that were sampled in the year  $y$ ; no data from living trees were used. The annual increment was converted to  $\log(\text{relbai})$  values (cf. Table 1, eqn 2).

The second data type, the forest inventory data, consisted of three repeated measurements (inventories) of tree radial growth. They were derived by calculating d.b.h. and tree survival information in the years  $y$ ,  $(y-10)$  and  $(y-20)$ , i.e. at the third, second and first inventory.

The interval length was fixed at 10 years because this time span is often used in large-scale forest inventories (e.g. Swiss National Forest Inventory, Brassel & Brändli 1999). We selected all trees that were alive at the first and second inventory and collected their survival information (dead/alive) at the third inventory. The 10-year  $\log(\text{relbai})$  calculated between the first and second inventory was used to explain the survival probability of the tree at the third inventory.

The combined data comprised forest inventory data derived from the living trees and tree-ring data derived from the dead trees, which may be collected in smaller, but more intensive, inventory efforts. For all trees that died in the last 5 years before the sampling year  $y$  (dead trees), the last five tree rings were collected to calculate the averaged 5-year  $\log(\text{relbai})$ . In contrast, for each tree living in the year  $y$ , we calculated the d.b.h. at two forest inventories in the years  $y$  and  $y-5$  years. The growth increment between these two inventories was condensed to an averaged 5-year  $\log(\text{relbai})$  value per tree.

In order to test a less comprehensive and therefore less expensive approach, we additionally created a reduced combined data set comprising all dead trees that died in the last 5 years prior to sampling but only a subset of the (many) living trees. According to the number of dead trees found in the inventory, we randomly selected an *equal* number of living trees with a similar d.b.h. from the pool of all living trees (cf. Wyckoff & Clark 2000), resulting in a 1 : 1 sample of living and dead trees. However, the advantage of this reduced sampling effort caused two additional uncertainties: first, the need to randomly select living trees, and secondly the uncertainty regarding the percentage of dead trees present in the forest at a given time.

#### EVALUATED GROWTH-MORTALITY MODELS

We evaluated eight growth-mortality models that required different data sources and featured different structural flexibility (Table 2); some of them were taken from the literature, whereas others were developed specifically for this study. The data sources include tree-ring data (T), forest inventory data (I), and a combination of both (C). The flexibility comprised an inflexible linear (L) and two more flexible nonlinear relationships (RCS = restricted cubic splines, NP = nonparametric) between the logit of the mortality probability

and tree growth. Below, we refer to methods with different data sources and model structure using the notation 'Data source<sub>Model structure</sub>', e.g. model  $T_L$  denotes a model based on tree-rings (T) analysed using logistic regression (L). In addition to the eight models, we evaluated a null model without any growth information, i.e. a constant annual mortality probability.

#### Tree-ring based models

We developed two tree-ring models that are based on logistic regression (tree-ring models with differing flexibility,  $T_L$  and  $T_{RCS}$ , Table 2). The response variable was the binary variable dead/alive, and the explanatory variable was the annual  $\log(\text{relbai})$ . For the less flexible model  $T_L$ , we used a logistic regression without further variable transformation (Table 1, eqn 3), whereas for the flexible model  $T_{RCS}$  we applied a restricted cubic spline transformation with three knots:

$$\log\left(\frac{\text{Pr}}{1-\text{Pr}}\right) = \beta_0 + \beta_1 x + \sum_{j=2}^4 \beta_j (x + \kappa_{j-1})_+^3, \quad (\text{eqn 6})$$

$$(z)_+ = z \text{ if } z > 0, 0 \text{ otherwise}$$

where  $x = \log(\text{relbai})$ ,  $\kappa_1 \dots \kappa_3$  are the knots of the restricted cubic spline transformation, and  $\beta_0 \dots \beta_4$  are parameter values. Restricted cubic splines are composed of third-order polynomials within intervals determined by the knots and thus result in a composite function that is constrained to be linear in the tails (Stone & Koo 1985; Harrell 2001).

#### Forest inventory based models

Our two forest inventory models were based on logistic regression (Wunder *et al.* 2007; forest inventory models  $I_L$  and  $I_{RCS}$ , Table 2). The response variable was the binary variable dead/alive and the explanatory variable was the 10-year  $\log(\text{relbai})$ . We derived a less flexible logistic regression model without further variable transformation ( $I_L$ , cf. eqn 3) and a more flexible logistic regression model with a restricted cubic spline transformation of the predictor variable ( $I_{RCS}$ , cf. eqn 6). Because both models  $I_L$  and  $I_{RCS}$  predicted

**Table 2.** Overview of the selected growth-mortality models. (L = linear model; RCS = restricted cubic splines, NP = nonparametric model; BY = model based on Bayesian approach)

		Data source	
		Dead trees	Living trees
Growth-mortality models			
Tree-ring models	$T_L$	Entire cores	–
	$T_{RCS}$		
Forest inventory models*	$I_L$	–	10-year-increment of all trees
	$I_{RCS}$		
Combined models†	$C_L$	5-year-increment of all trees that died in the last 5 years	5-year-increment of all trees
(based on tree-ring and forest inventory data)	$C_{NP}$		
	$C_{L,BY}$	5-year-increment of all trees that died in the last 5 years	5-year-increment of a random selection of trees,
	$C_{NP,BY}$		based on a 1 : 1 sample of dead and living trees

Notes: For model  $C_{NP,BY}$ , living trees with a similar d.b.h. as the dead trees were selected. For a detailed description of the methods see \*Wunder *et al.* (2007) and †Wyckoff & Clark (2000).

10-year survival probabilities based on a 10-year growth history we converted all predicted survival probabilities to annual survival probabilities by taking the 10th root.

### Models based on a combination of tree-ring and forest inventory data (combined models)

The four combined models were based on either logistic regression or nonparametric procedures (Wyckoff & Clark 2000), and they required either the data of the entire forest or a subset of those data. The former were analysed using the logistic regression model  $C_L$  (linear) and the nonparametric model  $C_{NP}$  (nonlinear). Reduced data sets were analysed with additional models based on Bayesian statistics designed for small data sets (Wyckoff & Clark 2000), i.e. a logistic regression model  $C_{L,BY}$  (linear, Bayes) and a nonparametric model  $C_{NP,BY}$  (nonlinear, Bayes).

The first combined model,  $C_L$ , was based on logistic regression. The response variable was the binary variable dead/alive, and the explanatory variable was the averaged 5-year  $\log(\text{relbai})$  (cf. eqn 3).

The second combined model,  $C_{NP}$ , was the nonlinear equivalent of model  $C_L$ . It was based on a nonparametric approach where the range of the growth variable  $\log(\text{relbai})$  was divided into several equally small bins, and for each bin the corresponding mortality rate was calculated by dividing the number of dead trees per bin by the number of all trees. We expanded the bin size by successive pooling of adjacent bins until the mortality rates described a decreasing monotonous function. The resulting step function was used as a mortality function. For a more detailed description of this approach, see Wyckoff & Clark (2000).

The third combined model,  $C_{L,BY}$ , was based on logistic regression applied to a reduced combined data set of a total of  $N_1$  trees (see above). The two uncertainties inherent in this reduced data set (see above) were treated with bootstrapping techniques and Bayesian statistics (Wyckoff & Clark 2000). To cope with the first uncertainty of randomly sampling living trees, we created 500 bootstrap samples, and for each of them we drew with replacement  $D_1$  dead trees from the pool of  $D_1$  dead trees and  $A_1$  living trees from the pool of  $N_1 - D_1$  living trees, with

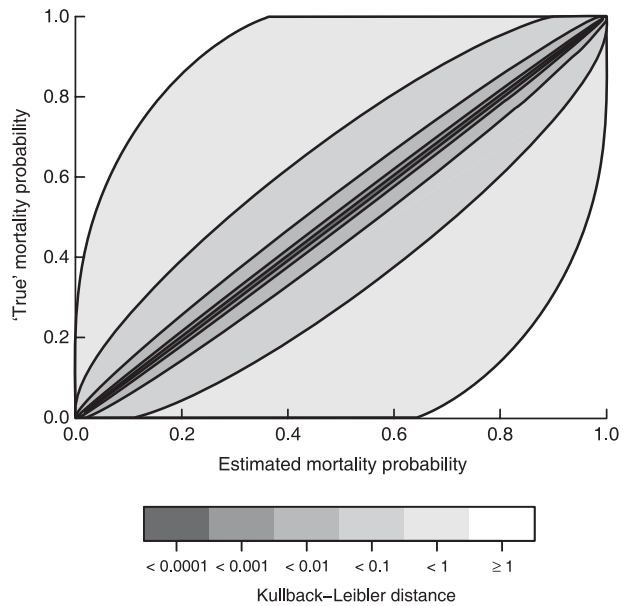
$$A_1 = D_1 \frac{1 - \theta}{\theta} \quad (\text{eqn 7})$$

where  $\theta$  represents the percentage of dead trees. To cope with the second uncertainty inherent in  $\theta$ , we used a Bayesian approach and calculated the probability distribution of  $\theta$  using a posterior density  $f(\theta)$ :

$$f(\theta | D_1, N_1) = \frac{\theta^{D_0+D_1-1} (1-\theta)^{N_0-D_0+N_1-D_1-1}}{B(D_0 + D_1, N_0 - D_0 + N_1 - D_1)} \quad (\text{eqn 8})$$

with  $D_0$  and  $N_0$  denoting the prior estimates of the number of dead and total (dead and living) trees, and  $B$  being the beta function (Wyckoff & Clark 2000). We used a non-informative prior for  $\theta$  that was determined by the data ( $N_0 = 0$ ,  $D_0 = 0$ ). Thus, each bootstrap sample contained a slightly different sample of trees and also a different percentage of dead trees. For each of these 500 samples, we fitted a logistic regression with the binary response variable dead/alive and the explanatory variable averaged 5-year  $\log(\text{relbai})$  (cf. eqn 3). The mean regression coefficients of the 500 bootstrap samples yielded the final parameter values of the model  $C_{L,BY}$ .

The fourth combined model,  $C_{NP,BY}$ , was the nonlinear equivalent of model  $C_{L,BY}$ ; it was applied to the same reduced combined data set. We calculated a monotonous mortality function according to



**Fig. 3.** Kullback-Leibler distance between underlying and estimated mortality probability. Areas of similar KL distances between the *a priori* specified and the estimated growth-mortality model are shown with grey colours. For example, the (inner) black lens represents an area with  $KL < 0.0001$ .

the model  $C_{NP}$ , resulting in the estimate  $C_{NP,BY}$ . The average step function of 500 bootstrap mortality step functions yielded the final growth-mortality model  $C_{NP,BY}$ .

The combined models predicted 5-year survival probabilities based on 5-year growth and survival information. The predictions were converted to annual survival probabilities by taking the fifth root.

### EVALUATION CRITERION: THE KULLBACK-LEIBLER DISTANCE

We quantified the deviation of the estimated growth-mortality relationship from the underlying relationship with the Kullback-Leibler (KL) distance (Kullback & Leibler 1951; see Fig. 3). KL is an information theory based measure of the distance between two models or probability distributions (Burnham & Anderson 2002). For a given growth value  $x$ , there is a correct (i.e. *a priori* specified) annual probability of survival  $\text{Pr}(x)$  according to the underlying virtual growth-mortality relationship, and an estimated probability  $\hat{\text{Pr}}(x)$  from the fitted growth-mortality model. The KL distance between these two values is given by

$$KL = \text{Pr}(x) \log \left( \frac{\text{Pr}(x)}{\hat{\text{Pr}}(x)} \right) + (1 - \text{Pr}(x)) \log \left( \frac{1 - \text{Pr}(x)}{1 - \hat{\text{Pr}}(x)} \right) \quad (\text{eqn 9})$$

where the growth value  $x$  equals  $\log(\text{relbai})$ . The smaller the difference between  $\text{Pr}(x)$  and  $\hat{\text{Pr}}(x)$ , the smaller the corresponding KL distance. For example, a KL distance of 0.001 means that a certain underlying survival probability (e.g.  $\text{Pr}(x) = 0.99$ ) is either under- or overestimated (e.g.  $\hat{\text{Pr}}(x) = 0.9849$  or  $0.9938$ ; cf. Figure 3). Under the assumption that 2% of all trees with such a constant underlying survival probability of  $\text{Pr}(x) = 0.99$  will reach their maximum age (Botkin *et al.* 1972), the correct maximum age would be 391 years,

and age estimations based on uncertain probability estimations ( $\hat{\text{Pr}}(x)$ , see above) would be either 259 or 633 years. Similarly, a lower  $\text{KL} = 0.0001$  corresponds to smaller errors of  $\hat{\text{Pr}}(x)$  (0.9885 or 0.9913) and of estimated maximum age (341 and 452, respectively). In the following, we will consider a KL distance of 0.001 as desirable. However, there are no general rules when a KL distance is acceptable, and whether a specific KL distance is sufficient depends on the context of application.

For the model comparison, we used the expected KL distance over all growth values, which we defined as the weighted average over all growth values:

$$\text{weighted KL} = \int_{-9}^0 \omega(x) \text{KL}(x) dx. \quad (\text{eqn 10})$$

The weights of the growth values corresponded to their probability density, which was estimated using a logspline density (Stone *et al.* 1997) of the  $\log(\text{relbai})$  values from a large virtual forest (simple or complex forest with 5000 trees). The integration limits were set to  $-9$  and  $0$ , which covered the most extreme growth values in the data set.

## SIMULATION EXPERIMENT

We constructed virtual forests with either the less flexible simple mortality model (simple forests) or the more flexible complex mortality model (complex forests). Both simple and complex forests were simulated 100 times for 500, 1000 and 2000 trees. These three forest sizes represent area-normalized reference sample sizes for the three sampling procedures, i.e. tree-ring, forest inventory and combined sampling. The effective sample sizes differed between the three procedures: forest inventory sampling used all trees in the reference sample, i.e. 500, 1000 or 2000 trees; tree-ring sampling used only standing dead trees, i.e. *c.* 60, 120 or 240 trees; finally, the

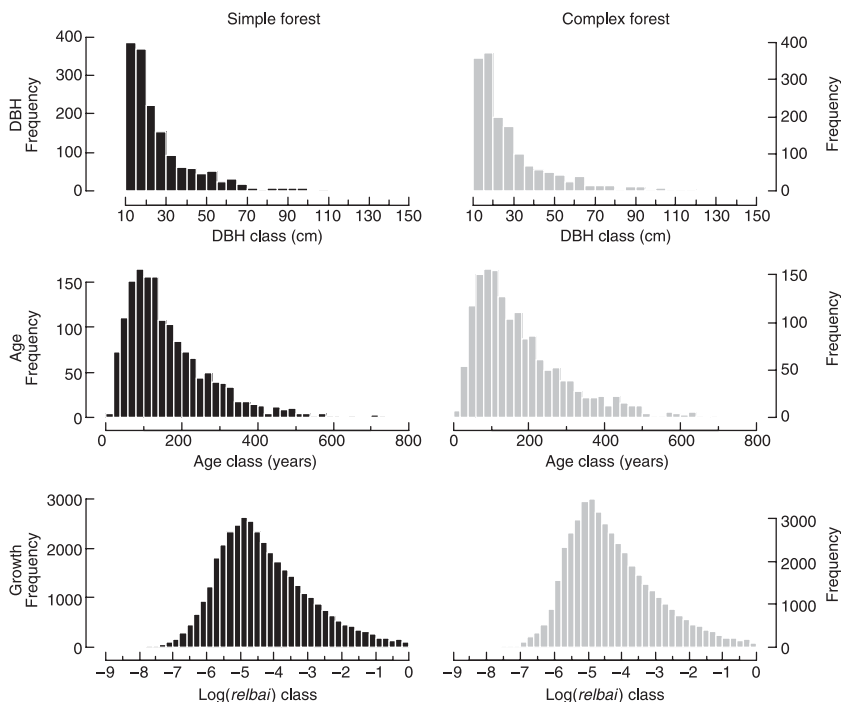
combined sampling used all recently ( $\leq 5$  years) dead trees and either all living trees or a number of living trees matching the number of recently dead trees. We separately simulated forests for the three different sizes to ensure independent samples. These virtual forests were sampled after 1500 years of succession, which assured an approximate equilibrium of the demographic processes. Thus, the resulting samples contained the entire growth histories of all trees and were converted to the data required by the different models, e.g. for the tree-ring based models the tree-ring information of all dead trees. The predicted probabilities of each of the eight models were used to calculate the corresponding KL distances, and the mean KL distances served as a measure of model accuracy.

All analyses were performed using R, a language and environment for statistical computing (R for Windows version 2.3.1; R Development Core Team 2006). Restricted cubic spline transformations were done using the Design package (R-package version 2.0–12; Harrell 2005); logspline density estimations were conducted using the Logspline package (R-package version 2.0.3; Kooperberg 2006).

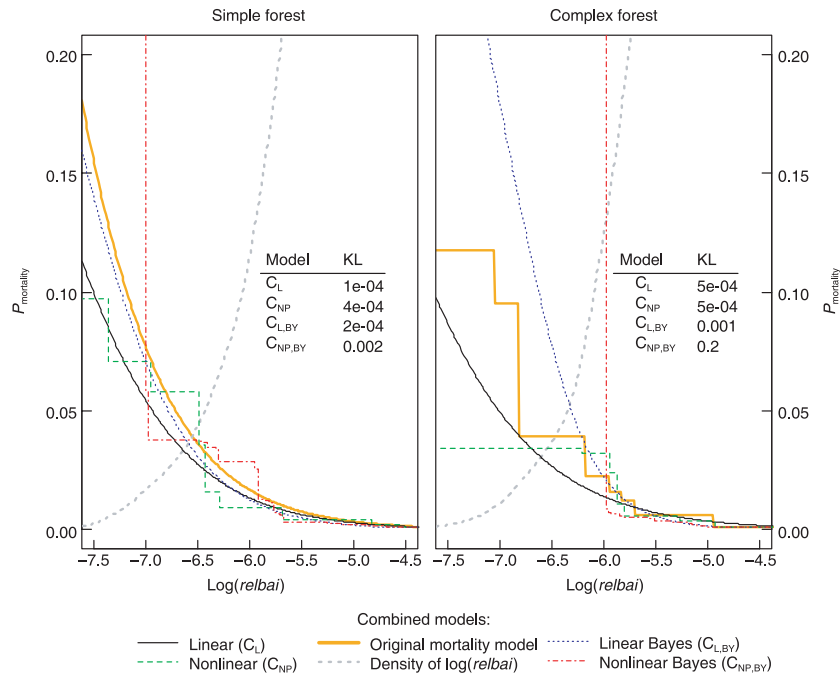
## Results

### KEY CHARACTERISTICS OF VIRTUAL FORESTS

The virtual forests exhibited characteristics typical of real forests (Leibundgut 1993; Peterken 1996; McElhinny *et al.* 2005). The d.b.h. distributions of the virtual forests showed a negative exponential or reversed J-shaped form, and many trees were between 60 and 140 years old (Fig. 4). The complex forests contained slightly more trees with higher d.b.h. and also slightly older trees than simple forests (Fig. 4). The proportion of snags in both virtual forest types ranged between 12 and 16%.



**Fig. 4.** Distribution of diameter at breast height (d.b.h.), age, and growth of simple and complex forests. d.b.h. and age frequencies are shown for a population sample of trees with d.b.h. > 10 cm from virtual forests (one realization per simple and complex forest with  $n = 2000$  trees after 1500 years of simulated succession).  $\log(\text{relbai})$  frequencies reflect the entire growth histories of all dead trees. Black bars, simple forest; grey bars, complex forest.



**Fig. 5.** Comparison of predicted mortality probabilities with the underlying virtual growth-mortality relationship using the Kullback-Leibler distance (KL). The combined growth-mortality models  $C_L$ ,  $C_{NP}$ ,  $C_{L,BY}$  and  $C_{NP,BY}$  were fitted to a population sample of trees from virtual forests and used to predict the mortality probabilities for a range of growth conditions (one realization per simple and complex forest with  $n = 2000$  trees after 1500 years of succession). The resulting mortality probability curves were compared against the corresponding *a priori* specified mortality model for the simple and complex forests (orange solid line). The KL distance between these curves is displayed in the figure (top right of each panel). Models:  $C_L$  = logistic regression (black solid line),  $C_{NP}$  = nonparametric approach (green dashed line),  $C_{L,BY}$  = logistic regression with Bayesian statistic (blue dotted line),  $C_{NP,BY}$  = nonparametric approach with Bayesian statistic (red dashed line). Densities of  $\log(\text{relbai})$  were calculated from large simple and complex forests ( $n = 5000$  trees, grey dashed line).

#### ESTIMATION OF THE *A PRIORI* SPECIFIED MORTALITY MODEL

The estimated growth-mortality relationships were used to predict annual mortality probabilities for a range of different growth conditions. The performance of the null model without growth information (KL = 0.005) was exceeded by all other models, independently of the data source (tree rings, inventory data, or a combination of the two). Thus, the eight models allow for a reasonable reconstruction of the *a priori* specified growth-mortality relationship. However, the combined models showed a KL < 0.005 only when applied to large forests (2000 trees). Furthermore, the accuracy of the growth-mortality models differed relatively strongly, as is evident from the distance between the mortality probability curve of the *a priori* specified mortality model and the corresponding probability curves estimated by the different models (Fig. 5).

Overall, the simpler forests were better represented by the different sampling procedures and model approaches than the complex forests. For both forest types, the tree-ring based models showed the highest accuracies compared with all other models (cf. Figures 6–8). Generally, the higher the number of trees in the virtual forests, the more accurate the corresponding model. On the one hand, with increasing sample size, the peak at the mode of the distribution (i.e. the most frequent value) got more pronounced, and shifted slightly

towards lower KL-distances. On the other hand, with increasing sample size, variances of the KL distance decreased, i.e. the frequency of large model discrepancies dropped.

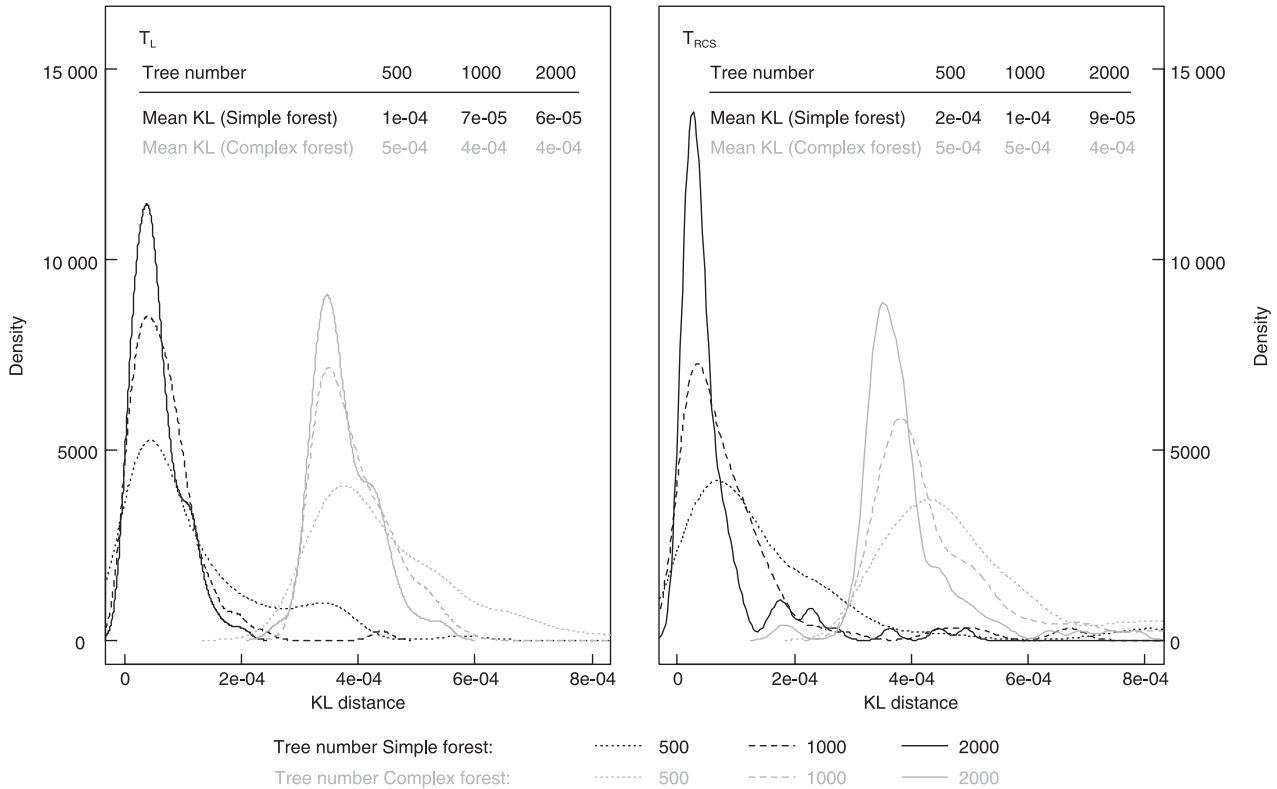
#### Tree-ring models

A nearly perfect match of the predicted probabilities was found for the maximum likelihood models  $T_L$  and  $T_{RCS}$  with KL distances very close to zero (Fig. 6). Still, both models ( $T_L$  and  $T_{RCS}$ ) showed markedly better performance for the simple forest than the complex forest. For the simple forest, the lowest KL distances were measured for model  $T_L$  (Fig. 6 left); for the complex forests, both models ( $T_L$  and  $T_{RCS}$ ) showed a similar performance.

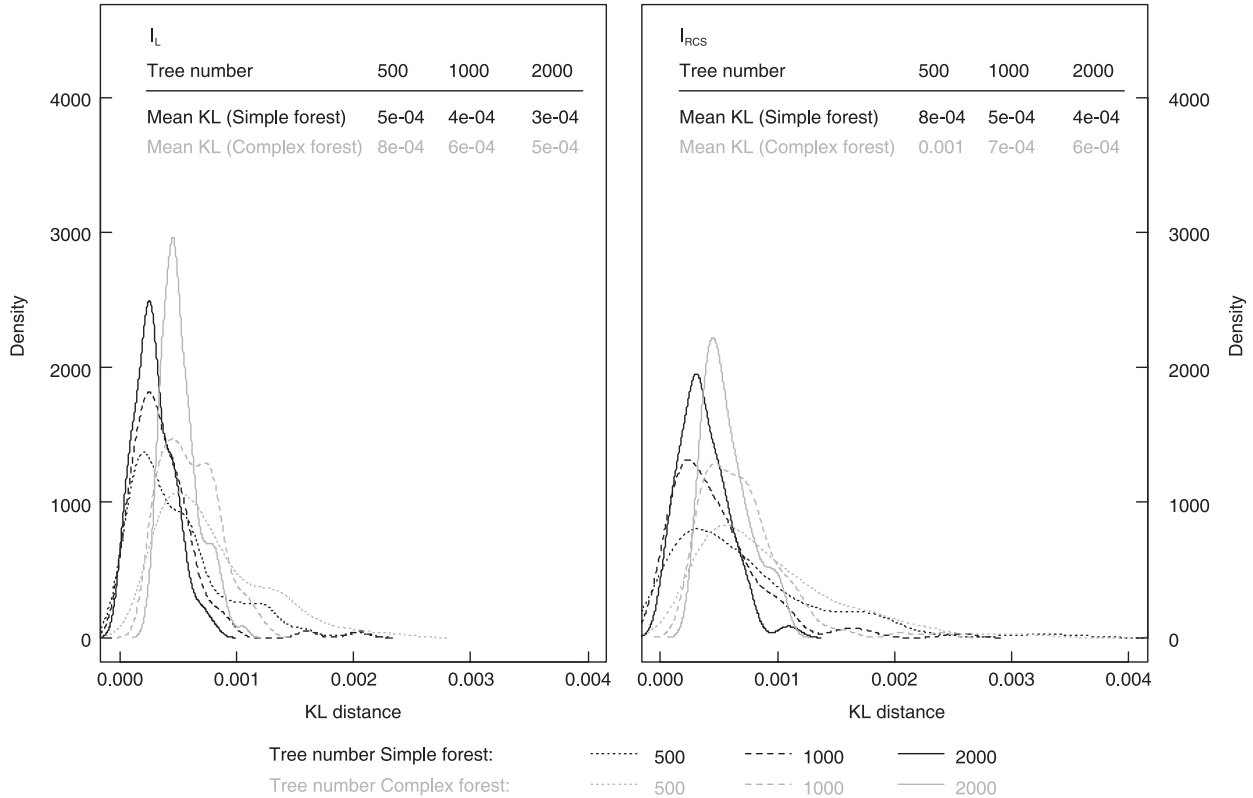
#### Forest inventory models

Both models ( $I_L$  and  $I_{RCS}$ ) exhibited relatively high accuracies (mean KL = [0.0005 ... 0.001], Fig. 7). The inflexible model  $I_L$  showed a slightly better performance in both forests. In contrast to the tree-ring models, there was considerably less difference in model performance between the two forest types. This was mostly due to the lower performance in simple forests. The KL distances of both inventory models applied to large complex forests (2000 trees) were very close to the KL distances measured for both tree-ring models (Fig. 6).

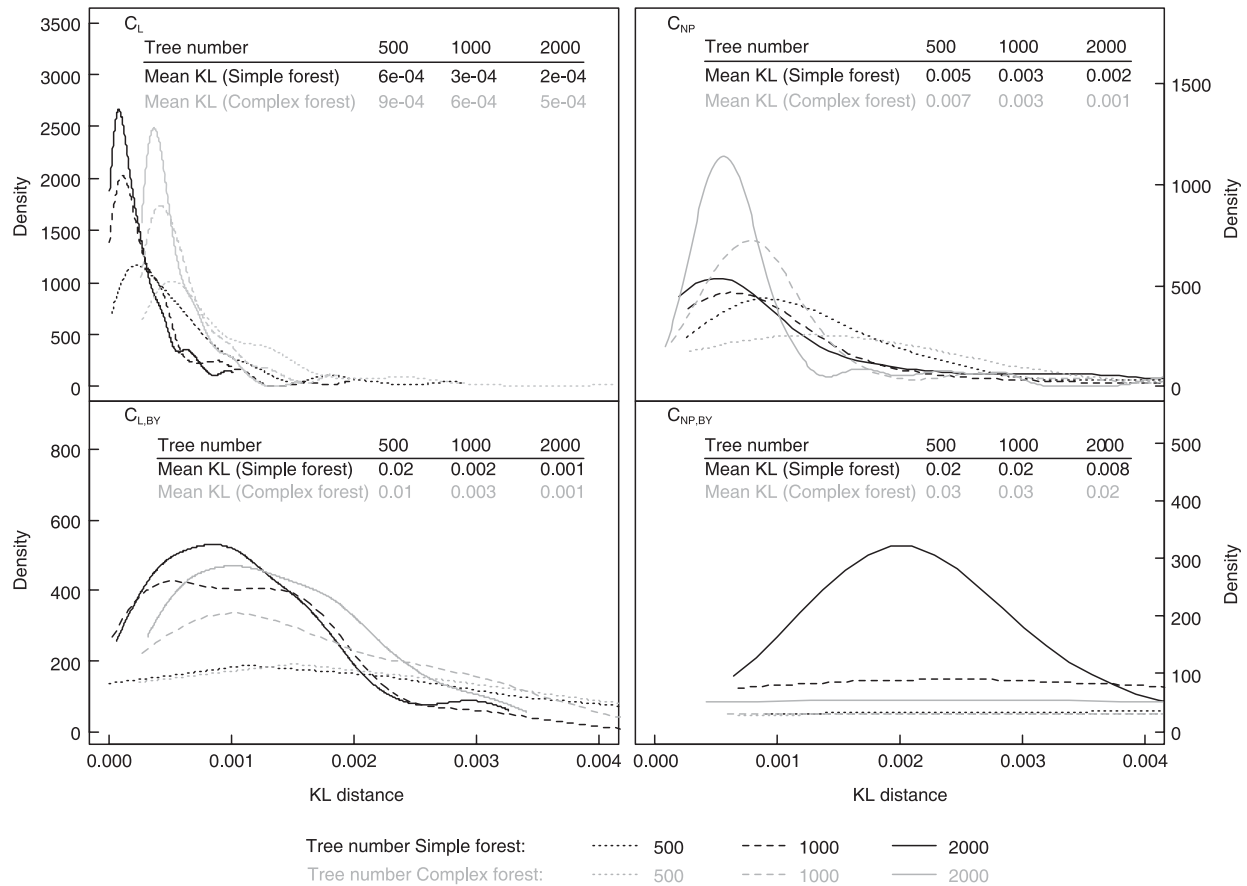




**Fig. 6.** Evaluation of the growth-mortality models based on tree-ring data. KL distances between the underlying virtual and fitted growth-mortality models are shown for 100 random realizations of different-sized simple forests (black lines) and complex forests (grey lines). Displayed are the KL distances for model  $T_L$  (linear tree-ring model, left) and model  $T_{RCS}$  (nonlinear tree-ring model, right).



**Fig. 7.** Evaluation of the growth-mortality models based on forest inventory data. KL distances between the underlying virtual and fitted growth-mortality models are shown for 100 random realizations of different-sized simple forests (black lines) and complex forests (grey lines). Displayed are the KL distances for the model  $I_L$  (linear inventory model, left) and model  $I_{RCS}$  (nonlinear inventory model, right).



**Fig. 8.** Evaluation of the growth-mortality models based on tree-ring and forest inventory data (combined models). KL distances between the underlying virtual and fitted growth-mortality models are shown for 100 random realizations of different-sized simple forests (black lines) and complex forests (grey lines). Displayed are the KL distances for the combined models, i.e. logistic regression (top left), nonparametric approach (top right), logistic regression with Bayesian statistics (bottom left) and nonparametric approach with Bayesian statistics (bottom right). Note the differences in the scale of the ordinate.

### Combined models

The model  $C_L$  was by far most accurate (Fig. 8, top left). In particular, the application of the model  $C_L$  to larger simple forests (1000 and 2000 trees) showed higher accuracies as compared with same-sized complex forests. The nonparametric model  $C_{NP}$ , which used the same data base as model  $C_L$ , showed a considerably lower accuracy (Fig. 8, top right). For example, even forests with 2000 trees analysed with the model  $C_{NP}$  revealed higher KL distances and consequently lower accuracies than a 500-tree forest analysed with the model  $C_L$ . The application of model  $C_{NP}$  to the complex forest resulted in more accurate predictions as compared with simple forests only for large sample sizes (2000 trees). In particular, only at sample sizes of at least 1000 trees did  $C_{NP}$  models outperform the null model without growth information, which had a KL distance of 0.005. Compared with the inventory models, there was no noticeable gain in accuracy in the combined models.

Both Bayesian models with a reduced data basis, i.e. the models  $C_{L,BY}$  and  $C_{NP,BY}$ , were less accurate than their corre-

sponding large sample models  $C_L$  and  $C_{NP}$ . The nonparametric approach with Bayesian statistic appeared to be least accurate (Fig. 8, bottom right). In contrast to the models  $C_L$  and  $C_{NP}$ , the KL distances for a simple and a complex forest of 500 trees were quite similar. However, with an increasing number of trees, the accuracy of the Bayesian model  $C_{L,BY}$  was consistently higher than the accuracy of the Bayesian model  $C_{NP,BY}$  (Fig. 8). The nonparametric Bayesian model  $C_{NP,BY}$  never reached the accuracy of the null model in our simulations, not even at a reference sample size of 2000 trees.

### Discussion

We shall first discuss the features of the virtual forests that were created using an *a priori* specified growth-mortality relationship. We then highlight the ability of several methods to capture that underlying virtual growth-mortality relationship, i.e. their accuracy. Lastly, we discuss the implications of these findings for the choice of an appropriate sampling design, as well as ecological consequences and future perspectives of this work.

## FEATURES OF VIRTUAL FORESTS

The virtual forests presented here are the result of strongly simplified processes of forest dynamics. Still, the distribution of the d.b.h. frequencies of the virtual forests showed a reversed J-shaped form (Fig. 4) that is considered typical for primary forests (Rubin *et al.* 2006). Also, the observed distribution of tree ages (Fig. 4) is comparable with that of uneven-aged forests (McCarthy & Weetman 2006). After 1500 years of simulated succession, the proportion of dead trees ranged between 12 and 16%, which lies well within the plausible range of 5–27% for the snag proportion of stems in primeval forests of the subalpine and boreal zones of Europe (Korpel 1995; Linder *et al.* 1997; Motta *et al.* 2002). Thus, the virtual forests exhibited quite realistic properties, in spite of the strongly simplifying assumptions that we made (cf. methods section).

## ACCURACY CHANGES WITH DATA SOURCE

*Tree rings*

Tree-ring based models showed an outstanding accuracy as expressed by the lowest measured KL distances for both forests (simple and complex forest, Fig. 6). The highest overall performance found for the model  $T_L$  within the simple forest is not surprising because of identical structures of the underlying virtual growth-mortality model and the fitted growth-mortality model. However, both methods depicted equally well the non-parametric model of the complex forest. The outstanding performance of the tree-ring methods may be explained by the fact that the complete growth information was available with annual resolution for every dead tree in the virtual forests, and also by the assumption of a fixed growth-mortality relationship. In reality, this relationship is likely to vary among populations of the same species, and also with age, climate and site factors.

*Forest inventories*

Both forest inventory models showed high model performance with slightly lower KL distances measured for the inflexible model  $I_L$  (Fig. 7). For small-sized forests (500 trees), the flexible  $I_{RCS}$  model showed for a few randomizations relatively high KL distances (see Fig. 7) with a strong influence on the mean KL. However, the larger the forest, the lower the differences between the two models; forests of 5000 trees showed no differences between the two methods (results not shown).

*Combined data.* The linear model  $C_L$  outperformed all other combined models ( $C_{NP}$ ,  $C_{L,BY}$ ,  $C_{NP,BY}$ ) for both forest types (simple and complex forests). The Bayesian model  $C_{L,BY}$  showed high accuracies only for forests of more than 1000 trees, whereas smaller samples of 500 trees showed low model accuracy, indeed lower than the null model that does not include any growth information. Finally, the Bayesian model  $C_{NP,BY}$  exhibited the lowest accuracy, which is in contrast to the findings by Wyckoff & Clark (2000), who found the non-

parametric approach to be the best model according to their data. One reason for this might be an overfitting of our non-parametric model, i.e. it was fitted too closely to the frequency distribution of the growth and survival data in the specific sample.

The different assessment of the nonparametric method between our study and the one by Wyckoff & Clark (2000) highlights a general issue when comparing flexible and inflexible methods. The strength of the nonparametric approach is that it can closely represent the specific underlying sample. However, if there is high variability in the data and the sample is small, chances are that the particular sample differs substantially from the relationship found in the whole population, even if there is no systematic bias in the sampling. At small sample sizes, flexible and inflexible methods therefore serve quite different purposes. Flexible methods are useful if the peculiarities of the sample at hand are of greatest interest. However, differences apparent in, for example, the growth-mortality relationships, as made visible by flexible methods, can often be due to chance alone rather than indicating differences in the underlying growth-mortality relationships. With small sample sizes, inflexible methods are thus usually more adequate when the aim is to draw inferences on the whole population, which is the case when, for example, using such growth-mortality relationships in forest simulation models.

## IMPLICATIONS FOR APPLIED ECOLOGY

*(a) Sampling design*

Our analyses are relevant for field ecologists because they help in selecting an appropriate sampling design. Tree-ring series from a few dead trees lead to highly accurate growth-mortality relationships so long as the underlying trees are drawn from a population sample. In our simulations, *c.* 60 dead trees were sufficient to yield models that exceeded the accuracy of models based on forest inventory data comprising 1000 trees. Thus, in spite of the relatively high effort that has to be put into field sampling and sample preparation, it may be very rewarding to core dead trees. This holds especially true in areas with low decay rates that are typical for sites at high elevations, high latitudes, or in dry areas (Bigler & Bugmann 2004; Kueppers *et al.* 2004; Storaunet & Rolstad 2004). However, at warm and moist sites high decay rates often result in fairly rapid ring erosion. Moreover, the absence of small dead trees due to relatively fast wood decay results in an over-representation of large dead trees. Such a sample of dead trees may cause a biased estimation of the underlying growth-mortality relationship (results not shown). In addition, tree-ring based methods may be less robust than inventory-based methods to deviations from our model assumptions, such as an identical growth-mortality relationship across all trees.

The proportion of dead trees in our virtual forests depends strongly on the submodel for snag standing time, which was derived from data from southern Norway (Storaunet &

Rolstad 2004), i.e. conifers from boreal forests that are known to have relatively low decay rates (Rouvinen & Kouki 2002; Mäkinen *et al.* 2006). Higher decay rates as expected for broad-leaved trees or generally for the temperate zone would result in somewhat shorter snag standing times (Kupferschmid Albisetti *et al.* 2003), which could have consequences for the minimum number of trees required to reliably estimate growth-mortality models.

The low temporal resolution of forest inventory data, i.e. only three measurements in 30 years, can be compensated for using large data sets (e.g. records from 2000 trees). Growth-mortality models obtained like this showed similarly high model accuracies as the tree-ring methods.

However, the extension of forest inventory data with short tree-ring series from dead trees (combined data) was shown to provide an excellent data source for Bayesian analysis if model flexibility is constrained (i.e.  $C_{L,BY}$ ). In contrast to the tree-ring and forest inventory data, the measurement effort of this method is comparatively low: given a population sample of 2000 trees, the short tree-ring cores from all dead trees can be easily collected and an equal number of even-sized trees need to be selected from the rest of the population. Of course, the accuracy of this method is lower as compared with methods using a small number of dead trees and annual growth resolution (tree-ring methods) or many trees with low temporal resolution (forest inventory methods). However, the accuracies that were obtained here may be sufficient (e.g.  $KL = 0.001$  for  $C_{L,BY}$ ), especially if tree-ring sampling is restricted (such as in national parks) or if no forest inventory records are available.

#### (b) Decision support in forestry

We propose that a better characterization of growth-mortality relationships is useful in practical forestry, i.e. in modern sustainable forest management. Simulation models have become an important decision support tool in forestry (cf. Pretzsch *et al.* 2007), but to date the growth-mortality relationships in these models largely lack a solid empirical basis, contributing to the uncertainty inherent in the simulation results (Keane *et al.* 2001). Forest management will usually directly affect the growth conditions of trees, and, consequently, it may indirectly affect tree mortality and hence forest dynamics. If this link were better reflected in forest management models, this should allow for a more realistic and comprehensive comparison and evaluation of management scenarios.

Similarly, forest models are often used to project the impacts of anthropogenic climate change and atmospheric  $CO_2$  fertilization on forest dynamics. Changes in mortality rates are an important determinant of the simulated magnitude and rate of change of simulated properties such as species composition, basal area, or carbon storage. Again, an improved representation of the growth-mortality relationship in these models is likely to have strong implications for the simulation results, with ensuing implications for sustainable forest management and adaptation practices.

#### IMPLICATIONS FOR BASIC ECOLOGY: STRESS TOLERANCE, SHADE TOLERANCE AND TREE MORTALITY

In many forest succession models, stress tolerance is related to shade tolerance (Keane *et al.* 1996; Bugmann 2001); hence competition for light is regarded as the most important stress factor influencing tree mortality. However, the classification of plants in shade tolerance classes is often based on field observations rather than on experiments (e.g. Ellenberg *et al.* 1992), which is especially evident for long-lived plants such as trees. Accurate growth-mortality models that were successful in this study might be applied to the growth histories of a range of tree species. This could help to elucidate the relationship between their stress and shade tolerances if we assume that competition for light is an important stress factor at the study sites. Such quantitative analyses would permit the classification of trees into functional groups with similar shade tolerance (Grime *et al.* 1989; Smith *et al.* 1997). As the qualitative classification of shade tolerance is widely used in forest succession modelling (e.g. Bugmann 2001; Seidl *et al.* 2005) accurate growth-mortality models would allow for corroboration and possibly a refinement of the existing classification of shade tolerance. Besides the consequences for forest succession modelling, a quantitative analysis of shade tolerance would help to further explain its role as one of the dominant life-history traits (Loehle 2000; Niinemets & Valladares 2006).

#### THE ROLE OF VIRTUAL ECOLOGY

In this study we have made extensive use of the virtual ecology approach. Virtual ecology has several potential uses for practical ecologists. First, virtual ecology helps to assess whether a particular statistical method or sampling design is *principally* capable of providing the desired answers. Next, virtual ecology allows us to compare alternatives in the general sampling design or statistical analysis, to identify the most efficient and/or robust ones, and it thereby helps to use resources (e.g. time) efficiently. Further, it can be used to identify necessary sample sizes for a desired level of accuracy, although these values should in general be regarded as lower bounds, because not all real-world complications can be accounted for in the virtual world. Finally (perhaps less tangible but no less important) virtual ecology helps to synthesize the current knowledge of an ecological system because it necessitates a precise description of the system that is then implemented on a computer. Thereby, virtual ecology can act as a heuristic to identify a system's salient features.

#### PERSPECTIVES

The excellent model accuracy obtained for the tree-ring based models and some combined models holds considerable potential for analysing growth-mortality relationships. As a first step, fairly accurate growth-mortality models can be obtained by analysing large existing forest inventory data

with at least three measurement periods, e.g. from the primeval forests of Białowieża, Poland (Faliński 1986), or from Barro Colorado, Panama (Hubbell *et al.* 2001). As a second step, existing forest inventory data from large permanent plot networks could be complemented by extracting cores from dead trees; the analysis of such combined forest inventory and tree-ring information is likely to result in highly accurate growth-mortality models.

The virtual forests presented here could also be used for investigating the influence of other variables such as tree size (cf. Wyckoff & Clark 2002), census interval length and varying census intervals on the performance of growth-mortality models (cf. Sheil *et al.* 1995; Sheil & May 1996; Kubo *et al.* 2000). Virtual forests have the potential to elucidate the shape of tree-size distributions by controlling species-specific growth-mortality relationships and disturbance-related mortality (cf. Coomes & Allen 2007; Woods 2004). Undoubtedly, the real-world growth-mortality relationship is more complex than the logistic regression applied here with  $\log(\text{relbai})$  as the explanatory variable. Therefore, it would be favourable to extend the evaluation to models using different explanatory variables describing the state of the tree (e.g. d.b.h. and tree height, Bravo-Oviedo *et al.* 2006). It would also be useful to assess the sensitivity of the different methods to deviations from the assumption that the growth-mortality relationship is constant in time and for all trees. In the long run, the phenomenological level of the growth-mortality relationship addressed here could be left behind entirely by focusing on physiological growth-mortality models relating mortality to carbon investment into plant growth, stability and defence (Martínez-Vilalta *et al.* 2002). However, for the time being, phenomenological growth-mortality models of high accuracy given the size and type of the underlying data, i.e. tree-ring data, forest inventory data or a combination of both, may be used to improve the reliability of two kinds of models, because their mortality routines often lack an empirical basis (Keane *et al.* 2001; Wunder *et al.* 2006): (i) forest growth models used in sustainable forest management (cf. Pretzsch *et al.* 2007), and (ii) forest succession models used for assessing the impacts of global change on long-term forest dynamics (cf. Bugmann 2001).

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## Supplementary material

The following supplementary material is available for this article:

**Appendix S1.** Parameters of the tree growth submodel of the virtual forests.

**Appendix S2.** Parameters of the tree mortality submodel of the virtual forests. S2.1: Simple mortality model. S2.2: Complex mortality model.

**Appendix S3.** Parameters of the snag standing time submodel of the virtual forests.

**Table S1.** Parameter matrix of the trees of the virtual forests (tree growth submodel).

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