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CHAPTER 5

Species traits drive contrasting wood decay rates: insights from a new short-term method to study long-term wood decomposition dynamics

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Submitted manuscript

Pinus sylvestris bole

SUMMARY

1. While the importance of wood decay for the global carbon balance is widely recognized, surprisingly little is known about its long-term dynamics and its abiotic and biotic drivers. Progress in this field is hindered by the long time-scales inherent to the low decay rates of wood and the lack of short-term methods to assess long-term decomposition dynamics in standardized field conditions.
2. Here we present such a method, which relies on the sampling and short-term incubation of wood from several decay stages covering the entire decay process. Together these short-term decay steps are used to model and discriminate between three potential decay dynamics (linear, exponential and sigmoid) using an iterative optimization procedure. We applied this method to analyse long-term wood decay of six subarctic tree species (six stems and two roots) and test the hypotheses that i) different wood species follow distinct decay dynamics and ii) interspecific variation in wood traits controls variation in wood decay rates in a standardized environment.
3. We found interspecific variation in long-term wood decay dynamics: decay of *Alnus* and *Salix* stems was best described by exponential models, whereas decay of *Sorbus* stems and *Betula* and *Pinus* roots were best fitted by linear models and *Betula*, *Pinus* and *Populus* stems each displayed a sigmoid decay dynamics (up to five-year initial lag-phase). A six-fold variation was observed between the decomposition half-lives of all eight wood types, from 6.8 years (6.1-7.5, 95% C.I.) for *Alnus* stems to 41.3 years (34.5-51.8) for *Pinus* roots. Initial wood traits such as pH (R^2=0.92), dry matter content (R^2=0.79) and lignin (R^2=0.73) were strong predictors of long-term wood decay rates.
4. *Synthesis.* Our findings suggest changing decay dynamics across wood species and types that are likely to arise from changing underlying wood decay processes (i.e. varying wood functional traits / decomposer community interactions). Our new method, which combines advantages of direct observations and the chronosequence approach, allows reliable comparisons of species contributions to long-term wood decay rates and provides future opportunities to experimentally disentangle intrinsic and external abiotic and biotic drivers of long-term wood decay processes.

Key-words: woody debris (WD), common-garden experiment, wood decomposability, decay rates, functional traits, climate, model, protocol

INTRODUCTION

Dead wood is a key driver of forest ecosystem functioning through its impact on carbon (C) and nutrient cycling (Harmon *et al.*, 1986) and its beneficial role to microbial, animal and plant diversity (Freedman *et al.*, 1996). The ecosystem processes associated with dead wood differ greatly from those of other litter materials owing to their large biomass, their temporally and spatially heterogeneous inputs and their low nutrient content and poor degradability. The substantial stocks of woody debris (WD) – forested ecosystems constitute as much as 50% of total C in the terrestrial biosphere (Malhi, 2002) and WD represents up to 20% of the total in old-growth forests (Delaney *et al.*, 1998) – and its ecological importance have stimulated studies on various aspects of their role in ecosystem processes (see reviews by Harmon & Sexton, 1996; Wirth, Gleixner & Heimann, 2009). Moreover, the urgent need for understanding and

predicting the consequences of current global climate and land-use changes has put increasing pressure on ecologists to quantify ecosystem C stocks and fluxes, with a special focus on forests and peatlands (IPCC, 2000). In this context, accurately measuring WD turnover and its sensitivity to (biotic and abiotic) environmental factors should be a first-order priority with respect to the improvement of C cycling models and consequently global climate predictions (Sitch *et al.*, 2003; Cornwell *et al.*, 2009).

Wood decomposition is a complex process which, like litter decomposition in general (Swift, Heal & Anderson, 1979), involves biotic and abiotic influences, as well as their interaction, and the quality of the wood itself (Harmon *et al.*, 1986). Micro-organisms, particularly fungi, and invertebrates are the main agents of wood decay (Käärik, 1974). The general pattern of succession and substrate exploitation by decomposing organisms over the different stages of WD decay are relatively well known, but largely context dependent (Käärik, 1974; Boddy & Watkinson, 1995; Boddy & Heilmann-Clausen, 2008; Olsson, 2008). The activity of decomposers is thought to be controlled to a large degree by local environmental factors such as temperature, humidity and to some extent fertility of the surrounding substrate (Harmon *et al.*, 1986; Boddy & Watkinson, 1995; Chen *et al.*, 2000; Progar *et al.*, 2000). However, results from field studies examining the relative importance of these factors show contrasting results (Harmon, Krankina & Sexton, 2000; Yatskov, Harmon & Krankina, 2003; Kueppers *et al.*, 2004). This may be due partly to the fact that the effects of these environmental factors are confounded with effects of variation in wood quality of different tree species. While the structural and chemical characteristics of wood strongly control its decomposition rate (Taylor *et al.*, 1991; Chambers *et al.*, 2000), we know very little about whether and how this control is species-specific and underpinned by interspecific variation in wood functional traits. This question is critical as climate or land-use-induced shifts in tree species composition may have major implications for carbon and nutrient dynamics via changes in wood traits and decomposition rates. The first few studies addressing this question (Chave *et al.*, 2009; Cornwell *et al.*, 2009; Weedon *et al.*, 2009; van Geffen *et al.*, 2010) have not yet shown clear common patterns. This inconsistency may be due partly to the difficulties of (1) studying the long time scale of wood decomposition whose complex dynamics could hinder extrapolation of short-term results and (2) singling out species trait effects in heterogeneous environments with multiple interactions among decomposition drivers.

Studying wood decomposition rates has remained a great challenge to date because of the extended timescale involved, up to centuries for complete wood decay under certain conditions (Kueppers *et al.*, 2004). In order to describe long-term WD decay dynamics and obtain estimates of decay rates, researchers have used direct and indirect methods. Direct approaches involve the monitoring of newly fallen wood pieces for varying periods (e.g. Romero, Smith & Fourqurean, 2005; Eaton & Lawrence, 2006). Long-term decomposition studies are often incompatible with the time frame of individual research projects and the current need for extensive comparative measurements of WD decay rates. Thus, when implemented over short time periods, they usually capture the first stages of wood decay only and therefore lack relevance for the entire course of decomposition. Direct approaches could nevertheless be particularly helpful for comparing different treatments and disentangling multiple environmental influences including the contribution of species characteristics. Indirect approaches, using chronosequences relying on historic records on extreme events (e.g. logging, massive windfall) or on other evidence indicating duration of WD decay (e.g. age of

regenerating stands, age of trees growing on the log, age of fire scars, radio-carbon-dating), allow the estimation of long-term decomposition dynamics within a much shorter time frame (e.g. Krankina & Harmon, 1995; Chen, Harmon & Griffiths, 2001; Yatskov, Harmon & Krankina, 2003; Hérault *et al.*, 2010; Kueppers *et al.*, 2004). Recently, promising progress has been made in comparing species contributions to wood decomposition rates using the chronosequence approach (Hérault *et al.*, 2010; van Geffen *et al.*, 2010), but the resolution is coarse because of the great uncertainties related to historic reconstruction and spatial and temporal heterogeneity (Harmon, Nadelhoffer & Blair, 1999), as compared to standardized experiments. Also, while most studies use negative exponential functions to describe WD decay, a few studies have suggested the inadequacy of assuming similar processes across tree species (Harmon *et al.*, 1995; Hale & Pastor, 1998; Harmon, Krankina & Sexton, 2000). Whether such variability in decomposition processes across species is marginal or the rule needs to be resolved. In order to disentangle the respective roles of biotic and abiotic factors influencing wood decay rate, experimental, standardized manipulation of WD decomposition is much needed. Here we present a new method that combines the advantages from the direct observation and chronosequence approaches and thereby minimizes the disadvantages associated with these methods. As described below, our new method uses wood relative density (RD; WD density divided by initial WD density) as a proxy for decay stage (Christensen, 1984) and, by analogy to the decomposition vectors' method (Harmon, Krankina & Sexton, 2000), relies on the sampling of several decay stages to cover the entire decay process. Our key innovation is to incubate multiple WD samples, covering a large range in decay stages (characterized by their RD) for each of a range of species, simultaneously for a set duration in a 'common garden' environment (cf. Cornelissen 1996). Then, for each species, we use a modelling procedure to combine all component short-term decay curves from all these decay stages into a long-term mass loss curve against time and test which decay model (linear, exponential, sigmoid) provides the best fit (Fig. 1). Thus, by relating the RD decrease of several decay stages of wood, this method enables direct and standardized comparison of long-term mass loss dynamics of different species using a short-term experiment. We demonstrate the applicability of this technique in a case study of six dominant tree species of Swedish subarctic forests, *Betula pubescens* (Ehrh.) *ssp. czerepanóvii*, *Pinus sylvestris* (L.), *Alnus incana* (L.), *Populus tremula* (L.), *Sorbus aucuparia* (L.) and *Salix caprea* (L.). It thereby provides the first explicit and direct test of the hypothesis that i) different wood species follow distinct decay dynamics in a similar environment. We then specifically test that ii) interspecific variation in wood traits controls variation in WD decay rates.

MATERIALS AND METHODS

Study area

Both plant material collection and experimental setup took place around the Abisko Research Station, North Sweden (68°21'N, 18°49'E) within the low altitude (350-400 m a.s.l.) forested area. Climatic data from the recent decade (1999-2008) showed a mean annual rainfall of 352 mm and mean January and July temperatures of -9.7 and 12.3 °C, respectively, with average daily temperatures ranging from -39.0 to 21.3 °C (meteorological data, Abisko Research Station). Throughout the Abisko valley, forests

are dominated by polycormic mountain birch trees *(Betula pubescens ssp. czerepanóvii)*, both in dry and wet areas. Four other deciduous tree species and one evergreen are commonly found within the area. *Pinus sylvestris* and *Populus tremula* are characteristic of the dry forest, while *Salix caprea*, *Sorbus aucuparia* and A*lnus incana* are mainly found in riparian areas. Following two successive episodes of severe tree defoliation by caterpillars of the moth *Epirrita autumnata* in 1954 and 1955, which killed a large number of birch stems, the forested area of Abisko valley consist mainly of rejuvenated birch stands of low stature (Tenow *et al.*, 2004).

Sampling

Our new method of estimating long-term wood decay requires the sampling of dead wood at various stages of decay. Thereto, all six tree species were sampled for dead woody stems and two of them, *Betula pubescens* and *Pinus sylvestris*, were also sampled for dead woody roots. The sampling was done from mid-August to mid-October 2007 and complemented in April 2008. Due to the young age and low stature of the forest, the average diameter of WD was relatively low. To ensure balanced species comparisons, only the common WD diameter class of 5 ± 1.2 cm was sampled, while the minimum length was 50 cm. From each log sample we obtained four subsamples of 10 cm for the decomposition experiment and a central cylinder of 10 cm for wood density, wood traits and residual humidity measurements (see below). To ensure the representativeness of the WD central cylinder for the neighbouring sub-samples used for the decomposition experiment, WD with heterogeneous external and internal aspect were discarded. In particular, WD with large branching knots, irregular shapes or uneven bark cover were avoided.

For each tree species and material (stem and root), between two and three samples of newly dead material were identified and sampled in the field, on standing trees, according to both internal and external aspects of the wood. After measurements of wood density on sub-samples of each material, only the denser wood sample of each species was kept as representative of newly dead wood and other samples were discarded. For each species and material, WD pieces were also sampled from various stages of decay. In this way we aimed to cover the widest range of wood decay stages. WD whose advanced state of fragmentation did not allow the direct estimation of volume for initial wood density calculation were avoided in this study. Nevertheless, in order to cover the latest stages of WD decay and therefore improve the range of decay models, such fragmented samples can still be used by estimating the initial stem diameter from less degraded parts of the stem, as described by Harmon & Sexton (1996). After sawing WD samples into five 10 cm long cylindrical sub-samples, these were cleaned of alien material, then air-dried and stored in paper bags pending further treatment and analyses.

Decomposition study

The central cylinder of each WD sample was used to estimate density, residual humidity and, on the newly dead WD sample only, WD chemical and structural traits of the sample. We estimated WD density (mg cm^{-3}) as the ratio of wood oven-dry mass (mg; 96h at 60°C) to volume (cm^3). The volume was estimated both by volume displacement in a graduated glass column and by measurement of length and diameter (taken as the average of three cross-section measures, i.e. 6 measurements) and taken as the mean of both estimates. Residual humidity of each sample was estimated on the

central cylinder as the ratio of the difference between air-dry and oven-dry mass to air-dry mass (the latter measured before volume estimation).

For each WD sample, the four remaining air-dry sub-samples were weighed separately and sealed into nylon litter bags of 1 mm mesh-size, which allowed exchange of microorganisms and small soil invertebrates. Measured air-dry masses were corrected for residual humidity to obtain true dry mass. The litter-bag samples were incubated in outdoor litter beds in an experimental garden surrounded by birch forest at Abisko Research Station, on 23 April 2008, following Cornelissen *et al.* (2004). The litter beds consisted of rectangular wooden frames sunk into the ground, including a layer of grit stones (particle sizes 10–20 mm) as a free-draining foundation on top of the original soil profile. They were covered by a 20 mm layer of mixed fresh and old litter collected in September 2007 from the surrounding dry and wet forests and ponds. The litterbags were laid out flat, without overlap, and covered by a 10 mm layer of the same mixed litter. Four separate blocks (c.a. 2 × 1 m) were used to host the four distinct groups of subsamples per sample. The litter beds were covered with a 10 mm mesh metal grid to protect them from birds and rodents. The litter bags were subject to the local climatic influences and did not receive any additional treatment.

The litter bags were harvested after two full years of incubation on 23 April 2010, while still frozen and stored at -16°C pending further processing. After defrosting, adhering soil, soil fauna and other alien material was removed from the decomposed litter by gentle brushing and rinsing with tap water. Litter subsamples were then dried (60°C, 96 h) and weighed. The % mass loss of each subsample was calculated as the ratio of its dry mass after decomposition to its original dry mass. For each replicate, WD density after decomposition was estimated by recalculating the pre-incubation WD density of the related sample central cylinders after accounting for the replicate % mass loss. These calculations assumed a constant volume before and after incubation in order to avoid biases related to material fragmentation leading to post-incubation density underestimation (Christensen, 1984).

Wood litter trait measurements

All newly dead WD types were measured for C, N, P and lignin content, as well as pH. For these analyses air-dried sub-samples were ground and subsequently oven-dried for 24h at 60°C. Carbon and nitrogen concentrations were measured by dry combustion on a NA 1500 elemental analyser (Carlo Erba, Rodana, Italy). Phosphorus was measured by acid digestion as referred to in Freschet *et al.* (2010). Lignin concentration was determined by extraction of non-ligneous compounds as described in Freschet *et al.* (2010). For pH, 0.15 ml of each ground sample was shaken with 1.2 ml demineralised water in an Eppendorf tube for 1h at 250 rpm. After centrifugation at 13,000 rpm for 5 min, pH of the supernatant solution was measured (Cornelissen *et al.*, 2006).

Modelling wood decomposition

For each woody debris type all density measurements (*n* 'WD decay stage' × pre- and post-incubation × 4 replicate subsamples) were standardized, i.e. divided by the density of the densest newly dead WD, to give relative wood density (RD) values, which ranged from 1 to 0 (100 to 0 %). For each pair of pre- and post-incubation RD, the set of 4 replicate subsamples was averaged to produce one single average 'two-year-decay-vector' (*sensu* Harmon, Krankina & Sexton, 2000). The data for each WD type (species) thus consist of *n* decomposition vectors (Fig. 1a), each representing the mean

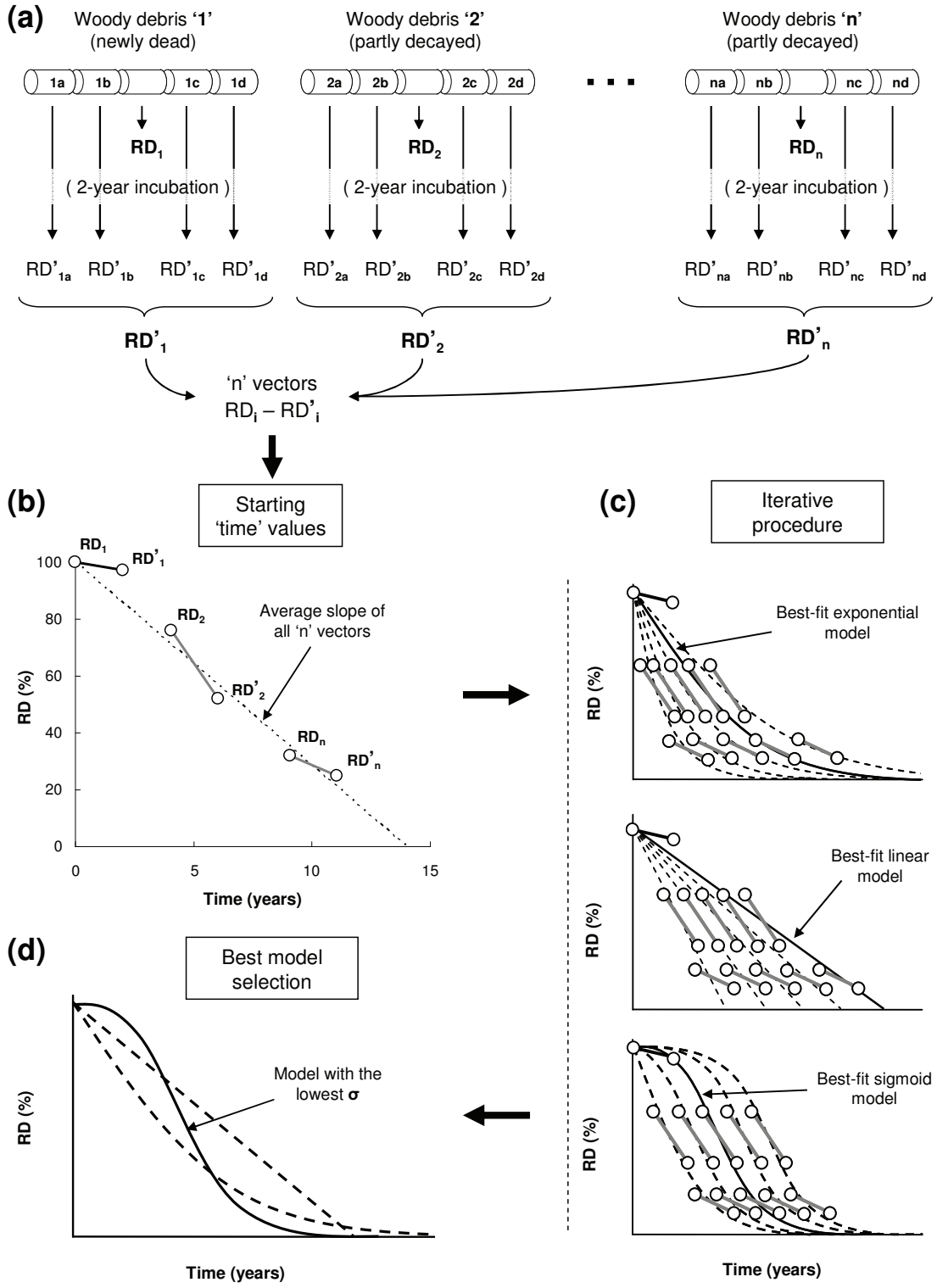

Fig. 1. Outline of the method used to model long-term wood decay dynamics based on short-term incubations of wood in various decay stages. Only the four main steps are shown **(a-d)**. Further details are provided in the text.

loss in relative density over the incubation interval (2 years) starting at a different phase of decay (with n from 5 to 16 depending on the WD type). To these data each of the following three decay models were fitted:

1) Linear $RD = 1 - mt$
2) Negative exponential $RD = e^{-kt}$
3) Negative sigmoid $RD = 1 - (1 - e^{-at})^b$

where t is time in years and m, k, a and b are parameters to be fitted. All models assume RD = 1 at t = 0 (i.e. the wood fragment with highest initial density represents "fresh" litter at the start of the incubation), and further that the parameters are subject to the constraints m, k and $a > 0$, $b \geq 1$ and $t \geq 0$.

An iterative optimization procedure was used to find the combination of both the model parameters, and the set of t values that minimized the residual variance in a (non)-linear regression using the following algorithm:

1) Fix the initial vector to begin at t=0 (Fig. 1b)
2) Choose initial values of t (for details see below) for the starting points of the remaining n-1 vectors (Fig. 1b)
3) Use linear- (model 1) or nonlinear- (models 2 & 3) least-squares regression to estimate the model parameters.
4) Output the residual variance from the model
5) Choose a new set of n-1 t values and repeat steps 3 and 4 until a stable minimum for residual variance (step 4) is obtained (Figure 1c).

The algorithm was implemented in R (R Development Core Team, 2009) using lm() and nls() for parameter estimates (step 3) and optim() to find the optimal set of t values for each dataset (step 5). Files containing the R scripts used are available from the authors upon request.

Initial tests on simulated data showed that the success or failure of the nls() fitting for model 3 was partly dependent on the choice of the initial set of t values at step 2, and the starting parameter estimates for the nonlinear regression at step 3. Best performance was achieved with a self-starter function (Ritz & Streibig, 2009) that generated initial t values by arranging the vectors along a straight line determined by the mean slope of all n decomposition vectors (Fig. 1b). Similarly, model failure was avoided when the mean slope of the decomposition vectors was used as the starting value for a, and the starting value of b was set to 1 (i.e when using realistic starting values of model parameters in the iteration procedure). For consistency, the same initial values of t were used for all three models and the mean slope was also used as a starter value for k in model 2.

Empirical time series of wood mass loss with sufficient temporal resolution are not available to independently test our estimation method so we used simulation testing to determine the range of decomposition dynamics over which our method can reliably estimate decay parameters. Simulated 'WD decay curves' were generated using a large range of parameter values. These decay curves were then 'sampled', that is, a number of 'decay vectors' were generated from each decay curve to which we added a random component with variance based on the observed within-log variance seen in our dataset.

These simulated data were then submitted to the same iterative optimization procedure as each of our real 'WD type' dataset. The estimated parameters were compared with those used to generate the simulated 'WD decay curve' to determine the accuracy and any biases in our estimation method. Briefly, we found that our procedure produced reliable estimates for linear and exponential models except for very low *m* and *k* parameter values and started to produce unreliable estimates in the sigmoid model only for very slowly-decomposing WD with long lag-phases (i.e. generated with a combination of low *a* and/or high *b* with the sigmoid model) that result in initial two year RD change of less than 2% (further details are given in Appendix S1 in Supporting Information). Based on the final selection of best-fit model for each WD type and the observed decay rate of newly dead wood litter in this experiment, all our WD types show only small *potential* relative error except *Pinus* stems (sigmoid model: 2.2% mass loss after two years) and *Pinus* roots (linear model: m=0.012). This suggests that, while the modelled output is reliable for most WD types, the duration of the lag phase of *Pinus* stem sigmoid model and the overall decay rate of *Pinus* roots might be slightly under- or over-estimated. Since 'newly dead' WD sample strongly influence the model for which the best fit is obtained, as well as the eventual estimate of lag-phase dynamics in case of sigmoid decay dynamics, it is advisable to increase replication of this initial decay class, and perhaps sample at more regular intervals, so as to obtain well constrained estimates of the decay rate in the initial period.

The output for each model fit is a set of modelled *t* values representing estimates of the age of the different decay stages, and model parameters. For each WD type (stem or root species), once optimization procedures had been performed for each distinct model (linear, exponential, sigmoid), the model fits were compared using the value σ derived from each model's residual variance by the following formula:

$$\sigma = \sqrt{\frac{1}{n-p}\sum_{i=1}^{n} R_i}$$

where n is the number of observations, p is the number of parameters fitted by the model (thus allowing for comparison of models with different numbers of parameters) and R represents the i-th residual after (non-)linear least squares regression. The decay model that provided the lowest σ was considered the best description of the underlying decay dynamics and used to estimate the WD type decomposition half-life ($T_{1/2}$; time (years) needed to reach 50% mass loss) for subsequent analyses (Fig. 1d). Using $T_{1/2}$ allows comparison of species for which different decay curves provided the best fit. 95% bootstrap confidence intervals (C.I.) for $T_{1/2}$ for each WD type and decay model combination were calculated from the 2.5 and 97.5 percentiles of the distributions of $T_{1/2}$ estimated from 1000 bootstrap samples of the wood decay stages within each WD type (Efron & Tibshirani, 1993). This measure includes uncertainty in our fitted values of *t* for each combination of WD type and model and avoids the unrealistically narrow confidence intervals that would result from calculations using the best fit only. The relatively large bootstrap confidence intervals found here stress the need to ensure an even distribution of wood decay stage samples across the whole decay process. Ordinary least square regressions were used to test predictions of WD $T_{1/2}$ from initial wood litter traits (to comply with normality assumptions, $T_{1/2}$, P, C/N and lignin/N were

Table 1. Model fits (best fits indicated in bold) and predictions for each wood substrate.

	Species	n	Lower limit of model prediction (% RD)	Linear				Single exponential				Sigmoid				
				σ	m	$T_{1/2}$	(95% C.I.)	σ	k	$T_{1/2}$	(95% C.I.)	σ	b	a	$T_{1/2}$	(95% C.I.)
Stem	*Alnus incana*	11	37	0.0209	0.065	7.7	(6.5-8.6)	**0.0145**	**0.102**	**6.8**	**(6.1-7.5)**	0.0146	1.06	0.108	6.8	(6.1-7.5)
	Betula pubescens	13	30	0.0193	0.039	13.0	(11.1-18.4)	0.0230	0.054	12.7	(10.9-20.5)	**0.0169**	**1.79**	**0.093**	**12.2**	**(10.5-15.3)**
	Pinus sylvestris	11	36	0.0140	0.031	16.1	(14.5-24.3)	0.0206	0.039	17.7	(15.0-32.0)	**0.0121**	**2.53**	**0.082**	**17.5**	**(14.3-20.1)**
	Populus tremula	12	23	0.0318	0.059	8.5	(7.0-12.4)	0.0473	0.072	9.6	(6.8-16.8)	**0.0244**	**2.79**	**0.199**	**7.6**	**(6.5-9.1)**
	Salix caprea	14	34	0.0312	0.071	7.1	(5.7-7.9)	**0.0296**	**0.098**	**7.1**	**(5.7-8.4)**	0.0302	1.00	0.098	7.1	(5.6-8.3)
	Sorbus aucuparia	16	42	**0.0131**	**0.052**	**9.6**	**(8.5-10.4)**	0.0173	0.069	10.1	(8.7-11.5)	0.0163	1.22	0.086	9.8	(8.5-11.2)
Root	*Betula pubescens*	11	44	**0.0123**	**0.037**	**13.6**	**(11.7-16.2)**	0.0145	0.050	13.9	(12.2-17.6)	0.0124	1.31	0.067	13.2	(11.1-15.9)
	Pinus sylvestris	5	39	**0.0042**	**0.012**	**41.3**	**(34.5-51.8)**	0.0073	0.014	48.5	(40.3-66.5)	0.0059	1.30	0.024	37.3	(20.8-52.5)

n is the number of distinct decay samples used in models. RD is relative wood density. σ is residual variance for a given decay model. m, k, b and a are predicted model parameters. $T_{1/2}$ is decomposition half-life. C.I. is bootstrap confidence interval. For each substrate best fit models are indicated in bold.

log_{10}-transformed before analysis). To assess the degree of correlation between explanatory variables Pearson's correlation coefficients were calculated for the relationships between lignin, DMC and pH.

RESULTS

Our model results showed that the wood decomposition dynamics differed across species as none of the three models tested could consistently provide the best fit for the decomposition process of all WD types (species-organ combinations; Table 1; Fig. 2). Long-term decay of three WD substrates was best fitted by a negative sigmoid function, three by a negative linear function and two by an exponential decrease function. Thus, only *Alnus* and *Salix* coarse stems displayed a constant *relative* mass loss over time (exponential model), while the relative mass loss of *Sorbus* coarse stems and *Betula* and *Pinus* coarse roots increased instead regularly as decomposition advanced (linear model) and that of *Betula*, *Pinus* and *Populus* coarse stems initially increased before stabilizing (sigmoid model) (Fig. 3).

A 2.5-fold variation in $T_{1/2}$ was observed across species for coarse stems, ranging from 6.8 y (6.1-7.5, 95% C.I.) for *Alnus incana* to 17.5 y (14.3-20.1, 95% C.I.) for *Pinus sylvestris*, and a 3-fold difference for coarse roots, from 13.6 y (11.7-16.2, 95% C.I.) for *Betula pubescens* to 41.3 y (34.5-51.8, 95% C.I.) for *Pinus sylvestris* (Table 1; Fig. 3). Across all species and organs, a 6-fold variation in $T_{1/2}$ was observed. A major difference in shape between root versus stem decay curves arose from the lack of initial lag-phase of both *Betula* and *Pinus* roots as compared to their respective stems (Fig. 3). However, while the $T_{1/2}$ of *Pinus* roots was double that of *Pinus* stems (19.0 vs. 39.9 y), *Betula* stems and roots had rather similar $T_{1/2}$ (14.5 and 13.6 y, respectively; Table 1).

Wood debris $T_{1/2}$ were strongly positively related to initial WD lignin content (R^2=0.73; P<0.01) and DMC (R^2=0.79; P<0.01) and negatively related to WD initial pH (R^2=0.92; P<0.001) but not significantly related to initial N, P, C/N, lignin/N and wood density. Lignin content, DMC and pH were strongly correlated ($r > 0.84$ and $p < 0.01$ for each pairwise correlation).

DISCUSSION

Our new short-term method has proven reliable in providing long-term estimates of wood decay dynamics (i.e. differentiate between decay models) from which decay rates can be derived and compared across species and substrate types. Moreover, the standardized conditions, including an optimal pool of fungi (WD gathered from a number of locations and assembled in a common litter bed with their respective biota), even contact of WD with the soil and consistent log size, minimize the interactive effects of environmental 'noise'. We believe that this relatively easy and rapid method will therefore find applications in any biome with slow-turnover litter. Here, we used it to single out species contributions to long-term variation in decomposition processes and rates of coarse woody debris and found empirical evidence in support of our hypotheses. Indeed, our results (i) indicate substantial inter-specific and inter-organ differences in the mass loss dynamics of coarse WD in a subarctic flora, with moreover (ii) strong predictive powers of several wood functional traits on long-term wood decay rates.

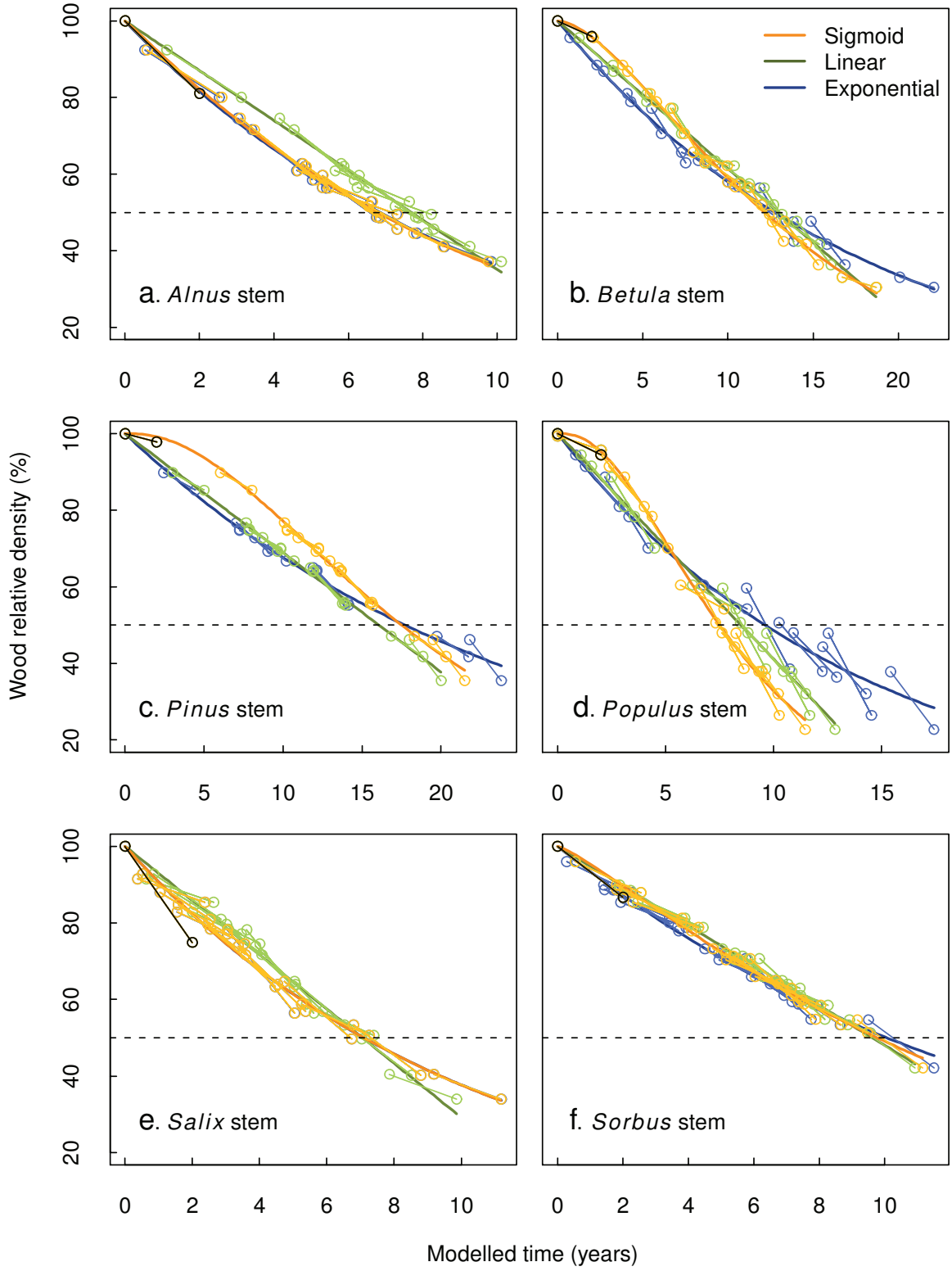

Fig. 2. Comparison of linear, exponential and sigmoid best fit decay model estimates for each substrate **(a-h)**. Model parameters' and residual variance estimates are provided in Table 1. Two-year decomposition vectors are displayed for each model type. Initial decomposition vectors are displayed in black because they are set at t=0 for all three model types. Estimated models do not extend beyond data range.

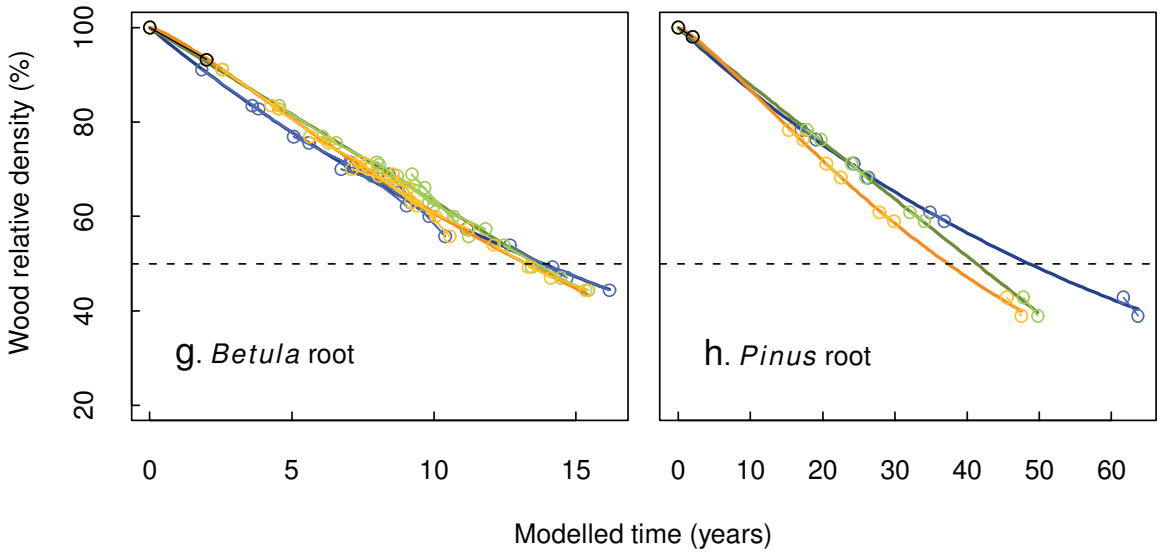

Fig. 2. (continued)

Interspecific variation in long-term wood decay dynamics

We found substantial interspecific variation in the mass loss models (Table 1, Fig. 2), which implies that wood decay dynamics differs among species. As discussed below, these interspecific differences in wood decay dynamics may, but do not necessarily, imply differences in wood decay processes. Nevertheless, these results contradict the widespread assumption that WD decay follows single (Olson, 1963) or multiple (Minderman, 1968) negative exponential functions, corresponding to constant or exponentially decreasing relative mass loss rates, respectively (Harmon *et al.*, 1986). The clearest indication that these models do not always describe wood decay processes adequately is found in the highly variable dynamics of mass loss rates observed across substrates in the initial phase of WD decay, which supports the additional use of linear and sigmoid models in our analysis. These results are in agreement with previous observations in both tropical and boreal ecosystems on *Coccothrinax readii* (Harmon *et al.*, 1995), *Picea abies* (Naesset, 1999), *Pinus contorta* (Laiho & Prescott, 1999) and *Pinus sylvestris* (Harmon, Krankina & Sexton, 2000), where WD decay was characterized by a slow initial decomposition phase, up to 5 years, before decay rate increased rapidly. These and our results need to be differentiated from others where observed lag times in decomposition may arise from prolonged periods where stems remained standing before entering in contact with the soil (e.g. Yatskov, Harmon & Krankina, 2003; Mäkinen *et al.*, 2006; Tuomi *et al.*, 2011). Our model estimations indicated a 5-year lag time for *Pinus* stems, and 2-year lag times for *Populus* and *Betula* stems. Such slow initial decomposition could relate to the preliminary phase of microbial and/or invertebrate colonization necessary to initiate decomposition (Swift, Heal & Anderson, 1979; Harmon *et al.*, 1986; Laiho & Prescott, 1999; Yatskov, Harmon & Krankina, 2003). Indeed, the complete spread of decomposers throughout large WD is a slow process that can take up to several years (Harmon, 2009). In the absence of mechanical injury colonization of sapwood may only begin once bark has dried and cracked (Käärik, 1974), galleries have been dug by invertebrates (Ausmus, 1977; Schowalter *et al.*, 1992) or bark defences have been overcome by microbes (Käärik, 1974). Differences in bark structure and composition might therefore explain interspecific differences in initial decay rates and thus in the decomposition model that

describes these processes. Once decomposing organisms have at least partly overcome bark defences, they typically attack the nutrient-richer, less chemically defended sapwood before feeding on heartwood (Käärik, 1974), suggesting that the early phase of decay may not yet concern WD heartwood. For a majority of tree species, the diameter of water-conducting cells or perforation plate apertures of WD should not limit fungal hyphae colonization (Cornwell *et al.*, 2009). However, depending on the species, the narrow pits connecting tracheids or vessels can potentially hinder fungal propagation. The large differences found between species (e.g. *Populus* vs. *Sorbus* stems) and organs (e.g. *Pinus* roots vs. stems) during the early stages of WD decay suggest that colonization by decomposers is strongly controlled by WD characteristics. For instance, while the resistance of sapwood to decay is marginal for most tree species, heartwood resistance is highly variable across species (Käärik, 1974) owing to large variations in their non-structural secondary compound contents (50-fold in angiosperms, 20-fold in gymnosperms; Cornwell *et al.*, 2009). Similarly, the short tracheids of gymnosperms might hinder fungal colonization more efficiently than typically much longer vessels of angiosperms (Carlquist, 2001; Cornwell *et al.*, 2009).

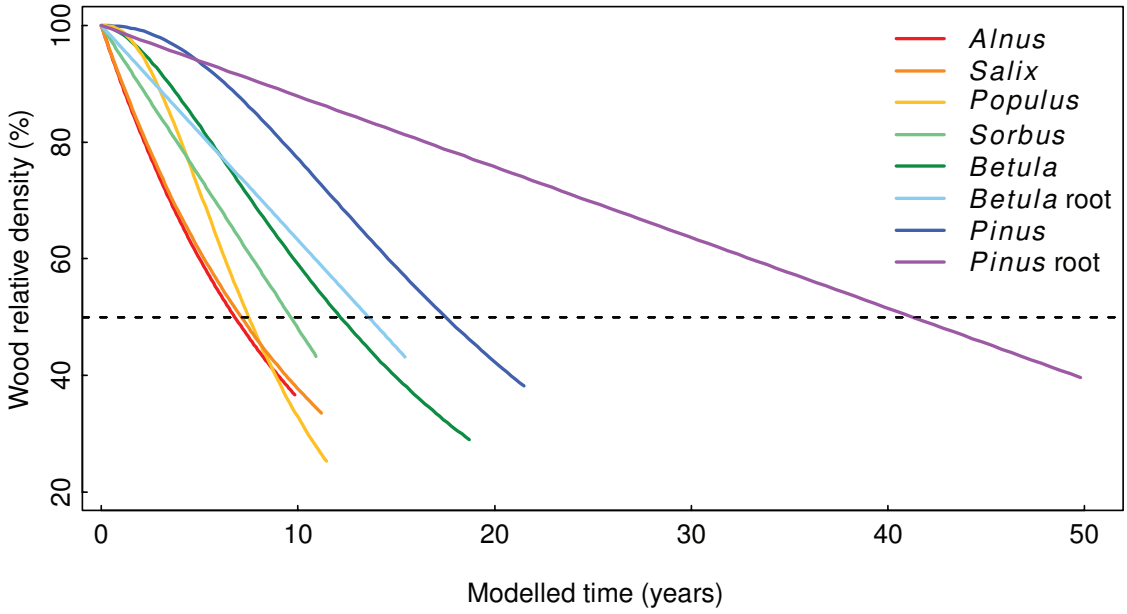

Fig. 3. Comparison of each substrate's best fit decay model on a common time axis.

The better performance of linear or sigmoid models, as opposed to exponential models, to describe the decomposition processes of a majority of WD indicates that relative decomposition rate might typically increase with WD age, at least up to 50-60% mass loss (Fig. 3). Our results thus confirm that WD decomposition processes may differ substantially from those of other litter types, as proposed by Harmon *et al.* (1986). Several factors could simultaneously account for this increase in relative decomposition rate from early to intermediate stages of decomposition. First, leaching of constitutive compounds of wood (e.g. dissolved organic carbon, polyphenols; Spears & Lajtha, 2004) should progressively increase with WD age as permeability to water and microbial colonization rises and the highly polymeric wood compounds are degraded

into soluble fractions (Harmon *et al.*, 1986). Second, as wood decay advances, nutrients limiting microbial growth and activity (such as N), which positively influence wood decomposition rates (Weedon *et al.*, 2009), are gathered and accumulated by microbial decomposers through a variety of mechanisms such as atmospheric N fixation, capture of atmospheric N deposition or retranslocation via extensive fungal hyphae (Cornwell *et al.*, 2009). The strong initial investment made by microbial decomposers towards nutrient acquisition may thus be progressively reinvested toward lignocellulolytic enzyme production as wood decay advances (Sinsabaugh *et al.*, 1993; Weedon *et al.*, 2009). Then, while non-structural secondary compounds initially give the heartwood of many species high decay resistance, this protection gradually decreases (Harmon *et al.*, 1986). Therefore, the constant relative mass loss rates over time displayed by *Alnus* and *Salix* WD (exponential model) may potentially be explained by a lack of heartwood defences. Finally, wood fragmentation by invertebrate decomposers or WD structure loss owing to both invertebrate and microbe action produce wood particles of various sizes that decompose more rapidly than the original WD because of their higher surface-to-volume ratio (Harmon *et al.*, 1986).

After 60-75% mass loss, the state of WD fragmentation makes it difficult to identify species and precisely measure WD density (Christensen, 1984). Nevertheless, methods exist to overcome this constraint, as advised in the Methods section. Despite lacking observations from the final phase of decay, our results suggest that most WD types may already show a stabilisation in their relative mass loss rate within our data range. Besides, the three substrates that did not show any inflection (linear model) were also those displaying the highest lower limit of model prediction (around 60%), which indicates that such stabilisation in their relative mass loss rate can potentially occur in their final phase of decay. Nevertheless, in all cases, the absence of data over 60-75% mass loss limits our interpretation of decomposition rates at the latest stages of WD decay. The very few studies documenting the latest stage of WD decay show variable results. For instance, while some studies described slow decay rates after only 50% mass loss (e.g. Harmon *et al.*, 1995; Krankina & Harmon, 1995), some others did not clearly support the view that decomposition rates decrease in the last phases of decay (Harmon, Krankina & Sexton, 2000; Mäkinen *et al.*, 2006). Besides, as suggested by our results, decomposition rates for the latest phase of decay may well be species-dependent (see also Harmon, Krankina & Sexton, 2000).

Interspecific variation in wood mass loss rates

Wood decay modelling, as applied here, can only provide estimations of mass loss curves and loses accuracy in the latest phase of WD decay. To minimize the impact of these factors on estimates of WD decomposition rates, we used here a measure of mass loss rate that both provides comparable values across models (Table 1) and does not extrapolate beyond our data range: decomposition half-life ($T_{1/2}$). The large differences in $T_{1/2}$ across species and organs of similar WD shape and diameter, when incubated in a common environment, suggest a strong control of wood traits on at least the initial and intermediate phases of WD decomposition (first hypothesis). This was confirmed by the strong relationships found between decomposition rates and several wood functional traits such as lignin content, dry matter content and especially pH (second hypothesis). Wood pH, which is generally negatively correlated with the nutritional status of decomposing material and positively correlated with the initial amount of antimicrobial organic acids (Cornelissen *et al.*, 2006), was a strong predictor (R^2=0.92) of WD decay

rates. Non-structural secondary compounds such as organic acids are known to provide WD heartwood with high decay resistance (Harmon *et al.*, 1986). Woody debris pH might therefore be a good indicator of the presence of antimicrobial compounds. Dry matter content generally represents the ratio of recalcitrant to more degradable tissues (Garnier & Laurent 1994). As one of the most recalcitrant compounds of wood (Käärik, 1974), lignin content also represents the ratio of recalcitrant to more degradable tissues and correlated strongly with dry matter content. Besides, the distribution of lignified structures throughout woody tissues likely constrains access of decomposers, particularly non-lignin degrading microbes, to more degradable materials such as cellulose (Scheffer & Cowling, 1966). Nevertheless, these results contrast with recent studies (e.g. van Geffen *et al.*, 2010) or literature surveys (Cornwell *et al.*, 2009; Weedon *et al.*, 2009) which did not find very strong predictive power of lignin with respect to WD decomposition rates. Thus, one cannot exclude that the good predictive powers of lignin and DMC partly stem from their correlation with wood pH.

Initial wood nutrient content (N, P, C/N) was non-significantly related to WD $T_{1/2}$, confirming that, while initial wood nutrient content generally matters for decomposition (Weedon *et al.*, 2009), its influence on wood decomposition is, as described for leaf litters (e.g. Hobbie, 2005), rather complex. For instance, van Geffen *et al.* (2010) proposed that wood nutrient content might not be a strong control on decomposition rates when wood C/nutrient ratios are within the range of those from wood decaying fungi – e.g. C/N of 40-400 (Dix & Webster, 1995) as compared to C/N of 70-395 in our study. Besides, microbial decomposers are potentially able to gather nutrients from external sources, alleviating thereby their potential nutrient limitation (Cornwell *et al.*, 2009).

CONCLUSION

This study has demonstrated the great potential for a novel short-term common-garden wood decomposition experiment to provide estimations of long-term wood decay dynamics and rates at the tree species level. As such, it also opens up promising perspective for comparing woody *versus* non-woody materials of highly contrasting decomposition rates and distinguishing between environmental (moisture or temperature regime, soil macro-fauna, etc.) and wood functional traits effects, while reducing environmental noise.

Our model estimates have also provided support for contrasting WD mass loss dynamics, displaying between one and three distinct phases depending on wood species and organ (stem *versus* root). As such, they suggest that the widespread use of exponential functions to model WD decay should be regarded more critically as it likely overlooks the complexity and diversity of wood decay processes. The 6-fold difference in decomposition rates across WD of similar shape and diameter decomposing in the same environment suggests, as shown for other litter types (Silver & Miya, 2001; Cornwell *et al.*, 2008), an important role for wood functional traits as drivers of wood decomposition. Here, initial wood pH, lignin and dry matter contents were strong predictors of wood decay rates. While our new method has been tested here in a specific flora, we believe it will open up exciting new research on species trait and external biotic and abiotic contributions to woody debris decomposition in many biomes. Considering the large stocks and inputs of woody debris in many ecosystems, this will

help to improve the predictions of terrestrial carbon pools and fluxes, also in ecosystems changing in species composition, e.g. in response to natural succession, climate or land-use change.

ACKNOWLEDGEMENTS

Thanks are due to the Abisko Scientific Research Station (ANS) for hosting this experiment. We are grateful to Bob Douma for constructive discussion on decomposition modelling. G.T.F. was supported by EU Marie Curie host fellowship grant MEST-CT-2005-MULTIARC 021143; R.A. by EU ATANS grant Fp6 506004; and J.H.C.C. by grants 047.017.010 and 047.018.003 of the Netherlands Organisation for Scientific Research (NWO).

REFERENCES

Ausmus, B. S. (1977) Regulation of wood decomposition rates by arthropod and annelid populations. *Ecological bulletins,* **25,** 180-192.

Boddy, L. & Heilmann-Clausen, J. (2008) Basidiomycete community development in temperate Angiosperm wood. *Ecology of Saprotrophic Basidiomycetes* (eds L. Boddy, J. Frankland & P. van West), pp. 211-238. Academic Press, London.

Boddy, L. & Watkinson, S. C. (1995) Wood decomposition, higher fungi, and their role in nutrient redistribution. *Canadian Journal of Botany,* **73,** S1377-S1383.

Carlquist, S. J. (2001) *Comparative Wood Anatomy: Systematic, Ecological, and Evolutionary Aspects of Dicotyledon Wood.* Springer, Berlin.

Chambers, J. Q., Higuchi, N., Schimel, J. P., Ferreira, L. V. & Melack, J. M. (2000) Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia,* **122,** 380-388.

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G. & Zanne, A. E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters,* **12,** 351-366.

Chen, H., Harmon, M. E. & Griffiths, R. P. (2001) Decomposition and nitrogen release from decomposing woody roots in coniferous forests of the Pacific Northwest: a chronosequence approach. *Canadian Journal of Forest Research,* **31,** 246-260.

Chen, H., Harmon, M. E., Griffiths, R. P. & Hicks, W. (2000) Effects of temperature and moisture on carbon respired from decomposing woody roots. *Forest Ecology and Management,* **138,** 51-64.

Christensen, O. (1984) The states of decay of woody litter determined by the relative density. *Oikos,* **42,** 211-219.

Cornelissen, J. H. C., Quested, H. M., Gwynn-Jones, D., Van Logtestijn, R. S. P., De Beus, M. A. H., Kondratchuk, A., Callaghan, T. V. & Aerts, R. (2004) Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Functional Ecology,* **18,** 779-786.

Cornelissen, J. H. C., Quested, H. M., van Logtestijn, R. S. P., Pérez-Harguindeguy, N., Gwynn-Jones, D., Díaz, S., Callaghan, T. V., Press, M. C. & Aerts, R. (2006) Foliar pH as a new plant trait: can it explain variation in foliar chemistry and carbon cycling processes among subarctic plant species and types? *Oecologia,* **147,** 315-326.

Cornwell, W. K., Cornelissen, J. H. C., Allison, S. D., Bauhus, J., Eggleton, P., Preston, C. M., Scarff, F., Weedon, J. T., Wirth, C. & Zanne, A. E. (2009) Plant traits and wood fates across the globe: rotted, burned, or consumed? *Global Change Biology,* **15,** 2431-2449.

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V., Díaz, S., Garnier, E., Gurvich, D. E., Kazakou, E., Klein, J. A., Read, J., Reich, P. B., Soudzilovskaia, N. A., Vaieretti, M. V. & Westoby, M. (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters,* **11,** 1065-1071.

Delaney, M., Brown, S., Lugo, A. E., Torres-Lezama, A. & Quintero, N. B. (1998) The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. *Biotropica,* **30,** 2-11.

Dix, N. J. & Webster, J. (1995) *Fungal ecology.* Chapman & Hall, London.

Eaton, J. M. & Lawrence, D. (2006) Woody debris stocks and fluxes during succession in a dry tropical forest. *Forest Ecology and Management,* **232,** 46-55.

Efron, B. & Tibshirani, R. J. (1993) *An Introduction to the Bootstrap.* Chapman & Hall, New York.

Freedman, B., Zelazny, V., Beaudette, D., Fleming, T., Johnson, G., Flemming, S., Gerrow, J. S., Forbes, G. & Woodley, S. (1996) Biodiversity implications of changes in the quantity of dead organic matter in managed forests. *Environmental Reviews,* **4,** 238-265.

Freschet, G. T., Cornelissen, J. H. C., van Logtestijn, R. S. P. & Aerts, R. (2010) Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology,* **98,** 362-373.

Garnier, E. & Laurent, G. (1994) Leaf anatomy, specific mass and water content in congeneric annual and perennial grass species. *New Phytologist,* **128,** 725-736.

Hale, C. M. & Pastor, J. (1998) Nitrogen content, decay rates, and decompositional dynamics of hollow versus solid hardwood logs in hardwood forests of Minnesota, U.S.A. *Canadian Journal of Forest Research,* **28,** 1276-1285.

Harmon, M. E. (2009) Woody detritus mass and its contribution to carbon dynamics of old-growth forests: the temporal context. *Old-growth forests: function, fate and value* (eds C. Wirth, G. Gleixner & M. Heimann). Springer-Verlag, Berlin Heidelberg.

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack Jr., K. & Cummins, K. W. (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research,* pp. 133-302. Academic Press, New York.

Harmon, M. E., Krankina, O. N. & Sexton, J. (2000) Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. *Canadian Journal of Forest Research,* **30,** 76-84.

Harmon, M. E., Nadelhoffer, K. J. & Blair, J. M. (1999) Measuring decomposition, nutrient turnover, and stores in plant litter. *Standard soil methods for long term ecological research* (eds G. P. Robertson, C. S. Bledsoe, D. C. Coleman & P. Sollins), pp. 202-240. Oxford University Press, New York.

Harmon, M. E. & Sexton, J. (1996) *Guidelines for measurements of woody detritus in forest ecosystems.* U.S. Long-term Ecological Research Network Office, Seattle, Washington.

Harmon, M. E., Whigham, D. F., Sexton, J. & Olmsted, I. (1995) Decomposition and mass of woody detritus in the dry tropical forests of the northeastern Yucatan peninsula, Mexico. *Biotropica,* **27,** 305-316.

Hérault, B., Beauchêne, J., Muller, F., Wagner, F., Baraloto, C., Blanc, L. & Martin, J.-M. (2010) Modeling decay rates of dead wood in a neotropical forest. *Oecologia,* **164,** 243-251.

Hobbie, S. (2005) Contrasting effects of substrate and fertilizer nitrogen on the early stages of litter decomposition. *Ecosystems*, **8**, 644-656.

IPCC (2000) IPCC Special Report: land use, land-use change, and forestry Intergovernmental Panel on Climate Change, Geneva.

Käärik, A. A. (1974) Decomposition of wood. *Biology of plant litter decomposition* (eds C. H. Dickinson & G. J. F. Pugh), pp. 129-174. Academic Press, London.

Krankina, O. N. & Harmon, M. E. (1995) Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. *Water, Air & Soil Pollution,* **82,** 227-238.

Kueppers, L. M., Southon, J., Baer, P. & Harte, J. (2004) Dead wood biomass and turnover time, measured by radiocarbon, along a subalpine elevation gradient. *Oecologia,* **141,** 641-651.

Laiho, R. & Prescott, C. E. (1999) The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. *Canadian Journal of Forest Research,* **29,** 1592-1603.

Mäkinen, H., Hynynen, J., Siitonen, J. & Sievanen, R. (2006) Predicting the decomposition of Scots pine, Norway spruce, and birch stems in Finland. *Ecological Applications,* **16,** 1865-1879.

Malhi, Y. (2002) Carbon in the atmosphere and terrestrial biosphere in the 21st century. *Philosophical Transactions of the Royal Society A,* **360,** 2925-2945.

Minderman, G. (1968) Addition, decomposition and accumulation of organic matter in forests. *Journal of Ecology,* **56,** 355-362.

Naesset, E. (1999) Decomposition rate constants of Picea abies logs in southeastern Norway. *Canadian Journal of Forest Research,* **29,** 372-381.

Olson, J. S. (1963) Energy storage and the balance of producers and decomposers in ecological systems. *Ecology,* **44,** 322-331.

Olsson, J. (2008) *Colonization patterns of wood-inhabiting fungi in boreal forest*. PhD, Umeå University, Umeå.

Progar, R. A., Schowalter, T. D., Freitag, C. M. & Morrell, J. J. (2000) Respiration from coarse woody debris as affected by moisture and saprotroph functional diversity in Western Oregon. *Oecologia,* **124,** 426-431.

R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Ritz, C. & Streibig, J. C. (2009) Nonlinear Regression with R. Springer, New York.

Romero, L. M., Smith, T. J., III & Fourqurean, J. W. (2005) Changes in mass and nutrient content of wood during decomposition in a south Florida mangrove forest. *Journal of Ecology,* **93,** 618-631.

Scheffer, T. C. & Cowling, E. B. (1966) Natural resistance of wood to microbial deterioration. *Annual Review of Phytopathology,* **14,** 147-168.

Schowalter, T., Caldwell, B. C., Carpenter, S. E., Griffiths, R. P., Harmon, M. E., Ingham, E. R., Kelsey, R. G., Lattin, J. D. & Moldenke, A. R. (1992) Decomposition of fallen trees: effects of initial conditions and heterotroph colonization rates. *Tropical Ecosystems : Ecology and Management* (eds K. P. Singh & J. S. Singh), pp. 373-383. Wiley Eastern Limited, New Delhi.

Silver, W. & Miya, R. (2001) Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia,* **129,** 407-419.

Sinsabaugh, R. L., Antibus, R. K., Linkins, A. E., McClaugherty, C. A., Rayburn, L., Repert, D. & Weiland, T. (1993) Wood decomposition: nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. *Ecology,* **74,** 1586-1593.

Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K. & Venevsky, S. (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology,* **9,** 161-185.

Spears, J. D. H. & Lajtha, K. (2004) The imprint of coarse woody debris on soil chemistry in the western Oregon Cascades *Biogeochemistry,* **71,** 163-175.

Swift, M. J., Heal, O. W. & Anderson, J. M. (1979) *Decomposition in terrestrial ecosystems.* Blackwell, Oxford.

Taylor, B. R., Prescott, C. E., Parsons, W. J. F. & Parkinson, D. (1991) Substrate control of litter decomposition in 4 Rocky-Mountain coniferous forests. *Canadian Journal of Botany,* **69,** 2242-2250.

Tenow, O., Bylund, H., Karlsson, P. S. & Hoogesteger, J. (2004) Rejuvenation of a mountain birch forest by an Epirrita autumnata (Lepidoptera: Geometridae) outbreak. *Acta Oecologica,* **25,** 43-52.

Tuomi, M., Laiho, R., Repo, A. & Liski, J. (2011) Wood decomposition model for boreal forests. *Ecological Modelling,* **222,** 709-718.

van Geffen, K. G., Poorter, L., Sass-Klaassen, U., Van Logtestijn, R. & Cornelissen, J. H. C. (2010) The trait contribution to wood decomposition rates of 15 neotropical tree species. *Ecology,* **91,** 3686-3697.

Weedon, J. T., Cornwell, W. K., Cornelissen, J. H. C., Zanne, A. E., Wirth, C. & Coomes, D. A. (2009) Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? *Ecology Letters,* **12,** 45-56.

Wirth, C., Gleixner, G. & Heimann, M. (2009) *Old-growth forests: function, fate and value.* Springer-Verlag Berlin Heidelberg.

Yatskov, M., Harmon, M. E. & Krankina, O. N. (2003) A chronosequence of wood decomposition in the boreal forests of Russia. *Canadian Journal of Forest Research,* **33,** 1211-1226.

Supporting Information

Appendix S1. Assessing model performance with simulated data

Here we describe in detail the procedure that we used to assess the performance of our iterative optimization procedure (expanding the outline presented in the main document). We then describe the main results of this assessment and discuss the reliability of our iterative optimization procedure. The main conclusions of this assessment are presented in the main document.

The simulation process used to assess the performance of our iterative optimization procedure and the accuracy of its estimation of decomposition half-lives ($T_{1/2}$) is as follows (R scripts are available on request from the authors). We describe the procedure followed for simulation of datasets using the sigmoid model, but the same principle applies for assessing the model performance using datasets generated from linear or negative exponential models.

We simulated sigmoid wood decay curves from a range of *a* and *b* parameter values. In total, 190 different curves were simulated, with each combination of *a* and *b* where $0.02 \leq a \leq 0.2$ (by increments of 0.01 = 19 values) and $1 \leq b \leq 4$ (by increments of 1/3 = 10 values).

For each combination of parameter values we generated 20 replicate datasets following the steps below:

- We used the selected parameter values to calculate the time (T_{70}) needed to reach 70% loss in wood relative density (RD). 70% RD loss corresponds to the average sampling limit of our real datasets of wood decay stages. For the sigmoid model T_{70} was calculated as:

$$\frac{\log\left(1-\left(\frac{7}{10}\right)^{\frac{1}{a}}\right)}{b}$$

- We divided the time needed to reach T_{70} into three equal tertiles.

- We set the initial simulated sample to correspond to $t = 0$ and then for each tertile we generated $(n\text{-}1)/3$ additional *t* values using sampling from a random uniform distribution with bounds determined by the borders of the tertile (with *n* the number of decay stage samples). This ensures that initial values for *t* of each of the simulated samples are more or less evenly distributed over the interval and simulates the selection of a range of decay stages in our method.

- We calculated the expected RD value for each *t* value based on the selected parameter values.

- For all but the initial ($t = 0$) sample we added a random noise component taken from a random normal distribution with mean = 0 and variance = σ^2 to simulate intra-sample variation in RD values. This simulated the pre-incubation RD

values. Then, we used the parameter values (i.e. *a* and *b* for sigmoid model) to generate *j* RD values (with *j* the number of within-decay stage replicates) for each generated (pre-incubation) value of *t* plus 2 (i.e. length of incubation in years) and added noise component as above. This simulates the post-incubation RD values.

Thus, for the sigmoid model, all 190 unique combinations of values of *a* and *b* were used to generate 20 unique datasets, for a total of 19 x 10 x 20 = 3800 simulations. All simulations used the average *n*, *j* and σ of our eight real wood decay stage datasets, i.e. *n*=10, *j*=4 and σ=0.025. An example simulated dataset for a sigmoid model with parameters *a*=0.1 and *b*=1.75, is shown in Fig. S1. Each plotting colour represents a different simulated wood decay stage.

These simulated datasets were then submitted to the iterative optimization procedure described in the main document. Fig. S2 shows the estimated curves for the three models using the simulated data in Fig. S1 (note that no information about the underlying model, or the generated *t* values is passed to the iterative optimization procedure). Black symbols show the original simulated data, and the black dashed curve shows the underlying model used to generate them.

For each of the 3800 simulations, $T_{1/2}$ was calculated from the estimated parameter values and the relative error (*RE*) was calculated by comparison with the actual $T_{1/2}$ calculated from the parameter values used to generate the simulated dataset:

$$RE = \frac{T_{\frac{1}{2}est.} - T_{\frac{1}{2}actual}}{T_{\frac{1}{2}actual}}$$

Fig. S3 visualizes the results of these simulations by plotting the absolute *RE* of the best-fit model from each simulation (z axis) against the values of the parameters used to generate the dataset. It shows that the modelling procedure makes satisfactory predictions at high values of *a* and low values of *b* (i.e. fast decomposing logs with short lag-phase), but makes increasingly poor and variable estimates as *a* decreases and/or *b* increases (increasing lag-phase and/or slow decomposition).

To show how these parameter values translate to initial relative density loss over two years (for which we have data available from our study) we plotted the same relative error data as a level-plot in Fig. S4, with overlaid isolines showing the relative density remaining after two years under each set of parameters. It shows that the region in parameter space where the model performs poorly describes wood substrates with very slow initial decay, resulting in more than 98% relative density remaining after two years. For our data only *Pinus* roots (98.0% remaining after two years) and *Pinus* stems (97.8%) have observed initial density loss that would place them in this region.

We performed similar simulations using datasets generated using linear or negative exponential models. The plots of absolute relative error versus *k* (negative exponential, Fig. S5) or *m* (linear, Fig. S6) show that relative errors in the estimation of $T_{1/2}$ are in general lower than for datasets generated from the sigmoid model, although an increase

in estimation error is also evident for very slow decomposing wood substrates (low k or m).

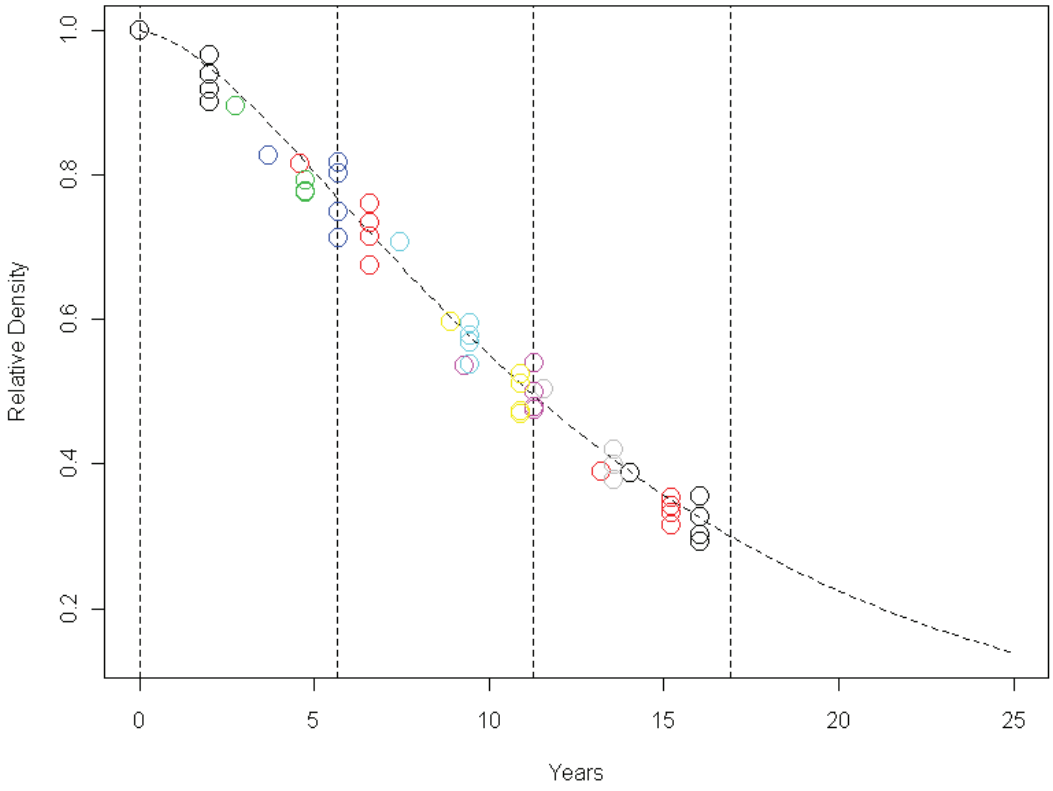

Fig. S1. Examples of a simulated dataset using the parameter values a = 0.1, b = 1.75, n = 10, j = 4, σ = 0.025. Each colour represents a different simulated wood stage. The dashed vertical lines indicate the positions of the three tertiles over which the t values of the simulated wood stages are distributed. The curved line indicates the underlying decay model from which the data points are generated.

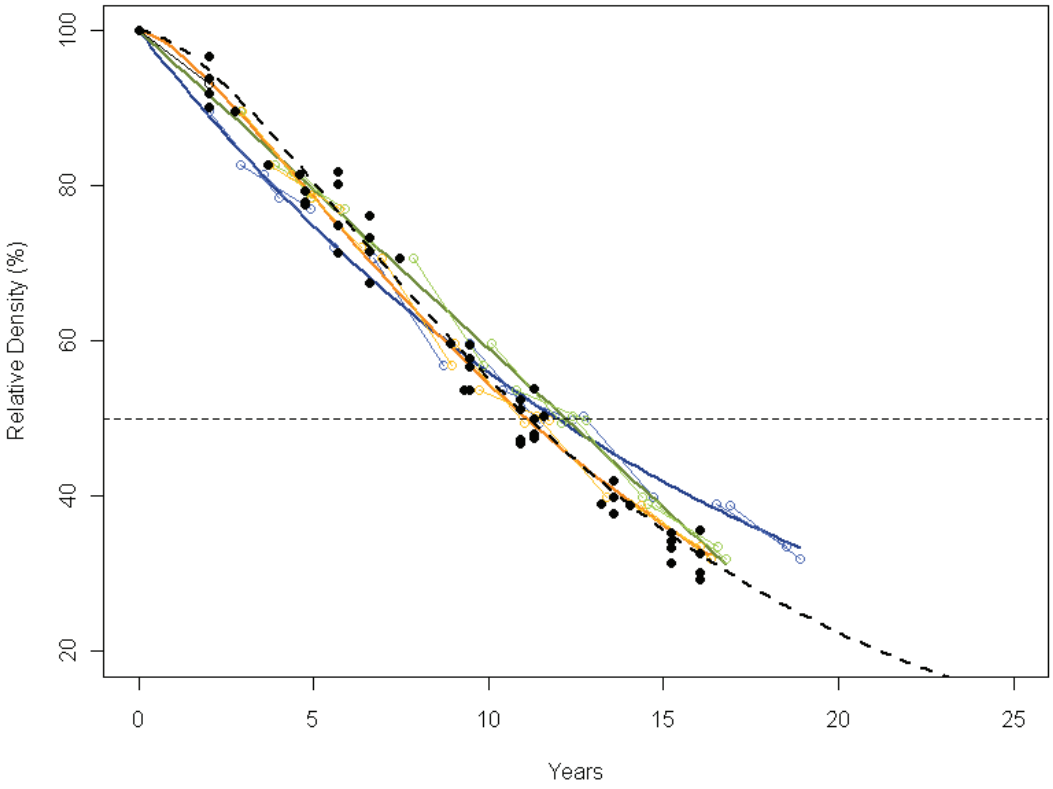

Fig. S2. Data from figure S1 after processing using the iterative optimization procedure. Blue curve and vectors represent the best fit under the assumption of negative exponential decay, green curve and vectors under a linear model, and orange curve and vectors under sigmoidal decay. The black points and black dashed line indicate the true values and underlying model of the original simulated dataset.

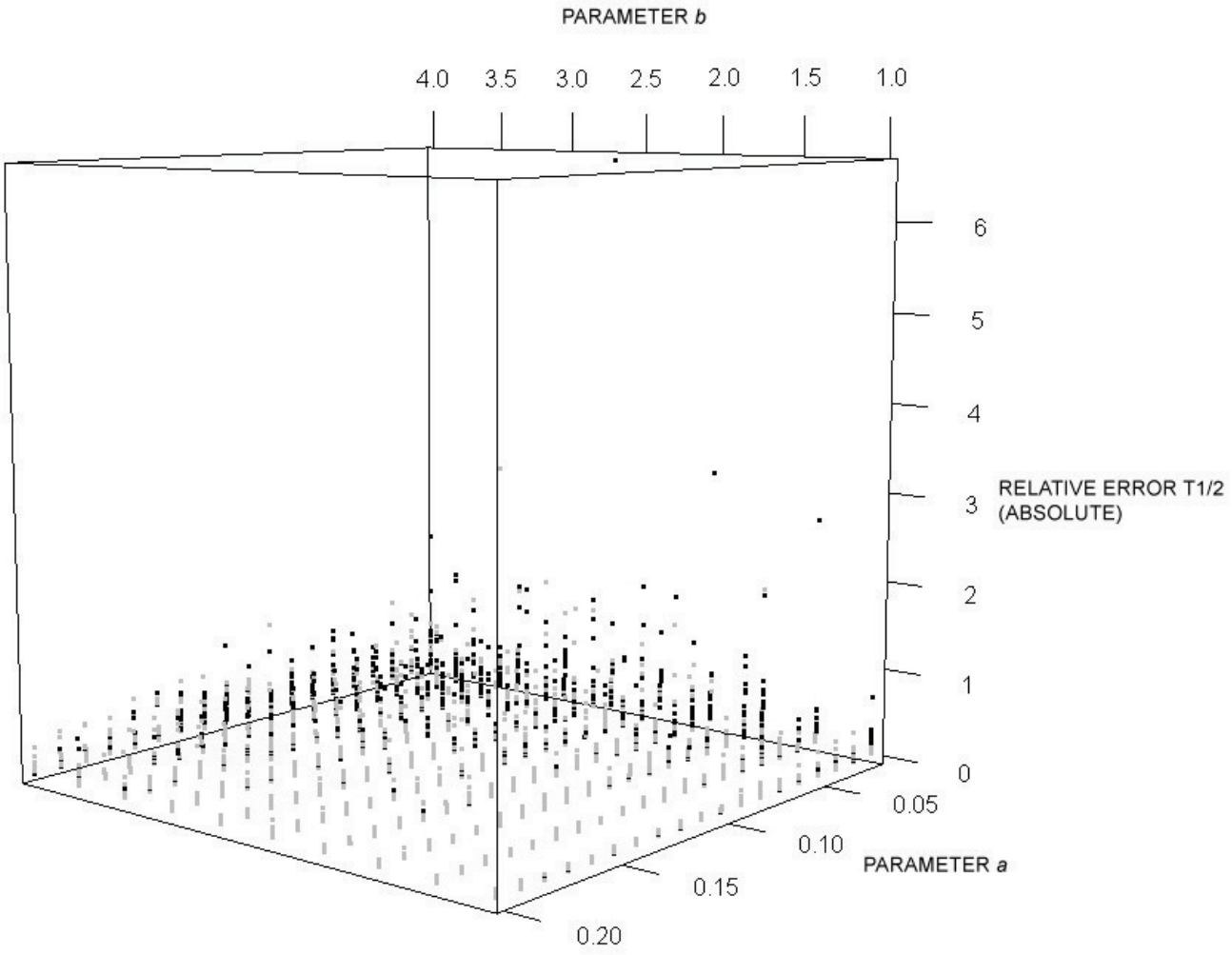

Fig. S3. Absolute values of relative error of estimates of $T_{1/2}$ from 3800 simulated datasets under 190 combinations of *a* and *b* parameter values. Grey points are simulation runs for which the estimated $T_{1/2}$ was within 20% of the true value (i.e. absolute relative error < 0.2). The plot shows how $T_{1/2}$ estimates become unreliable at lower values of *a* and/or higher values of *b*.

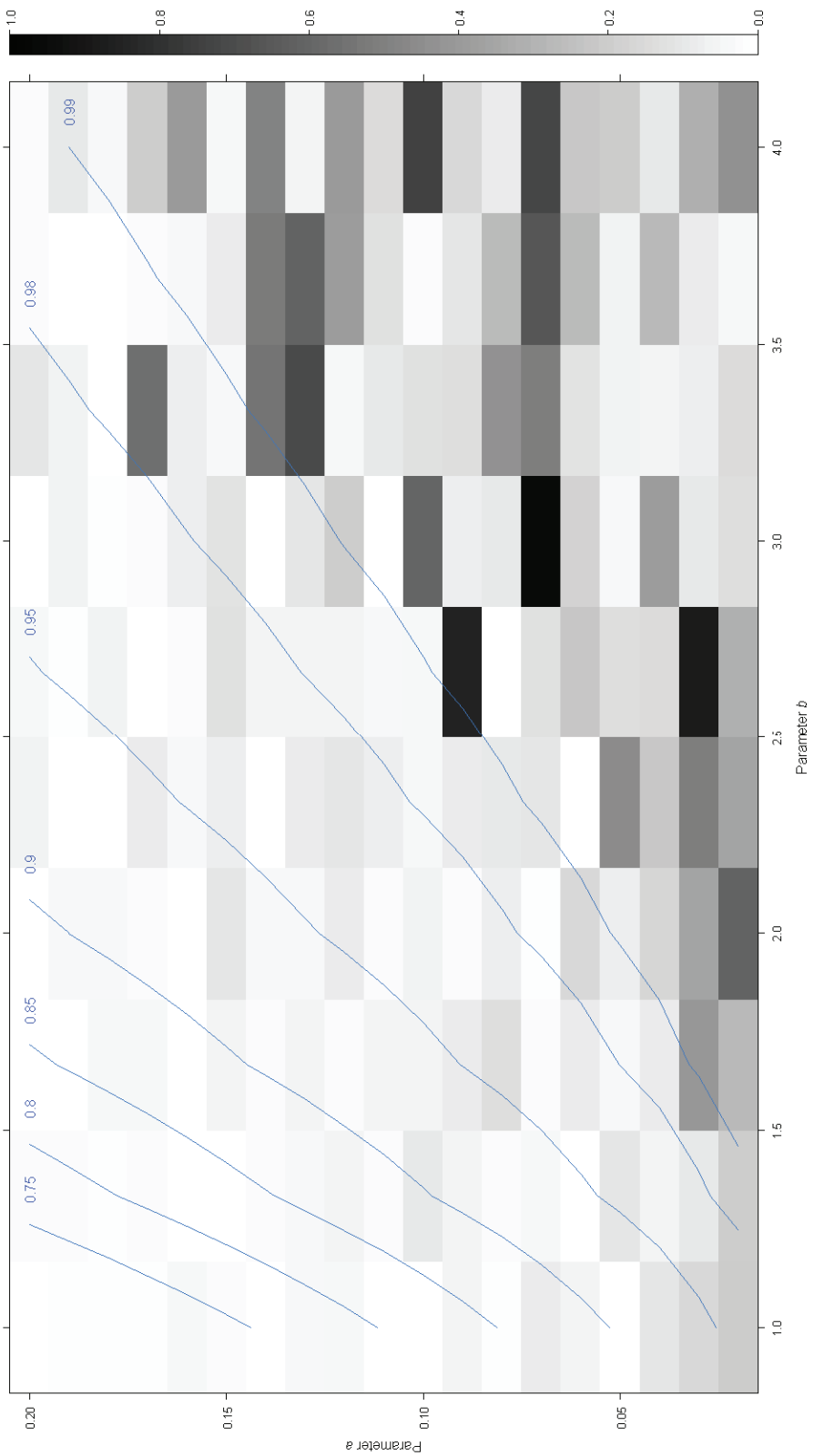

Fig. S4. Contour plot of mean absolute relative error of estimates of $T_{1/2}$ under the simulated datasets visualized in Fig S3. Darker colours indicate higher mean absolute relative error. Overlaid isolines indicate the expected relative density remaining after two years incubation under the different combinations of *a* and *b*.

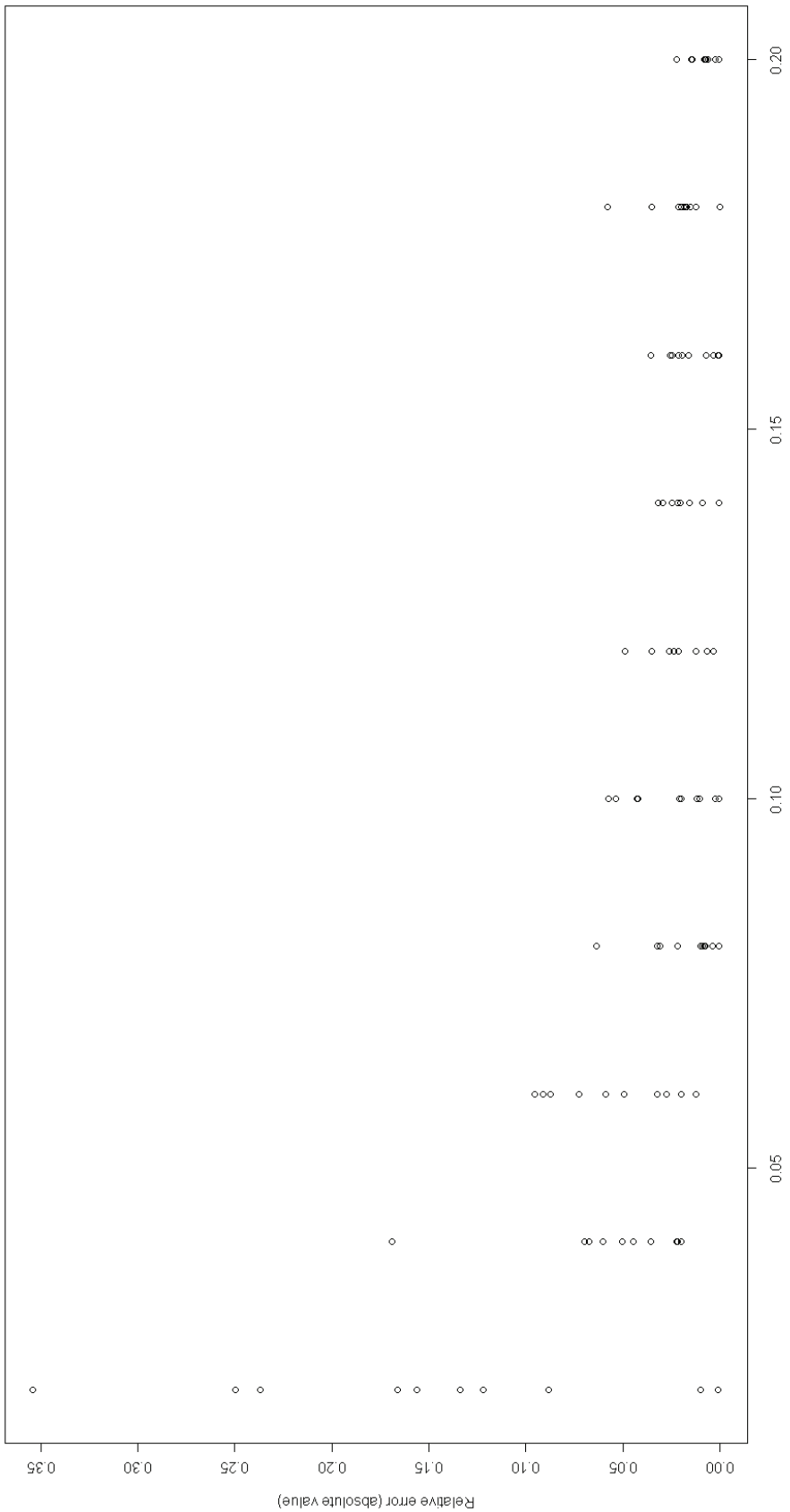

Fig. S5. Absolute relative error for estimates of $T_{1/2}$ using 100 datasets generated from a negative exponential model with a range of k values from 0.02 to 0.20. For each value of k 10 replicate datasets were generated, n = 10, j= 4 and σ = 0.025 for all simulations.

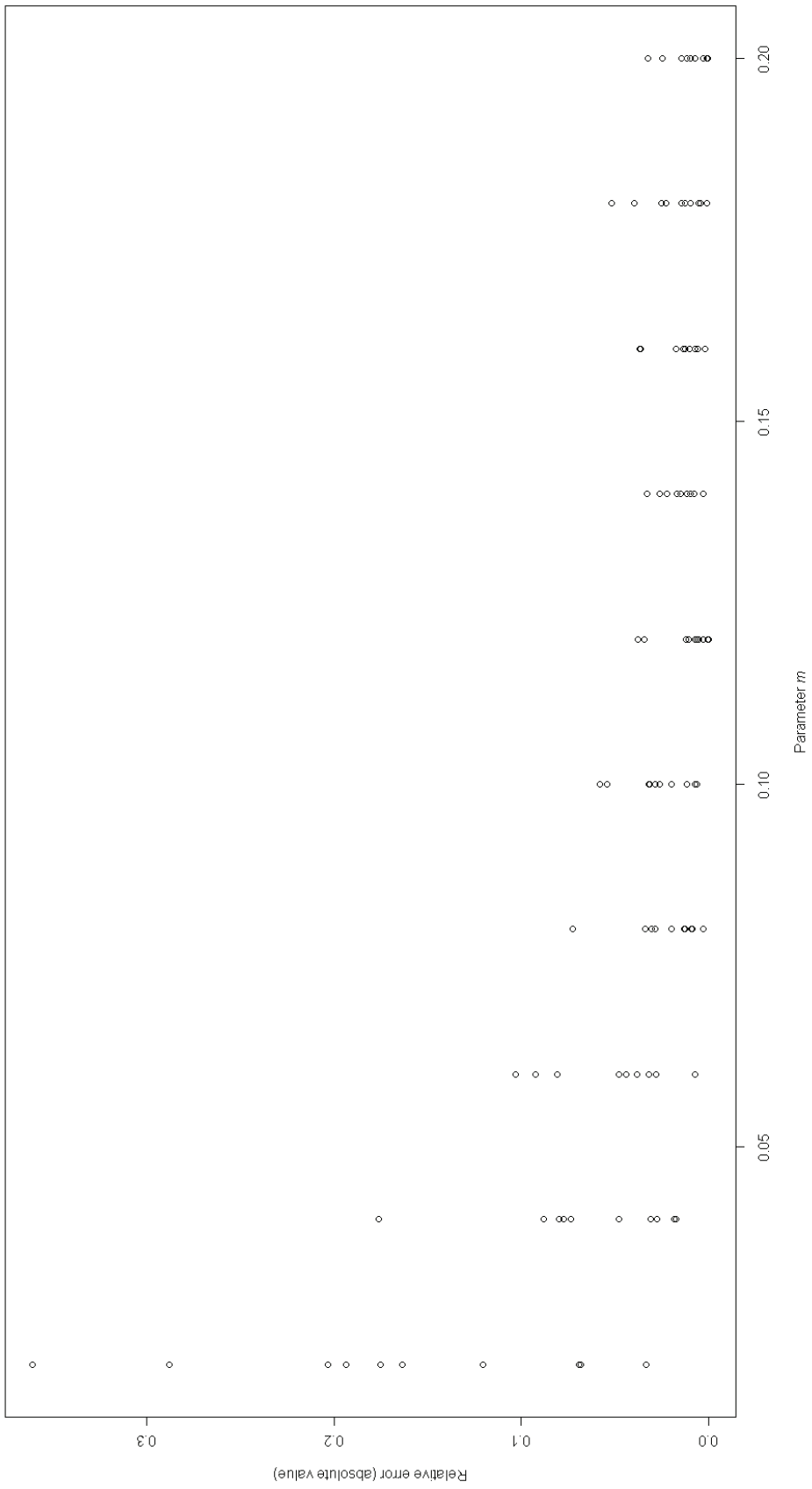

Fig. S6. Absolute relative error for estimates of $T_{1/2}$ using 100 datasets generated from a linear model with a range of *m* values from 0.02 to 0.20. For each value of *k* 10 replicate datasets were generated, $n = 10$, $j = 4$ and $\sigma = 0.025$ for all simulations.