Biases in the estimation of size-dependent mortality models: advantages of a semiparametric approach

Ghislain Vieilledent, Benoît Courbaud, Georges Kunstler, Jean-François Dhôte, and James S. Clark

Abstract: Mortality rate is thought to show a U-shape relationship to tree size. This shape could result from a decrease of competition-related mortality as diameter increases, followed by an increase of senescence and disturbance-related mortality for large trees. Modeling mortality rate as a function of diameter is nevertheless difficult, first because this relationship is strongly nonlinear, and second because data can be unbalanced, with few observations for large trees. Parametric functions, which are inflexible and sensitive to the distribution of observations, tend to introduce biases in mortality rate estimates. In this study we use mortality data for *Abies alba* Mill. and *Picea abies* (L.) Karst. to demonstrate that mortality rate estimates for extreme diameters were biased when using classical parametric functions. We then propose a semiparametric approach allowing a more flexible relationship between mortality and diameter. We show that the relatively shade-tolerant *A. alba* has a lower annual mortality rate (2.75%) than *P. abies* (3.78%) for small trees (DBH <15 cm). *Picea abies*, supposedly more sensitive to bark beetle attacks and windthrows, had a higher mortality rate (up to 0.46%) than *A. alba* (up to 0.30%) for large trees (DBH ≥50 cm).

Résumé : La relation entre taux de mortalité et taille des arbres présente une forme en U. Cette forme serait associée à une diminution de la mortalité due à la compétition pour les faibles diamètres, suivie d'une augmentation de la mortalité due à la sénescence et aux perturbations. La modélisation du taux de mortalité en fonction du diamètre est difficile, car la relation est fortement non-linéaire et car les données sont déséquilibrées, avec peu d'observations pour les gros arbres. Les fonctions paramétriques habituellement utilisées sont peu flexibles et sensibles à la répartition des données. Nous avons étudié la mortalité d'*Abies alba* Mill. et de *Picea abies* (L.) Karst. pour démontrer que l'estimation du taux de mortalité pour des diamètres extrêmes était biaisée lorsque l'on utilisait des fonctions paramétriques. Nous proposons une approche semi-paramétrique plus flexible pour représenter la relation entre mortalité et diamètre. Nous montrons qu'*A. alba*, l'espèce la plus tolérante à l'ombre, a un taux de mortalité annuel plus faible (2,75 %) que *P. abies* (3,78 %) pour de faibles DBH (<15 cm). *Picea abies*, plus sensible aux attaques d'insectes et aux coups de vent, a un taux de mortalité supérieur (jusqu'à 0,46 %) à *A. alba* (jusqu'à 0,30 %) pour les forts DBH (≥50 cm).

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Introduction

Understanding how mortality risk is influenced by tree size is frustrated by the fact that tree death is rarely observed, especially for large trees. The relationship between size and mortality risk varies among species, in part because of differences in shade tolerance and longevity, and it influences forest stand dynamics (Monserud 1976; Franklin et al. 1987; Harcombe 1987). Mortality rate is generally modeled as a U-shape function of diameter. Smaller individuals present high mortality rates as a result of competition from overstory trees. Large trees can also have high mortality rates owing to senescence and susceptibility to insect attacks or windthrows (Harcombe 1987). Because trees have a long life-span, small differences in annual mortality rates can translate to huge differences in terms of population dynam-

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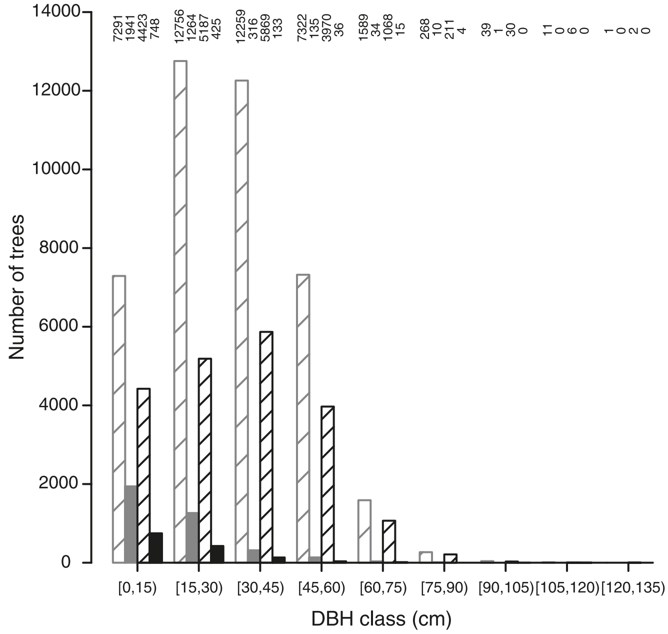


Fig. 1. Data distribution by DBH class. The number of living trees is represented by bars with shaded lines for *Abies alba* (black) and *Picea abies* (grey). The number of dead trees is represented by colored boxes. The exact number of trees is provided above each box.

ics (Pacala et al. 1996). Thus, even small differences among species and size classes can have a dramatic effect on production of offspring and life expectancy, thus determining community composition, structure, and carbon storage.

The data sets that are used for mortality estimation come from long-term or permanent plots that contain few large trees, and only a limited number of these die in any given year (Hawkes 2000; Lorimer et al. 2001). Permanent plots are rarely followed for more than several years, thereby limiting the number of tree death observations (Wunder et al. 2007). National forest inventories are principally based on managed forest plots, where logging also limits natural tree death for large trees. Moreover, methods vary among inventories (e.g., a minimum diameter of 7.5 cm for the French national forest inventory and 12 cm for the Swiss national forest inventory (Ulmer 2006)), so that data are less numerous for small diameters than for other diameters when we combine data sets. The U-shape mortality–diameter curve is usually modeled using a parametric logistic (Yao et al. 2001; Wunder et al. 2007) or a parametric log-normal function (Uriarte et al. 2004). Parametric models assume strict model shapes, although the exact shape of the mortality–diameter relationship is uncertain a priori (Lavine 1991; Draper 1995). This assumption may lead to biased estimates where the mortality–diameter curve is highly skewed (Wyckoff and Clark 2000). In addition, when using parametric models, estimation at one diameter depends on estimations at all other diameters. When data sets are unbalanced and relations are strongly nonlinear, the disproportionate influence of intervals with many observations can lead to biased estimations in intervals with few observations (Lavine 1991; Wyckoff and Clark 2000), with misleading results for small and large diameters in our context.

In this study we analyzed mortality–diameter relationships for *Abies alba* Mill. (silver fir) and *Picea abies* (L.) Karst. (Norway spruce). Data came from French and Swiss national forest inventories and a data set from a permanent-plot network. We compared a semiparametric model with three classical parametric models described by (*i*) a logistic function including a second-degree polynomial on DBH (Yao et al. 2001), (*ii*) a more flexible logistic function including a third-degree polynomial on DBH, and (*iii*) a log-normal function implying a slight upturn of the mortality rate for large trees (Uriarte et al. 2004). We used a Bayesian framework to estimate parameters, both for the semiparametric model and for the three parametric models, and we compared the models' goodness of fit for each diameter class using the deviance criterion. We simulated unbalanced and balanced data sets and tested for the effect of unbalanced data on the shape of the four model. Our objectives in this study were to demonstrate (*i*) that parametric approaches lead to divergent results when estimating mortality for extreme diameters (DBH <15 cm and ≥45 cm), (*ii*) that an unbalanced data set dramatically affects the shape of the parametric models, but it does not affect the shape of the semiparametric model (*iii*) that the semiparametric approach results in unbiased estimations, allowing a more accurate comparison of species ecological strategies.

Materials and methods

Field data

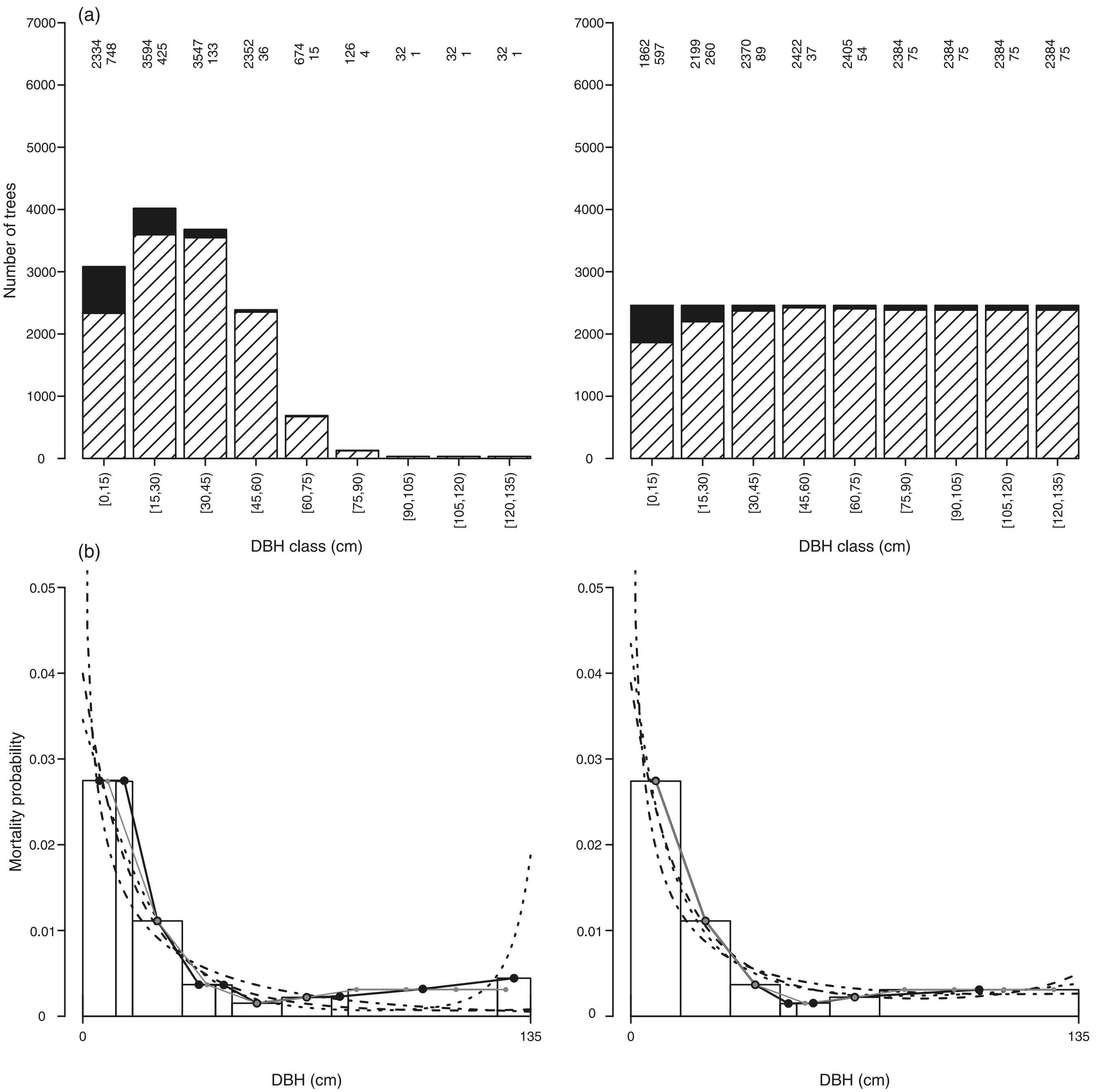
Mortality rate estimations for *A. alba* and *P. abies* were based on three different data sets: (*i*) Swiss national forest inventory (NFI), (*ii*) French NFI, and (*iii*) permanent plots from the Cemagref network.

The Swiss NFI includes 1982 permanent sample plots established between 1983 and 1985 and measured again between 1993 and 1995. Tree attributes (tree species, state (dead or alive), and DBH) were collected on two concentric circular plots, 200 m^2 for trees of 12–35 cm in DBH and 500 m^2 for trees ≥36 cm in DBH (Ulmer 2006). Logged trees were not taken into account. The Swiss NFI stands were dominated by *A. alba* or *P. abies* and had an elevation from 800 to 1800 m (mountain-belt elevation). Plots were all situated in the Swiss Alps.

The French NFI was analyzed for the 12 administrative areas that constitute the French Alps. Measurements were taken from 1992 to 2002 on 4776 temporary plots and are part of the third NFI. Tree attributes were taken on three concentric circular plots with radiuses of 6, 9, and 15 m for trees with a DBH between 7.5 and 22.5 cm, between 22.5 and 37.5 cm, and greater than 37.5 cm, respectively. Trees that had apparently been dead for less than 5 years were identified by using records of past storms and by evaluating the state of their bark. As for the Swiss NFI, logged trees were not included in the analysis.

The two NFIs were complemented by seven permanent plots from the Cemagref network located in the French Alps. Plots were installed from 1994 to 2002 and measured again from 2005 to 2006. No silvicultural operations had

Fig. 2. Comparing model fits for unbalanced and balanced data sets generated from the semi parametric model estimates. (*a*) Data repartition for the unbalanced (left) and balanced (right) data set. The number of living trees is represented by transparent boxes with black lines, and number of dead trees is represented by black boxes. The exact numbers of living and dead trees are provided at the top of each vertical bar. (*b*) Corresponding model fits for the unbalanced (left) and the balanced (right) data sets. For each data set, we fitted a semiparametric model (—), a parametric logistic model with a second-degree polynomial (– – –) and with a third-degree polynomial (· · · ·), and a parametric log-normal model (– · –). Bar widths and bar heights represent bin values and maximum likelihood estimates obtained from the modified Ayer's algorithm, respectively. Grey points indicate the mortality rate estimates used to generate the two data sets.



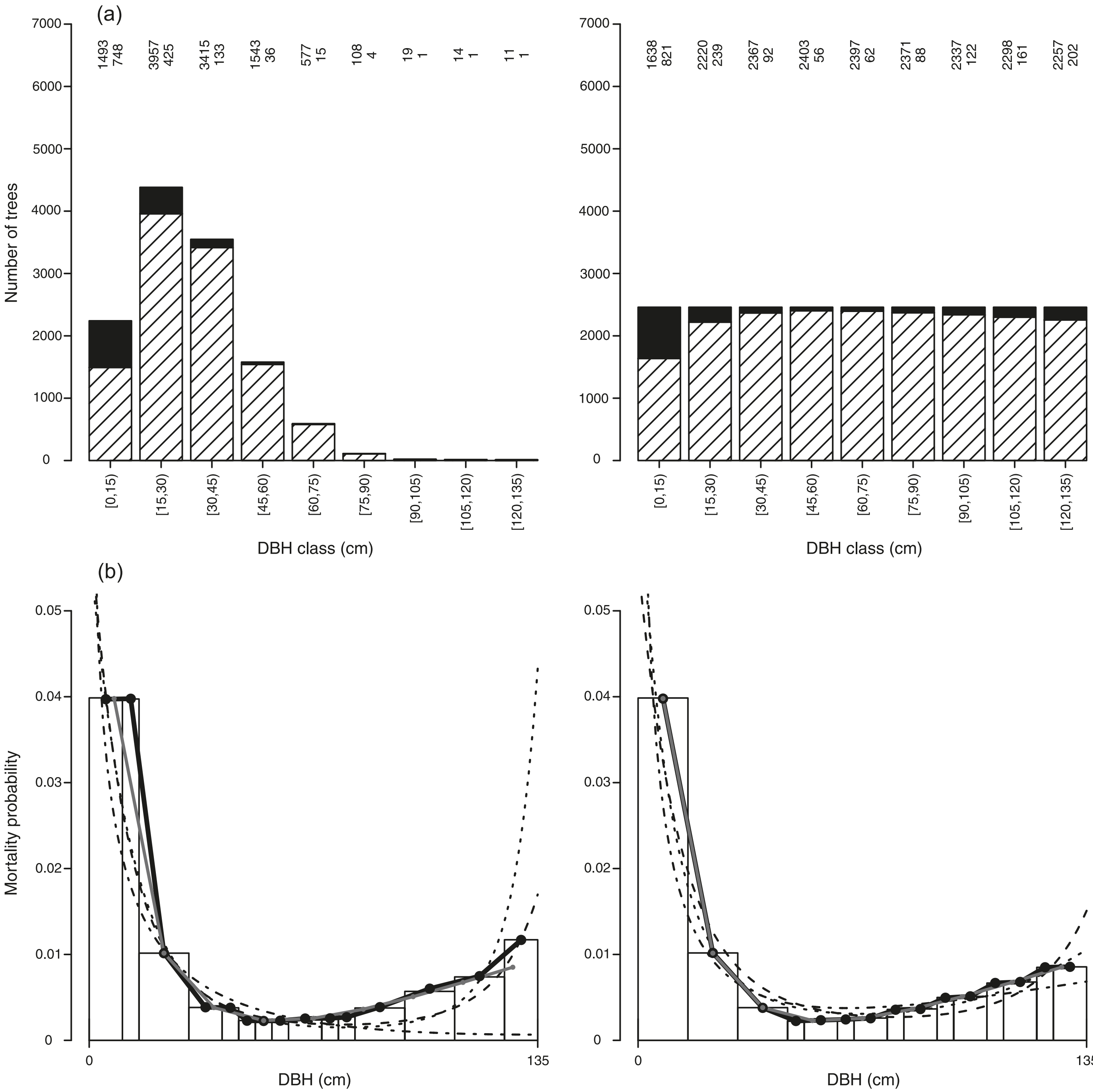
been performed on these plots for at least 10 years before installation. Plots ranged from 0.25 to 1 ha. Stands were dominated by *A. alba* and *P. abies*. Plot elevations ranged from 800 to 1800 m. All trees with a DBH of at least 5 cm were measured.

Death was categorized as having resulted from either windthrow or another cause (standing dead trees). By combining these three data sets, we obtained a large sample size with a total of 22 127 *A. alba* and 45 237 *P. abies*. Nevertheless, the data set was highly unbalanced with numerous trees with a DBH between 15 and 45 cm and few trees with a DBH <15 cm or >45 cm (Fig. 1).

Parametric models to compute mortality rate as a function of DBH

Mortality rate was modeled separately for both species.

Fig. 3. Comparing model fits for unbalanced and balanced data sets generated from the log-normal model estimates. (*a*) Data repartition for the unbalanced (left) and balanced (right) data sets. The number of living trees is represented by transparent boxes with black lines, and number of dead trees is represented by black boxes. The exact numbers of living and dead trees are provided at the top of each vertical bar. (*b*) Corresponding model fits for the unbalanced (left) and the balanced (right) data sets. For each data set, we fitted a semiparametric model (—), a parametric logistic model with a second-degree polynomial (– – –) and with a third-degree polynomial (· · · ·), and a parametric log-normal model (– · –). Bar widths and bar heights represent bin values and maximum likelihood estimates obtained from the modified Ayer's algorithm, respectively. Grey points indicate the mortality rate estimates used to generate the two data sets.



Let z_i be the event that individual i survives (z_i = 1) or dies from (z_i = 0) during a time interval Y_i (in years) with probability $1 - \mu'_{D_i}$: $z_i \sim$ Bernoulli$(1 - \mu'_{D_i})$.

The parameter μ'_{D_i} was expressed as a function of the annual mortality rate μ_{D_i} and the time interval between censuses Y_i for tree i (Monserud 1976):

$$[1] \qquad \mu'_{D_i} = 1 - (1 - \mu_{D_i})^{Y_i}$$

We tested three common parametric functions to link μ_{D_i}, the annual mortality rate of tree i, to DBH_i, the diameter at breast height of tree i. First, we used a logistic function including a second-degree polynomial on DBH:

$$[2] \quad \text{logit}(\mu_{D_i}) = \mu_0 + \alpha\text{DBH}_i + \beta\text{DBH}_i^2$$

Second, we used a logistic function including a more flexible third-degree polynomial on DBH:

$$[3] \quad \text{logit}(\mu_{D_i}) = \mu_0 + \alpha\text{DBH}_i + \beta\text{DBH}_i^2 + \gamma\text{DBH}_i^3$$

Third, we used a log-normal function implying a slight upturn of the mortality for high DBH values (Uriarte et al. 2004):

$$[4] \quad \mu_{D_i} = 1 - K\exp\left[-\frac{1}{2}\left(\frac{\log\ (\text{DBH}_i/X_0)}{X_b}\right)^2\right]$$

We used a Bayesian framework to infer parameters values. Priors were chosen noninformative with very large variances. Parameters μ_0, α, β, and γ, which belong to the set of real numbers $\mathbb{R}$ were drawn in a flat normal distribution: μ_0, α, β, $\gamma \sim$ Normal(0,1.0 × 10^6). Parameter K, which corresponds to the minimum mortality rate, has a value between 0 and 1 and was therefore drawn in a flat beta distribution: $K \sim$ Beta(1,1). Parameters X_0 and X_b which have non-null positive real values, were drawn in a flat log-normal distribution: X_0, $X_b \sim$ LogNormal(0,1.0 × 10^6).

We obtained a posterior distribution for each parameter from which we computed the mean, the standard deviation, and the 95% quantiles. We used R version 2.5.0 software (Ihaka and Gentleman 1996) for data manipulations and graphs, WinBUGS version 1.4 (Gilks et al. 1994) for Bayesian modelling, and R2WinBUGS (Sturtz et al. 2005) to link R to WinBUGS. We checked the convergence of two Markov Chain Monte Carlo (MCMC) runs for each parameter using the potential scale reduction factor Rhat (at convergence, Rhat = 1). We performed 50 000 iterations for each MCMC with a burning period of 25 000 steps and a thinning of 50. We then obtained 1000 estimations per parameter.

Semiparametric model to compute mortality rate as a function of DBH

Modified Ayer's algorithm to determine minimum mortality and DBH bins

We used a fourth model with a semiparametric Bayesian approach to compute mortality rate as a function of DBH. The semiparametric model consisted of dividing the range of diameters in bins (which can have different widths) and calculating associated probabilities of mortality. The model relied on the assumption that mortality risk decreases until a given diameter DBH_0, afterwards mortality risk increases.

We used a modified Ayer's algorithm (Ayer et al. 1955; Wyckoff and Clark 2000) to determine (*i*) the value of DBH_0 in the set {0, 5, 10,…, 135} and (*ii*) the values of the bins of the DBH classes respecting our assumption of decreasing mortality on the interval [0, DBH_0] and increasing mortality on [DBH_0, 135].

We implemented the algorithm for each DBH_0 in the set of values {0, 5, 10,…, 135}. Our algorithm began with an arbitrarily small bin width of 5 cm DBH. The DBHs of all living and dead trees were partitioned into bins j = 1,2,…,m_D, and a corresponding annual mortality rate μ_{D_j} for each bin j was estimated with the maximum likelihood approach. The likelihood of the model for each bin was

$$[5] \quad \text{Likelihood}_j = \prod_{k=1}^{d_{D_j}} 1 - (1-\mu_{D_j})^{Y_k} \times \prod_{l=1}^{n_{D_j}-d_{D_j}} (1-\mu_{D_j})^{Y_l}$$

where d_{D_j} and n_{D_j} are the number of dead trees and the total number of trees (dead and living) in bin j, respectively. Y_k and Y_l were, respectively, the number of years between censuses for dead tree k and living tree l in bin j. The likelihood accounted for the different time intervals for the three inventories. The algorithm checked separately for a monotonic decrease of mortality rate estimates for DBH ∈ [0, DBH_0] and for a monotonic increase of mortality rate estimates for DBH ∈ [DBH_0, 135]. On the interval [0, DBH_0], the algorithm started at j = 1. Bins for which $\mu_{D_j} \leq \mu_{D_{j+1}}$ were merged as $\text{bin}_j \hookleftarrow \text{bin}_j + \text{bin}_{j+1}$, and data were rebinned as $d_{D_j} \hookleftarrow \text{d}_{D_j} + d_{D_{j+1}}$ and $n_{D_j} \hookleftarrow \text{n}_{D_j} + n_{D_{j+1}}$. Each time a bin was modified, the algorithm restarted from j = 1. The process was continued until a monotonic decrease was achieved on the interval [0, DBH_0]. The algorithm was the same on the interval [DBH_0, 135], except that it merged bins for which $\mu_{D_j} \geq \mu_{D_{j+1}}$, until a monotonic increase was achieved on the interval [DBH_0, 135].

For each DBH_0 in the set of values {0, 5, 10, …, 135}, the initial number of bins $m_{D,\text{Start}}$ was equal to 135/5 = 27. When monotonicity was achieved with a decrease on [0, DBH_0] and an increase on [DBH_0, 135], the final number of bins $m_{D,\text{Final}}$ could be between two (one large bin on each side of DBH_0) and $m_{D,\text{Start}}$. The final number of bins depended on the value taken by DBH_0. Final bin widths were also variable, with a minimum of 5 cm and a maximum of (DBH_0 – 0) cm on the interval [0, DBH_0] and of (135 – DBH_0) cm on the interval [DBH_0, 135]. The model structure was not entirely specified a priori but was instead determined from data, and the number and values of the parameters were flexible and not fixed in advance.

We were interested in selecting the semiparametric model with the best goodness of fit, as determined by the model's deviance. For each DBH_0 in the set of values {0, 5, 10, …, 135}, we computed model's deviance:

$$[6] \quad \text{Deviance} = -2\ \text{logLikelihood} = -2\ \log \sum_{j=1}^{m_{D,\text{Final}}} (\text{Likelihood}_j)$$

We selected the model with the lowest deviance and identified the best DBH_0 with the corresponding bins repartition. The modified Ayer's algorithm was implemented using the R language (Ihaka and Gentleman 1996). The code is available upon request.

Bayesian model to infer mortality rate considering DBH

After having identified the minimum mortality rate DBH_0 and the bin values for each DBH class, we estimated the mortality rate of each DBH class using a Bayesian approach. Let z_{ij} be the event that individual i of diameter class j survives (z_{ij} = 1) or dies from (z_{ij} = 0) during a time interval Y_i (in years) with probability $1-\mu'_{D_{ij}}$, $z_{ij} \sim \text{Bernoulli}(1-\mu'_{D_{ij}})$. We expressed $\mu'_{D_{ij}}$ as a function of the annual mortality rate μ_{D_j} associated with diameter class j and Y_i:

$$[7] \qquad \mu'_{D_{ij}} = 1 - (1 - \mu_{D_j})^{Y_i}$$

We used a logit transformation for mortality rate:

$$[8] \qquad \mathrm{logit}(\mu_{D_j}) = \lambda_{D_j}$$

and priors for the m_D parameters λ_{D_j} were taken noninformative with a large variance: $\lambda_{D_j} \sim \mathrm{Normal}(0, 1.0 \times 10^6)$.

Deviance and AIC comparison among models

To compare the models' goodness of fit for extreme DBH values, we computed the deviance of the four models, taking into account observations in each DBH class. The deviance of model $M \in \{1, 2, 3, 4\}$ for bin j was

$$[9] \qquad \mathrm{Deviance}_{j,M} = -2 \log \mathrm{Likelihood}_{j,M}$$

$$[10] \qquad \mathrm{Likelihood}_{j,M} = \prod_{k=1}^{d_{D_j}} 1 - (1 - \mu_{D_k,M})^{Y_k} \times \prod_{l=1}^{n_{D_j}-d_{D_j}} (1 - \mu_{D_l,M})^{Y_l}$$

Annual mortality rates $\mu_{D_i,M}$ of tree i were obtained from eqs. 2, 3, 4, and 8.

The four models were also compared for the whole data set using the Akaike's information criterion (AIC). For each model $M \in \{1, 2, 3, 4\}$, $\mathrm{AIC}_M = \mathrm{Deviance}_M + p_M$, with p_M being the number of parameters for each model and $\mathrm{Deviance}_M = \sum_j \mathrm{Deviance}_{j,M}$. For the logistic model including a second-degree polynomial, $p_1 = 3$. For the logistic model including a third-degree polynomial, $p_2 = 4$. For the log-normal model, $p_3 = 3$. For the semiparametric model, $p_4 = 2m_{D,\mathrm{Final}} - 1$ with one parameter for each μ_{D_j} and $(m_{D,\mathrm{Final}} - 1)$ parameters to fix bin boundaries in the DBH interval [0, 135].

Fitting models on simulated unbalanced and balanced data sets

To test for the effect of unbalanced data sets on parametric model shapes, we fitted the three parametric models and the semiparametric model on two types of simulated data sets; the first data set was unbalanced in regard to diameter, such as real mortality data sets are, and the second data set was balanced.

We generated unbalanced and balanced data sets using 15 cm DBH classes with dead and living trees. To generate the data, we first used mortality rate estimates produced by the semiparametric model for *A. alba*. With this first approach, we tested whether parametric models were able to match the estimations of the semiparametric model, when data were unbalanced and when data were balanced. Second, we used mortality rate estimates produced by the log-normal model for *A. alba*. With this second approach, we tested whether the semiparametric model was able to match the estimations of one of the parametric models.

Both simulated balanced and unbalanced data sets were based on fixed 10 year time intervals between censuses for dead and living trees (Y_k and Y_l), eliminating the additional complexity of heterogeneous time intervals.

In the two simulated unbalanced data sets, each 15 cm DBH class had the same number of dead trees than the original *A. alba* data set, with the exception that the number of dead trees had to be at least one in each class to be able to compute the number of living trees corresponding to the estimated mortality rate in the class. We then had one dead tree for class [90, 105], class [105, 120], and class [120, 135] (Figs. 2*a* and 3*a*). For other 15 cm DBH classes, the number of dead trees was equal to that of the original *A. alba* data set: 748, 425, 133, 36, 15, and 4 (Fig. 1). The corresponding number of living trees for each class was computed in regard to the estimated mortality rate obtained first from the semiparametric model (Fig. 2*a*) and second from the log-normal model (Fig. 3*a*). For each 15 cm DBH class, we used the mortality rate estimate that corresponded to the one obtained at the middle of the class (at 7.5 cm for the first class [0, 15], 22.5 cm for the second class [15, 30], etc.; see grey points in Figs. 2*b* and 3*b*). Tree diameters where regularly distributed in the DBH class.

For the two balanced data sets, each 15 cm DBH class had an equal number of observations (2459) with a total of 22 131 observations, a number close to the total number of observations in the original *A. alba* data set (22 127) (Figs. 2*a* and 3*a*). The number of dead trees for each 15 cm DBH class corresponded first to the annual mortality rate estimates obtained from the semiparametric model for *A. alba* (Fig. 2*a*) and second to the annual mortality rate estimates obtained from the log-normal model (Fig. 3*a*). Tree diameters were fixed in the same way as for the two unbalanced data sets.

Results

The large data set allowed us to estimate mortality rates on a large diameter range (from 5 to 125–130 cm), with relatively narrow 95% confidence envelopes (Table 1 and Fig. 4).

Different estimates of mortality rates with parametric approaches

Parametric functions led to dramatically different estimates for large and small diameters, where data were sparse (Table 2). For small diameters (DBH <15 cm), the logistic function with second- and third-degree polynomials gave mortality rate estimates for *P. abies* that were larger than those for *A. alba*. At the minimum DBH (5 cm), the mortality estimates for the two species were much higher than those obtained with the semiparametric approach (Fig. 5), with estimates of about 7% for *P. abies* and 4% for *A. alba* (Figs. 4*a* and 4*b*). Mortality rate estimates were higher still for these DBH values when using the log-normal function, with 8.04% for *P. abies* and 5.59% for *A. alba*. For small diameters, the log-normal function, unlike the other parametric functions, led to a nonsignificant difference in mortality between the two species (Fig. 4*c*).

The logistic function with a second-degree polynomial resulted in an increase in mortality estimates for large *P. abies* trees, with rates reaching 11.90% for trees with DBH = 130 cm (Fig. 4*a* and Table 2). By contrast, such an increase

Table 1. Values of parameters for the semiparametric approach and the parametric functions.

	Abies alba		*Picea abies*	
Parameter	Mean	SD	Mean	SD
Parametric approach				
Logistic function – 2nd-degree poly.				
μ_0	–5.096	0.033	–5.083	0.024
α	–1.096	0.038	–1.136	0.018
β	0.127	0.035	0.267	0.014
Logistic function – 3rd-degree poly.				
μ_0	–5.070	0.033	–5.099	0.024
α	–1.229	0.034	–1.122	0.023
β	0.051	0.031	0.287	0.021
γ	0.049	0.009	–0.005	0.005
Log-normal function				
K	0.998	0.001	0.998	0.000
X_0	56.336	8.736	48.981	2.388
X_b	7.282	0.582	5.653	0.168
Semiparametric approach				
λ[0,15)	–3.569	0.038	–3.237	0.024
λ[15,20)	–3.851	0.060	–3.884	0.035
λ[20,25)	–4.488	0.084	–4.553	0.055
λ[25,30)	–5.180	0.127	–4.924	0.075
λ[30,35)	–5.416	0.157	–5.312	0.098
λ[35,40)	–5.603	0.122	–5.706	0.089
λ[40,45)	–5.737	0.133	–5.919	0.104
λ[45,50)	–6.766	0.207	–6.145	0.105
λ[50,55)	–6.489	0.346	–5.914	0.171
λ[55,70), λ[55,75)*	–6.117	0.156	–5.761	0.098
λ[70,135), λ[75,135)*	–5.770	0.301	–5.426	0.291

Note: For equations see Materials and methods.
*The first parameter applies to *Abies alba*; the second to *Picea abies*.

in mortality rates did not occur for *A. alba* (Fig. 4*a* and Table 2). For both species, the logistic function with a third-degree led to a strong upturn of the mortality–DBH curve high DBH values, with mortality estimates much higher than those obtained with the semiparametric approach (Fig. 5). For both species, the log-normal function led to a slight increase of the mortality rate for high DBH values (Fig. 4*c*). The mortality rate estimates for large diameters obtained with the log-normal function were lower than those obtained with the two logistic functions (Fig. 5). At the maximum diameter, *P. abies* had a higher mortality rate (1.71% at DBH = 130 cm) than *A. alba* (0.82% at DBH = 125 cm), but the difference was nonsignificant (Fig. 4*c*).

For medium diameters (DBH between 15 and 75 cm), where data were more numerous, there was less difference in mortality estimates among the parametric functions (Table 2). With all the parametric functions, we observed a minimum mortality rate of about 0.3% around 45 cm of DBH for both species (Figs. 4 and 5).

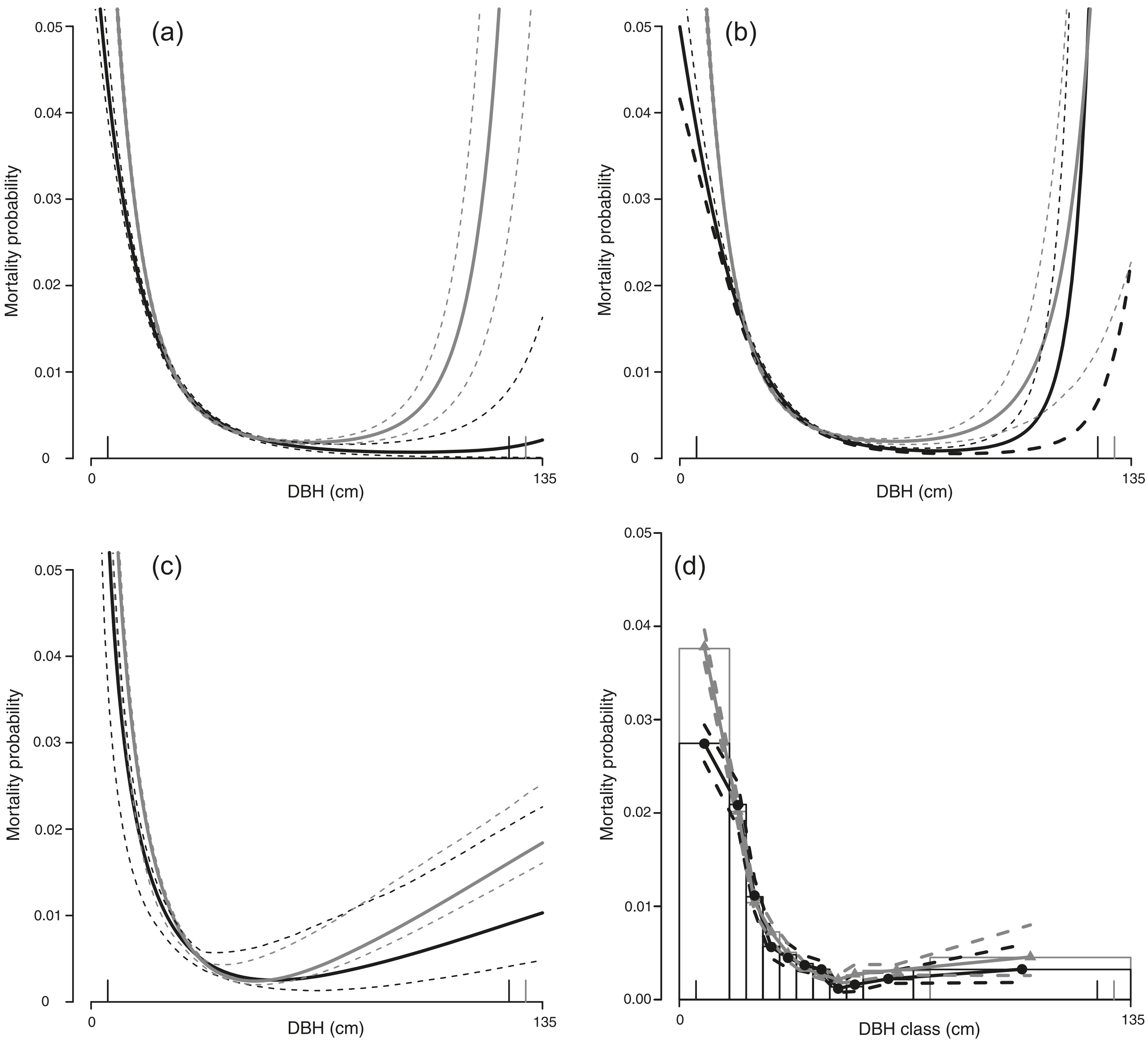
An unbalanced data set affects the parametric model shapes

For the two simulated balanced data sets, parametric models gave almost equivalent mortality rate estimations (Figs. 2 and 3). The strong differences among parametric models for large diameters observed when using real and simulated unbalanced data sets (Figs. 2, 3, and 4) were not observed when using simulated balanced data (Figs. 2 and 3).

In contrast, an unbalanced data set had a negligible effect on the predictions of the semiparametric model, regardless of the model used to generate mortality data (Figs. 2 and 3). When mortality data were generated with the log-normal model, the semiparametric estimates matched almost perfectly the log-normal estimates (Fig. 3). On the contrary, for unbalanced data sets, the log-normal estimates did not match the original estimates, even when the data were generated with the log-normal model (Figs. 2 and 3).

When using the unbalanced data sets, the gain in deviance with the semiparametric model was high both at extreme diameters, where data were scarce (Tables 3 and 4), and between 45 and 60 cm of DBH for the data set generated with the semiparametric model, where the mortality–DBH curve was highly skewed (Table 3 and Fig. 2). On the contrary, when using a balanced data set generated with the semiparametric model, the gain in deviance for the semiparametric model was more important (from 6% to 15%) on the skewed portion of the curve but was not large (≤3%) for extreme diameters (Table 4 and Fig. 5).

Fig. 4. Comparison of parametric and semiparametric models estimating mortality rate as a function of DBH. (*a*) Logistic function with second-degree polynomial, (*b*) logistic function with third-degree polynomial, (*c*) log-normal function, and (*d*) semiparametric model. Models for *Abies alba* (black lines and dots) and *Picea abies* (grey lines and triangles) are represented with posterior mean (—) and 95% quantiles (– – –). In Fig. 4*d* bar widths represent bins values obtained from the modified Ayer's algorithm, and bar heights represent maximum likelihood estimates obtained with Ayer's algorithm. Vertical lines on the DBH axis indicate the data range for *A. alba* (black) and *P. abies* (grey).



Improved goodness of fit for the semiparametric model

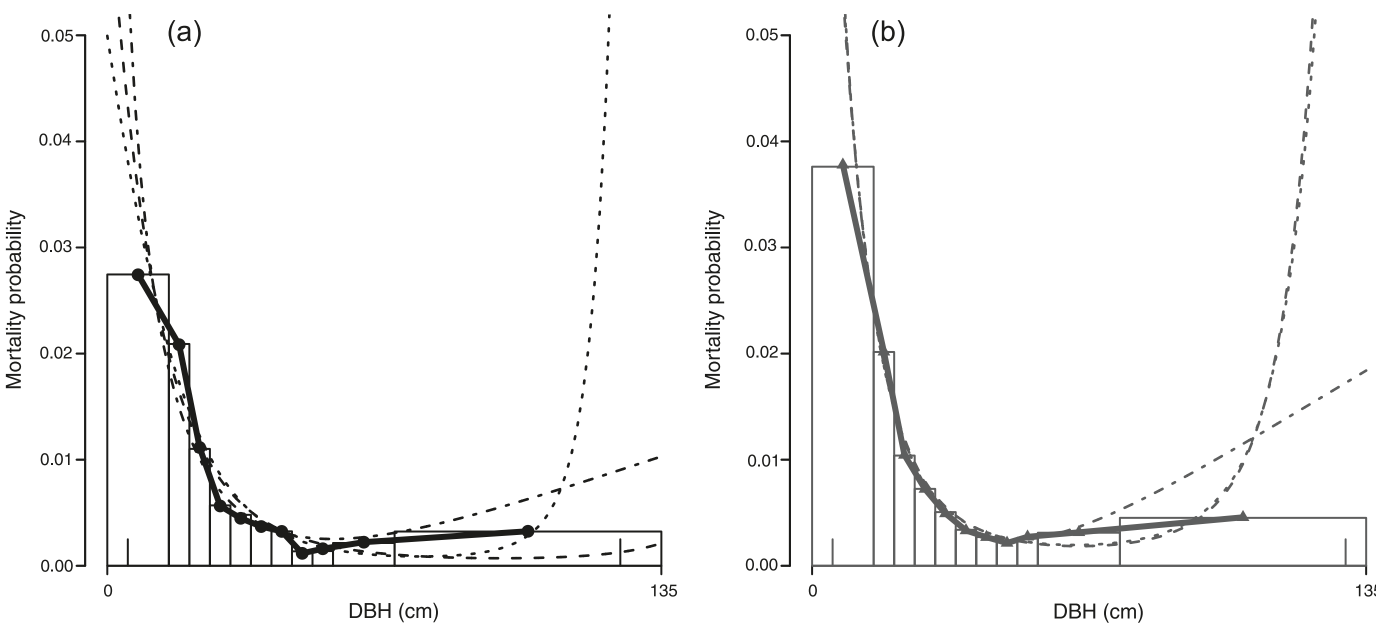
Of the four models we compared for the two real data sets with *A. alba* and *P. abies* mortality observations, the semiparametric model was the best, as it had the lowest AIC (Table 5). For all DBH classes the semiparametric model had the lowest deviance and therefore the best goodness of fit (see eqs. 9 and 10 and Table 5). For the central DBH range (15–60 cm), the gain in deviance was low (<1%); however, for extreme DBH values, where data were scarce (DBH <15 cm and especially for DBH ≥60 cm), the gain in deviance was large, increasing from 1% to 12% (Table 5).

A U-shape mortality–DBH function with substantial differences between species for extreme diameters was obtained when using the semiparametric approach. The deviance study for the semiparametric approach showed that the best models had a minimum mortality rate at DBH_0 = 45 cm for *A. alba*

Table 2. Mortality rate for specific values of DBH estimated with three different parametric models and a semiparametric model for *Abies alba* and *Picea abies*.

DBH (cm)	Logistic model 2nd-degree poly.	Logistic model 3rd-degree poly.	Log-normal	Semipara.
Abies alba				
5	0.0432	0.0381	0.0559	0.0274
15	0.0197	0.0205	0.0186	0.0208
45	0.0029	0.0027	0.0027	0.0012
75	0.0009	0.0009	0.0030	0.0033
125	0.0006	0.0591	0.0082	0.0033
Picea abies				
5	0.0717	0.0739	0.0804	0.0378
15	0.0242	0.0241	0.0240	0.0202
45	0.0028	0.0028	0.0025	0.0022
75	0.0020	0.0022	0.0052	0.0046
130	0.1190	0.0927	0.0171	0.0046

Fig. 5. Curves comparison for *Abies alba* (*a*) and *Picea abies* (*b*) with real unbalanced data set. The semiparametric curve (—) is compared with a logistic function with a second-degree polynomial (– – –), a logistic function with a third-degree polynomial (· · · ·), and a log-normal function (– · –). Bar widths represent bins values obtained from the modified Ayer's algorithm for the semiparametric model, and bar height represent maximum likelihood estimates obtained within Ayer's algorithm. Vertical lines on the DBH axis indicate the data range for observations.



and *P. abies*, with an annual mortality rate estimate of 0.12% for *A. alba* and 0.22% for *P. abies* (Fig. 4*d*). For small diameters (DBH <15 cm), *A. alba* had a significantly smaller annual mortality rate (2.74%) than *P. abies* (3.78%). For trees with DBH ≥50 cm, the semiparametric approach led to an increase in the mortality rate for both species. This increase was substantial but not as strong as that suggested by the third-degree polynomial parametric or the log-normal approaches (Fig. 5). *Picea abies* had a higher mortality rate (up to 0.46%) for high DBH values (≥50 cm) than *A. alba* (up to 0.33%) (Fig. 4*d*). The difference was nevertheless not significant for the last DBH class (DBH ≥75 cm) because of the very small number of observations.

Discussion

Bias in the estimation of a mortality — diameter function with parametric models

In this study, parametric methods provided reasonable estimates of the mortality rates for DBH intervals containing numerous observations (15–60 cm DBH). In this range, estimates did not strongly depend on the model. However, para-

Table 3. Comparing model deviances for the simulated data obtained from the semiparametric model.

DBH (cm)	Logistic model: 2nd-degree poly.	Logistic model: 3rd-degree poly.	Log-normal	Semipara.	% gain vs.: 2nd-degree poly.	% gain vs.: 3rd-degree poly.	% gain vs.: Log-normal	$n_j - d_j$	dj
Deviance comparison for unbalanced data									
[0,10)	2298	2287	2393	2278	1	0	5	1556	499
[10,15)	1174	1164	1221	1138	3	2	7	778	249
[15,30)	2738	2741	2737	2713	1	1	1	3594	425
[30,40)	783	783	792	765	2	2	3	2365	89
[40,45)	379	380	383	379	0	0	1	1182	44
[45,60)	386	379	413	373	3	1	10	2352	36
[60,75)	147	152	145	144	2	5	0	674	15
[75,80)	10	10	10	10	2	6	–3	42	1
[80,125)	51	52	47	45	12	13	5	158	5
[125,135)	11	9	10	8	21	10	18	22	1
Total	7978	7957	8150	7854	2	1	4	12 723	1364
No. of parameters	3	4	3	19					
AIC	7981	7961	8153	7873	1	1	3	12 723	1364
Deviance comparison for balanced data									
[0,15)	2772	2786	2907	2726	2	2	6	1862	597
[15,30)	1672	1676	1678	1660	1	1	1	2199	260
[30,45)	785	778	784	766	2	2	2	2370	89
[45,50)	141	139	147	125	11	10	15	807	12
[50,60)	275	274	289	259	6	6	10	1615	25
[60,75)	520	521	529	519	0	0	2	2405	54
[75,135)	2712	2694	2692	2685	1	0	0	9536	300
Total	8877	8868	9026	8739	2	1	3	20 794	1337
No. of parameters	3	4	3	13					
AIC	8880	8872	9029	8752	1	1	3	20 794	1337

Note: Mortality data were generated from the semiparametric model estimations. We computed the deviance of each model for each diameter class and the gain obtained by using the semiparametric approach. n_j and d_j are the total number trees and the number of dead trees for class j, respectively. AIC is Akaike's information criterion. There were 2459 observations for each 15 cm DBH class for the balanced data set. Unlike the unbalanced data set, the higher gain in deviance using the semiparametric model on the balanced data set was not observed for extreme large diameters but for the skewed portion of mortality–DBH curve, i.e., between 45 and 60 cm of DBH.

metric methods were unable to estimate mortality rates for extreme DBH values with fewer observations (DBH <15 cm and especially DBH ≥60 cm), as shown by the large variation in estimates among functions and by model deviances that were dramatically higher than those obtained with the semiparametric model.

For parametric models, estimation at one data point depends on estimations at all other data points and therefore on the distribution of the data (Lavine 1991). While comparing estimates for parametric models with balanced and unbalanced data sets, we demonstrated that the part of the curve where data are numerous correctly fits the data. Because parameter estimates depend mostly on these data and because of the inflexibility of parametric models in comparison with the strong nonlinearity of the relationship, biased mortality rate estimates are obtained where data are scarce. Unbalanced data sets are common in mortality studies, but the consequent bias in estimations made with parametric approaches are rarely taken into account. Wyckoff and Clark (2000) also demonstrated this problem for the estimation of a monotonic decreasing mortality–growth relationship, comparing results of parametric and semiparametric approaches. For the mortality–diameter relation, Muller-Landau et al. (2006) used regression based on the mean mortality rate within equal diameter classes to avoid undue influence of the many small individuals. Semiparametric models avoid bias associated with unbalanced data sets, as estimation at one data point does not depend on estimations at all other data points.

With the simulated balanced data set, the gain in deviance for the semiparametric model was more important on the data range where the mortality–diameter curve was highly skewed (45–55 cm DBH). Whereas the exact shape of the mortality–diameter relationship is uncertain, parametric models assume a strict inflexible shape. Putting aside the problem due to unbalanced data, parametric models fail to represent the strong nonlinearity of the true mortality–diameter relationship (Lavine 1991; Draper 1995). Semiparametric models perform better in this case, as unlike parametric models, they do not assume a strict model shape (Lavine 1991; Draper 1995; Wyckoff and Clark 2000).

Bias in mortality estimation may lead to inaccurate demographic models and poor predictions at extreme diameters. Mortality rates for extreme DBH values are especially important, as they provide a quantitative description of species life-history strategies, such as longevity or shade tolerance (Harcombe 1987). Difference in survival at small diameters can be related to difference in shade tolerance (Nakashizuka 2001). At small diameters, a trade-off between survival in resource-limited environments and rapid growth in rich en-

Table 4. Comparing model deviances for the simulated data obtained from the log-normal model.

	Logistic model				% gain vs.				
DBH (cm)	2nd-degree poly.	3rd-degree poly.	Log-normal	Semipara.	2nd-degree poly.	3rd-degree poly.	Log-normal	$n_j - d_j$	dj
Deviance comparison for unbalanced data									
[0,10)	1934	1928	2032	1903	2	1	6	995	499
[10,15)	1025	1019	1076	951	7	7	12	498	249
[15,30)	2831	2837	2810	2791	1	2	1	3957	425
[30,40)	772	772	787	759	2	2	4	2277	89
[40,45)	376	376	379	376	0	0	1	1138	44
[45,50)	116	115	119	114	1	1	4	514	12
[50,55)	115	115	117	115	0	0	2	515	12
[55,60)	114	115	115	114	0	0	1	514	12
[60,70)	94	95	94	93	1	2	0	385	10
[70,75)	47	48	47	47	1	2	1	192	5
[75,80)	9	10	9	10	–2	0	–1	36	1
[80,95)	27	28	28	26	4	7	8	78	3
[95,110)	8	9	10	8	6	8	17	17	1
[110,125)	8	8	10	7	4	6	25	13	1
[125,135)	7	7	10	7	1	8	36	8	1
Total	7484	7481	7642	7320	2	2	4	11 137	1364
No. of parameters	3	4	3	29					
AIC	7487	7485	7645	7349	2	2	4	11 137	1364
Deviance comparison for balanced data									
[0,15)	3227	3263	3504	3132	3	4	11	1638	821
[15,30)	1599	1588	1581	1568	2	1	1	2220	239
[30,45)	815	799	797	785	4	2	2	2367	92
[45,50)	183	179	182	173	5	4	5	801	18
[50,60)	368	367	373	361	2	1	3	1602	38
[60,65)	189	189	192	188	0	1	2	799	20
[65,75)	391	392	398	391	0	0	2	1598	42
[75,80)	253	251	251	251	1	0	0	790	29
[80,90)	512	508	510	508	1	0	0	1581	59
[90,95)	328	321	320	320	3	1	0	779	40
[95,105)	661	652	651	651	2	0	0	1558	82
[105,110)	401	395	395	393	2	1	1	766	53
[110,120)	801	797	800	796	1	0	0	1532	108
[120,125)	465	464	471	464	0	0	1	752	67
[125,135)	950	935	942	933	2	0	1	1505	135
Total	11 143	11 102	11 367	10 914	2	2	4	20 288	1843
No. of parameters	3	4	3	29					
AIC	11 146	11 106	11 370	10 943	2	1	4	20 288	1843

Note: Mortality data were generated from the log-normal model estimations. We computed the deviance of each model for each diameter class and the gain obtained by using the semiparametric approach. n_j and d_j are the total number of trees and the number dead trees for class j, respectively. AIC is Akaike's information criterion. There were 2459 observations for each 15 cm DBH class for the balanced data set. For the unbalanced data set, the goodness of fit of the semiparametric model for high diameters (DBH ≥80 cm) was much better than that of the log-normal model used to generate mortality data. Differences among models for high diameters were less important when the data set was balanced.

vironments can promote coexistence, as formalized in the successional niche theory (Pacala and Rees 1998). Low mortality for high diameters contributes to a longer life-span and may promote species coexistence by allowing adults to survive over long periods of poor recruitment, as formalized in the storage effect theory (Warner and Chesson 1985). A small difference in the annual mortality rate can substantially modify population and community dynamics on a long time scale, with a huge impact on tree life-span. Indeed, annual mortality rate cumulates each year, so that for an initial number of 1000 trees, a small difference of 1‰ for the annual mortality rate on a 100 year time interval leads to a difference of $1000 \times [1 - (1 - 0.001)^{100}] = 95$ dead trees.

The semiparametric approach we developed allowed us to make the most of existing data by combining several data sets, despite variable time intervals between censuses, and by avoiding the bias related to unbalanced data sets. The semiparametric model provided maximum flexibility to accommodate patterns in data with minimal assumptions. Our only assumption was that the mortality–diameter relation would be characterized by a monotonic decrease followed by a monotonic increase. Although the estimate of mortality

Table 5. Comparing model deviances for the real *Abies alba* and *Picea abies* data sets.

	Logistic model				% gain				
DBH (cm)	2nd-degree poly.	3rd-degree poly.	Log-normal	Semipara.	2nd-degree poly.	3rd-degree poly.	Log-normal	$n_j - d_j$	dj
Abies alba									
[0,15)	4451	4433	4488	4381	2	1	2	4423	748
[15,20)	1629	1624	1638	1620	1	0	1	1787	255
[20,25)	845	846	845	846	0	0	0	1623	111
[25,30)	536	539	530	527	2	2	1	1777	59
[30,35)	385	385	383	383	0	1	0	1446	41
[35,40)	428	428	427	426	0	0	0	1889	44
[40,45)	472	472	472	471	0	0	0	2534	48
[45,50)	165	163	165	159	4	2	4	1783	14
[50,55)	112	111	113	110	2	1	3	1256	10
[55,70)	239	242	237	236	1	3	0	1770	22
[70,135)	98	101	90	88	10	12	2	478	9
Total	9360	9344	9388	9248	1	1	1	20 766	1361
No. of parameters	3	4	3	21					
AIC	9363	9348	9391	9269	1	1	1	20 766	1361
Picea abies									
[0,15)	10 163	10 169	10 182	10 036	1	1	1	7291	1941
[15,20)	4720	4721	4720	4708	0	0	0	4616	741
[20,25)	2412	2410	2410	2403	0	0	0	4104	316
[25,30)	1713	1712	1711	1708	0	0	0	4036	207
[30,35)	1026	1025	1025	1019	1	1	1	3176	115
[35,40)	1022	1021	1017	1017	0	0	0	4196	108
[40,45)	905	905	902	903	0	0	0	4887	93
[45,50)	553	554	553	552	0	0	0	3502	55
[50,55)	417	417	417	416	0	0	0	2269	43
[55,75)	679	676	668	664	2	2	1	3140	71
[75,135)	99	98	94	91	8	7	3	319	11
Total	23 708	23 708	23 699	23 518	1	1	1	41 536	3701
No. of parameters	3	4	3	21					
AIC	23 711	23 712	23 702	23 539	1	1	1	41 536	3701

Note: We computed the deviance of each model for each diameter class and the gain obtained by using the semiparametric approach. The minimum deviance is obtained with the semiparametric model for every diameter class, with gain mostly in high diameter classes. n_j and d_j are the total number of trees and the number of dead trees for class *j*, respectively. For each model, we computed the Akaike's information criterion (AIC) on the whole diameter range. The semiparametric model had the lowest AIC.

risk in any one bin depended on that in adjacent bins (to achieve monotonicity), the dependency was weak relative to that of parametric models.

One of the pitfalls often underlined for nonparametric and semiparametric models, in comparison with parametric models, is the difficulty of extrapolating predictions outside the data range used for the inference (in our case, beyond 125 and 130 cm of DBH for *A. alba* and *P. abies*, respectively). With the semiparametric model we propose that the last class can be extended to a desired DBH value beyond 125 or 130 cm (see the upper 135 cm boundary in Fig. 5). Extending the last class leads to a constant mortality rate beyond the data's upper boundary, a result that may not be in agreement with the senescence hypothesis. Nevertheless, the use of parametric models would not necessarily lead to better extrapolations. The three parametric models had different and biased estimations for large diameters, and the logistic model with a second-degree polynomial and the log-normal model may not detect the increase of mortality in data for high diameters (Figs. 2 and 3). Another inconvenience of the semiparametric model is the discontinuity between estimates from one DBH class to another, which finds little empirical support in reality. This problem may be resolved using nonparametric continuous models such as penalized spline regressions (Crainiceanu et al. 2005; Gimenez et al. 2006).

Advantages of the semiparametric method for forest dynamics study

The estimates of mortality obtained with parametric approaches are dramatically dependent on the function chosen, without a clear statistical advantage for one or the other, to confidently identify ecological differences between species. The semiparametric approach, which is more flexible and less dependent on the balance in the data, appeared to be more reliable for identifying species strategies. We showed that *A. alba* had a smaller annual mortality rate (2.74%) than *P. abies* (3.78%) for low DBH values (<15 cm) and that *P. abies* had a higher mortality rate (up to 0.46%) than *A. alba* (up to 0.33%) for high DBH values (>50 cm).

Few studies have tried to compare *A. alba* and *P. abies* in terms of mortality as a function of diameter, although these species commonly coexist in the Alps at the mountain-belt elevation (800–1800 m). In an analysis on the Austrian National Forest Inventory data, Monserud and Sterba (1999) found opposite results for low DBH values (DBH <20 cm). In their study, *A. alba* had a higher annual mortality rate (around 1.6%) than *P. abies* (around 1.1%), but parameter uncertainty led to a nonsignificant difference between the two species. The difference between the two studies may be attributed to the different modelling approaches or to site characteristics, which were not taken into account in both cases. Another study by Eid and Tuhus (2001) based on the Norwegian National Forest Inventory gave mortality estimates similar to ours for *P. abies* at low DBH values (around 3.5% for DBH <15 cm). For high DBH values (DBH ≥60 cm), species comparison is often not performed, as data for large trees are missing (Monserud and Sterba 1999; Eid and Tuhus 2001; Wunder et al. 2007). This lack of data motivates the combination of national data sets.

Small trees are potentially those receiving low levels of light in the subcanopy, and the lower small-tree mortality rate for *A. alba* than for *P. abies* is in agreement with species life-history strategies. The relative shade tolerance of *A. alba* and *P. abies* has previously been observed and demonstrated by various authors (Schütz 1969; Wasser and Frehner 1996; Grassi and Bagnaresi 2001; Stancioiu and O'Hara 2006). The characteristics describing photosynthetic performance at low light levels (dark respiration rate, apparent quantum yield, and light compensation point) suggest that *A. alba* is better suited to maintain a positive carbon balance in shaded conditions than *P. abies* (Grassi and Bagnaresi 2001). The shorter longevity of *P. abies* compared with that of *A. alba*, associated with a higher vulnerability to disturbances such as rock falls (Stokes et al. 2005), storms (Lundström et al. 2007), and insects attacks (Zolubas 2003), is also in agreement with our results reporting a higher mortality rate for *P. abies* than for *A. alba* for high DBH values.

Diameter covariate has been widely used to estimate tree mortality, especially for large adult trees (see PROGNAUS (Sterba and Monserud 1997; Monserud and Sterba 1999) or SORTIE simulator (Canham et al. 2001; Papaik et al. 2005)). Nevertheless, for modeling mortality of young trees suffering competition, a growth covariate, or equivalent covariate (for instance a competition index), is often added to the diameter covariate (Pacala et al. 1996; Yao et al. 2001; Wunder et al. 2007). Although simple in regard to the number of covariates, our approach emphasizes the interest of using semiparametric models to accurately represent tree mortality. We believe that the potential bias of parametric methods in the estimation of mortality for extreme diameters has been largely overlooked in previous studies. We showed that this bias can have important consequences on the estimation of tree species life-history traits such as shade tolerance and longevity. We believe further studies of tree survival should account for this potential bias. The semiparametric approach presented in this study can be used to construct more complicated semiparametric models that would include complementary covariates such as growth and diameter to simulate tree mortality at all stages (Clark et al. 2007; Vieilledent et al. 2009).

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