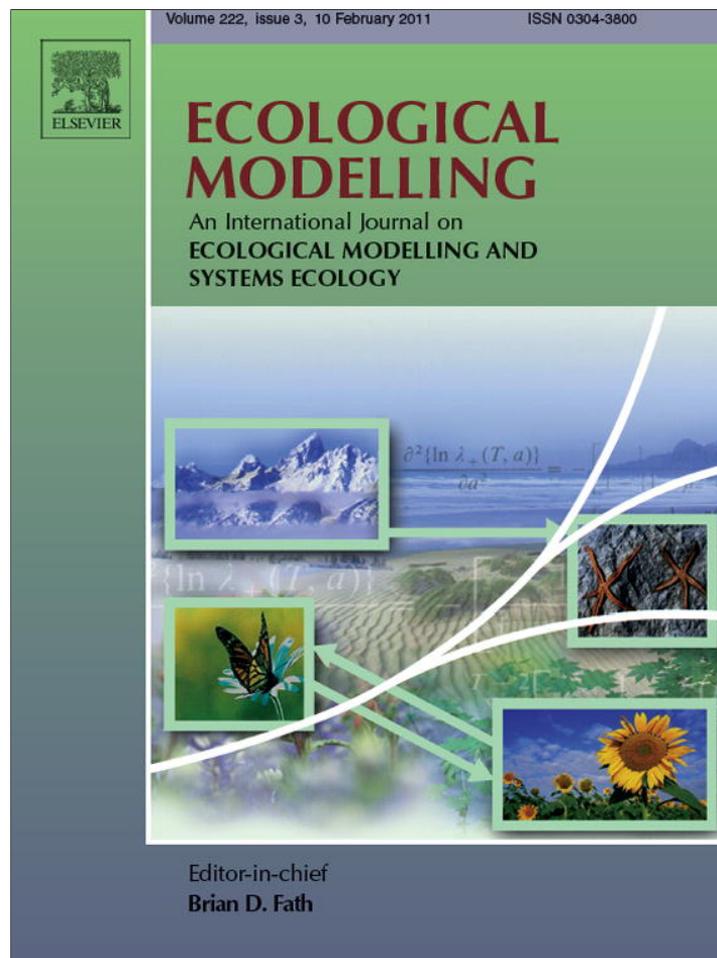


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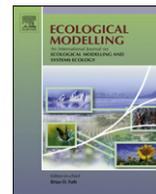
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## Ecological Modelling

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## Model-based analysis of the influence of ecological processes on forest point pattern formation—A case study

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### ARTICLE INFO

#### Article history:

Received 5 July 2010

Received in revised form 19 October 2010

Accepted 23 October 2010

Available online 22 November 2010

#### Keywords:

Ecological processes

Individual-based models

Sensitivity analysis

Spatio-temporal analysis

Shot-noise competition field

### ABSTRACT

Many different spatio-temporal individual-based models (IBM) for forests have been developed for studying the development of trees in space and time. Such models typically depend on various numerical parameters that represent the ecological processes of growth (G), inter-plant competition (C) and birth-and-death (B&D; also called regeneration and mortality). Until now little work has been done to systematically trace the influence of these processes and their model parameters on the spatial structure of forest ecosystems.

This paper attempts to fill this gap by addressing an important aspect of forest structure, spatial variability, characterised by the mark variogram as a summary characteristic. The model used was inspired by components of various well-established IBMs including a shot-noise competition field. Time series data from monospecies forests in three different countries of the northern hemisphere provided ecological reference scenarios. Though a case study, the paper's methodology is rather general and can be applied to any model and forest ecosystem.

Methods of sensitivity analysis revealed that only a small number of model parameters is crucial for forming spatial variability. Particularly important is the range of competition between trees; with increasing range the variability increases. Growth processes have considerable importance particularly with short observation periods and in young forests, whereas mortality processes become more influential in the long-term. Naturally, these statements depend upon the initial structure and on the length of the observation period.

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### 1. Introduction

Spatial patterns in plant populations are the result of complex dynamics involving three main processes: plant growth (G), inter-plant competition (C, hereafter termed just competition) and birth-and-death processes (B&D) (Vanclay, 1994; Hasenauer, 2006). These three ecological processes interact in a complicated dynamic way making it difficult to disentangle them. Part of the difficulty in isolating relative influences is that the only firm evidence of the G, C and B&D processes are the resulting spatial patterns. Therefore linking spatial patterns to processes is of particular interest in plant ecology, since this allows diagnosing the development of plant communities and even to understand successional stages from ad hoc field data (Perry et al., 2006; Law et al., 2009). However, there is no unique solution; similar spatial patterns can be the

result of different underlying processes, see for example Comas and Mateu (2007).

An important property of plant patterns is their spatial variability (see for example Perry et al., 2006). Only recently suitable statistical measures have been developed, namely various correlation functions (Cressie, 1993; Illian et al., 2008), including the mark variogram. Papers such as Walder and Stoyan (1996), Stoyan and Walder (2000), Kint et al. (2003) and Suzuki et al. (2008) have demonstrated the power of the mark variogram in ecological research.

Clearly, long-term field experiments will improve our understanding of how changing ecological conditions affect vegetation dynamics. However, computer experiments based on suitable models offer an immediate and efficient way of studying processes of spatial pattern formation. This line of analysis is also very flexible, since ecological conditions can be freely determined, not necessarily depending on the particular conditions of concrete field experiments. As always in computer experiments, there is the slight risk that situations may be constructed in the model which cannot appear in nature.

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In models used for this purpose, the three ecological processes are described mathematically. Particular aspects are characterised by numerical model parameters. This provides the opportunity to study the relevance and influence of these parameters on spatial pattern formation. For example, the undoubted influence of C can be analysed in greater detail by investigating the influence of range and strength of competition, expressed by suitable parameters.

Spatio-temporal individual-based models (IBM) are ideal for this kind of computer experiments, because they simulate the development of plant communities in sufficient detail (Grimm and Railsback, 2005). We applied such a model to the case of tree communities, since spatio-temporal data from forests are currently more readily available. However, the same methodology could be applied to other plant communities.

For our study, we developed an IBM using ideas from spatial statistics and experience from existing spatio-temporal individual-based models. We implemented well-established components of existing models with the aim to obtain results which have the potential to be of a general nature. In the modelling and parameterisation process principles of *pattern-oriented modelling* (Grimm and Railsback, 2005) were used, involving real patterns of tree density, mean stem diameter and spatial forest structure. To simplify the analysis, we excluded births. (These did not occur in the time series data available to this study.) We demonstrated the suitability of our model by fitting it to three spatio-temporal forest data sets. The parameters estimated were used as starting values for the simulations.

The objective of this paper is to reveal and to quantify the influences of model parameters on spatial pattern formation through computer experiments and thus to understand the related ecological processes.

In analysing the influences of the model parameters we used methods of sensitivity analysis (SA), namely a modified version of a classical screening method, a so-called one-at-a-time experiment (OAT), and a modern method, the extended Fourier amplitude sensitivity test (eFAST) as described in Saltelli et al. (2000).

The systematic application of these methods to forest models is still uncommon. Most of the studies in the literature were for biogeochemical models (see for example Matsushita et al., 2004; Rüger et al., 2007; White et al., 2008), which are, however, less relevant to the research question addressed in this paper. Berger et al. (2002) investigated the influence of a model parameter controlling the range of competition on the resulting skewness of the tree diameter distribution and on a self-thinning characteristic using an individual-based model and OAT. All these papers did not consider spatial variability characteristics. The focus was rather on model outputs that are by their nature real-valued variables and that characterise means like plant density and mean stem diameter or the variability behaviour of single trees measured as the skewness of the stem diameter distribution.

However, “spatial patterns” or “spatial variability” are numerically diffuse notions that cannot be sufficiently expressed by a single real number. The usual way in spatial statistics is to use *functions* as summary characteristics. We decided to choose the mark variogram for this purpose, because it characterises spatial correlations between tree sizes, in our case stem diameters. The mark variogram was then used to construct a suitable real-valued output variable as required in SA.

## 2. The spatio-temporal model

### 2.1. Model description

Our model belongs to the class of spatio-temporal individual-based models. Examples of spatio-temporal IBM include the models

Moses (Hasenauer, 2006), Silva (Pretzsch et al., 2002) and the mangrove-specific tree model KiWi (Berger and Hildenbrandt, 2000). Also the Tree and Stand Simulator (TASS) model developed by Mitchell (1975) belongs to this group, whereas SORTIE (Pacala et al., 1993, 1996) is a so-called process-based model, which explicitly models biogeochemical processes in plants. There are also a number of spatio-temporal models which use point process models of a more mathematical nature, e.g. Renshaw and Särkkä (2001) and Särkkä and Renshaw (2006).

For presenting our model we follow the standard protocol (ODD—Overview, Design concepts and Details) for describing individual-based models as proposed by Grimm et al. (2006, 2010).

#### 2.1.1. Purpose

The model was developed for analysing spatio-temporal dynamics of even-aged forests consisting of only one species. It was a particular objective to understand how intraspecific competition, growth and mortality affect the spatial structure of a forest, in particular its spatial variability. The model was parameterised for three tree species occurring in separate forests in Switzerland, Austria and Canada (see Section 2.4).

#### 2.1.2. State variables and scales

The model has two hierarchical levels, individual trees and the forest, i.e. the population to which the trees belong. At individual level, growth, competition and mortality are considered. An individual tree  $i$  is described by (1) an identity number, (2) a location,  $\xi_i$ , of the stem centre expressed in Cartesian coordinates, (3) a stem diameter (=diameter at breast height, measured at 1.3 m above ground in cm, denoted as  $dbh_{i,t}$ ) and (4) an annual diameter increment,  $id_{i,t}$ , the latter two depending on time  $t$ , given in years. Tree competition is spatially explicit, see Section 2.1.4, *Interaction*. The rectangular observation window (typically between 0.10 and 5 ha) defines the boundaries of the forest and can be arbitrarily selected. The nine model parameters are tree species-specific.

#### 2.1.3. Process overview and scheduling

The trees' life cycle is described by two biological sub-models operating in discrete, annual time steps. The first sub-model determines the stem diameter increment depending on a tree's potential diameter increment and its competition load. The second sub-model deals with mortality and consists of two components. The first component simulates natural tree mortality depending on the diameter growth during a reference period of the last five years. The second component takes care of natural disturbances and cutting. To keep the model simple, the establishment of new trees was not considered.

At the beginning of each time step, all tree diameters are updated synchronously. Then the mortality rule is applied and afterwards the competition load is calculated for the remaining trees. Finally diameter growth is determined for the next time step.

#### 2.1.4. Design concepts

*Basic principles:* The growth sub-model reflects the well-known fact that diameter growth of trees inside a forest is reduced compared to that of open-grown trees, which typically face no competition (Newnham, 1964; Botkin et al., 1972). In our model, as a substitute of growth data from open-grown trees increment data of the most dominant trees were used (Pretzsch et al., 2002). The competition sub-model is based on a random field for describing the competition load of single trees in a forest, following Adler (1996), Berger and Hildenbrandt (2000) and Illian et al. (2008), p. 435f. The additive superposition of competition effects exerted by single trees describes the competition load or competition intensity that

a tree would face at a given location. The deterministic mortality component utilises the well-known observation that trees have to maintain some level of diameter growth at all times for their survival.

**Emergence:** We explicitly model the life of each tree depending on growth, local competition and mortality. Emergent system dynamics include (1) the spatial structure of the forest, (2) the distribution of tree sizes, (3) self-thinning behaviour and (4) response to human management.

**Adaptation:** Mortality and cutting enlarges the growing space available to some trees. As a consequence these trees have access to more resources, which increases the growth of stem diameters.

**Objectives:** The objective of the adaptive trait mentioned above is individual survival through continuous growth.

**Sensing:** Individual trees are assumed to be aware of their own state variables, of the model parameters related to the tree processes and of their competition load.

**Interaction:** The competition for spatially distributed resources is modelled using the idea of the *shot-noise field*, see Illian et al. (2008). According to this approach every tree exerts a local competition effect, which depends on its stem diameter and decreases with increasing distance from the tree. To derive the competition load of a tree, the competition effects of all other trees are additively aggregated. The resulting total competition load is then weighted by the stem diameter of the tree considered. This determination of competition load mainly reflects asymmetric competition, which is defined by Weiner (1988) as an unequal sharing of resources as a consequence of larger individuals having a competitive advantage over smaller ones.

Incidentally, Berger and Hildenbrandt (2000) use the term “field of neighbourhood” (FON) instead of “shot-noise field” in their IBM. There have been other papers that have considered multiplicative aggregation of competition effects, such as Wu et al. (1985) and Miina and Pukkala (2002), who refer to an “ecological field” in this context.

**Stochasticity:** The second component of the mortality sub-model includes a stochastic element to account for variability of death and survival events, for which it is unimportant to model the actual causes. All other sub-models are completely deterministic.

**Observation:** At the end of each model run the model allows saving all state variables but also the derived variables such as the competition load of each tree. In addition, summary characteristics such as the empirical mark variogram, mean stem diameter and tree density averaged over  $N$  model runs can be saved. The output files are in ASCII format and can easily be imported by spreadsheet and statistical software for further analysis and visualisation.

### 2.1.5. Initialisation

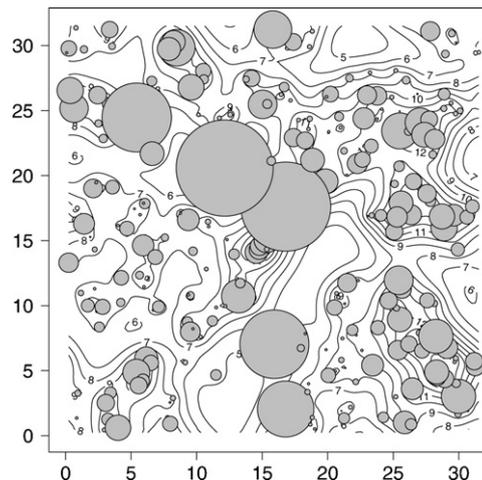
The model is initialised with a starting configuration of trees, i.e. tree locations and stem diameters. In our applications, we used the data from the original time series for this purpose. Also the length of the observation period,  $T$ , in this study ranging from 10 to 50 years, was in most cases taken from the time series data, once we worked with a shorter  $T$ . Furthermore, the model is initialised with a set of nine model parameters, which are read from an input file and are specific for each investigated forest. This initialisation is fixed for all  $N$  runs of a simulation. In this study we used  $N = 500$  runs.

### 2.1.6. Input data

The model does not use input data to represent varying environmental processes.

### 2.1.7. Submodels

**2.1.7.1. Growth.** The biological core of the model is the G process. Growth is modelled using the potential-modifier approach (Newnham, 1964; Botkin et al., 1972). In this approach, potential



**Fig. 1.** Map of monitoring plot 3 (Douglas fir [*Pseudotsuga menziesii* var *glauca* (MIRB.) FRANCO], Canada) at the beginning of the time series in 1988. The filled grey circles represent tree locations, circle sizes indicate relative diameters. The contour lines represent the shot-noise field calculated according to Eq. (3). The largest field values between 14 and 15 can be observed in the bottom right corner between  $27 < x < 30$  and  $3 < y < 7$ .

annual diameter increments are determined, i.e. increments that would be observed if the trees grew largely in absence of any competition from other trees. These increments are then reduced based on inter-tree competition,  $C$ .

The potential diameter increment  $id_{i,t}^{pot}$  is modelled for each tree  $i$  and time  $t$  according to a Chapman-Richards-type growth function, similar to Pretzsch et al. (2002) and Pretzsch (2009):

$$id_{i,t}^{pot} = A \cdot (1 - \exp(-k \cdot dbh_{i,t}))^p \cdot k \cdot p \cdot \exp(-k \cdot dbh_{i,t}), \quad (1)$$

where  $A$ ,  $k$  and  $p$  are model parameters. In the original Chapman-Richards function, the parameter  $A$  is an asymptote representing the maximum diameter for all trees of a given forest, parameter  $k$  scales the growth rate and  $p$  determines the location of the inflection point of the growth function, as explained in Pienaar and Turnbull (1973).

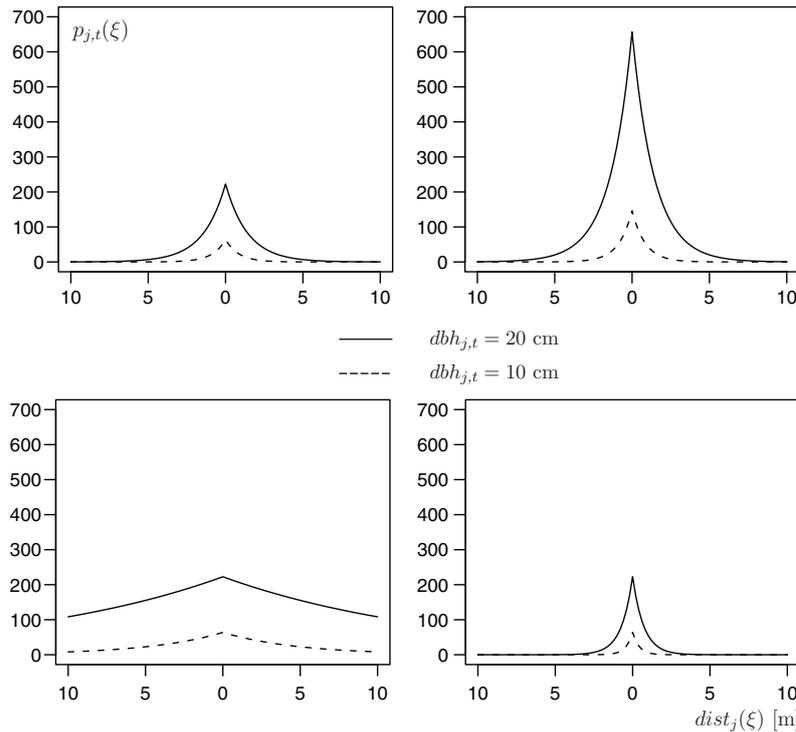
Finally, using the competition load  $c_{i,t}^{trans}$ , a growth modifier, as determined in Eq. (5) below, the annual diameter increment,  $id_{i,t}$ , is obtained as

$$id_{i,t} = id_{i,t}^{pot} \cdot \nu \cdot (1 - c_{i,t}^{trans}). \quad (2)$$

Here  $\nu$  is a further model parameter, which can be interpreted as another modifier. This parameter allows us to equate both sides of the equation. Without  $\nu$  both terms in Eq. (2) would only be proportional; incidentally, parameter  $\nu$  will play no individual role in the SA.

**2.1.7.2. Competition.** Tree growth and consequently diameter growth is hampered by competition among trees. To model this impact, in each time step first a competition field was constructed based on the actual forest configuration, given by tree locations and stem diameters. The value of  $c_{i,t}$  (see Eq. (4)) of this field at the position of tree  $i$  was considered the corresponding competition load and was then used to determine the increment,  $id_{i,t}$ , by means of Eq. (2).

The distance-related decrease of the local competition effect is modelled using a negative exponential function. The local competition effects of all trees in a forest are additively aggregated. This results in a competition field (see also the illustration in Fig. 1), which gives for any location  $\xi$  and time  $t$  the competition load  $c_t(\xi)$



**Fig. 2.** The local competition effect  $p_{j,t}(\xi)$  (Eq. (3)) of a tree  $j$  with 20 cm and 10 cm  $dbh_{j,t}$ . *Top left:* Original model parameters  $\alpha$ ,  $\beta$  and  $\delta$  for the beech (*Fagus sylvatica* L., Embrach, Switzerland) time series as compiled in Table 1. *Top right:*  $\alpha$  increased by 20%,  $\beta$  and  $\delta$  fixed to the values of Table 1. *Bottom left:*  $\beta$  increased by 100%,  $\alpha$  and  $\delta$  fixed. *Bottom right:*  $\delta$  increased by 100%,  $\alpha$  and  $\beta$  fixed.

as

$$c_t(\xi) = \sum_j p_{j,t}(\xi) = \sum_j dbh_{j,t}^\alpha \cdot \exp\left(-\frac{\delta \cdot dist_j(\xi)}{dbh_{j,t}^\beta}\right) \quad (3)$$

with positive model parameters  $\alpha$ ,  $\beta$  and  $\delta$ ;  $dist_j(\xi)$  is the Euclidean distance between the location of an arbitrary tree  $j$  and another location in the forest,  $\xi$ .

Consequently, the competition load of tree  $i$  at time  $t$  can be expressed as

$$c_{i,t} = \sum_{j \neq i} p_{j,t}(\xi_i) = \sum_{j \neq i} dbh_{j,t}^\alpha \cdot \exp\left(-\frac{\delta \cdot dist_j(\xi_i)}{dbh_{j,t}^\beta}\right). \quad (4)$$

The  $c_{i,t}$  values are computed with periodic boundary conditions (Illian et al., 2008) to reduce edge effects. The value of  $c_{i,t}$  is only dependent on the diameter of the trees influencing tree  $i$  and the distance  $dist_j(\xi_i)$  between tree  $i$  and tree  $j$ .

However, the impact of competition load also depends on the size of the affected tree  $i$ . Therefore, a further transformation of  $c_{i,t}$  is required, which is inspired by Adler (1996). This transformation combines the size of the affected tree  $i$  with its competition load  $c_{i,t}$  and is given by

$$c_{i,t}^{trans} = \frac{c_{i,t}}{dbh_{i,t}^\alpha + c_{i,t}}. \quad (5)$$

By construction,  $c_{i,t}^{trans}$  is scaled between 0 and 1. Note that the exponent  $\alpha$  in Eq. (5) is the same parameter  $\alpha$  as in Eqs. (3) and (4).

**2.1.7.3. Mortality.** First, following Berger et al. (2004), the trees' growth information over the last 5 years (=5 growth periods) was used for the deterministic component. The basic premise is that trees with low increments tend to die. However, refining the approach in Berger et al. (2004), diameter multipliers  $md_{i,t}$  were

used instead of absolute diameter increments, and defined as

$$md_{i,t} = \frac{dbh_{i,t}}{dbh_{i,t-1}} \quad (6)$$

following Wenk (1994). Clearly, the  $md_{i,t}$  values all satisfy  $md_{i,t} \geq 1$ , and  $md_{i,t} = 1$  indicates “no growth”, which can be the result of heavy competition, senescence or disease. Again following Berger et al. (2004), five subsequent  $md_{i,t}$  are combined by quadratic averaging to obtain

$$\overline{md}_{i,t} = \sqrt{\frac{1}{5}(md_{i,t}^2 + md_{i,t-1}^2 + \dots + md_{i,t-4}^2)}. \quad (7)$$

If this quadratic mean is smaller than a prescribed critical value  $md^{crit}$ , the corresponding tree dies. For convenience, the parameter  $md^{crit}$  is expressed in the form

$$md^{crit} = 1 + \frac{c}{1000}, \quad (8)$$

where  $c$  is a further model parameter, which replaces  $md^{crit}$  as a mortality parameter in the sensitivity analyses that follow, in order to obtain a reasonable parameter scale. The deterministic mortality component represents regular mortality resulting from competition.

Second, for the stochastic mortality component, a tree  $i$  dies during a growth period with probability

$$prob_{i,t} = a \cdot \left(\frac{dbh_{i,t}}{dg_t}\right)^b \quad (9)$$

with model parameters  $a$  and  $b$ . Here,  $dg_t$  is the quadratic mean diameter and is calculated as

$$dg_t = \sqrt{\sum_{i=1}^n \frac{dbh_{i,t}^2}{n}} \quad (10)$$

from all  $n$  trees in the forest at time  $t$ . The quadratic mean diameter is a well-established summary characteristic in forest biometrics

that has often been successfully used in the context of mortality modelling (see Chen et al., 2008; Crecente-Campo et al., 2009; Sims et al., 2009).

The model was constrained to ensure that  $p_{i,t} \leq 1$ . To implement the stochastic component, a tree dies, if a random number between 0 and 1 is less than its probability of mortality.

## 2.2. Role and interpretation of the model parameters

For purposes of the sensitivity analyses, a separate use of parameters  $A$  (from Eq. (1)) and  $\nu$  (from Eq. (2)) is not necessary. It is easy to see that the product of  $A$  and  $\nu$  can be viewed as a single parameter, denoted as  $Av$ .

The parameters of Eqs. (3) and (4) can be easily interpreted. The exponent  $\alpha$  scales resource allocation as a function of tree diameter (Adler, 1996); a large value of  $\alpha$  increases the strength of the local competition effect of tree  $j$  (see top section of Fig. 2) and therefore we refer to  $\alpha$  as *strength parameter*.  $\beta$  and  $\delta$ , on the contrary, are *range parameters* (see bottom section of Fig. 2). The parameter  $\beta$  scales the decrease of the competition signal with distance  $dist_j(\xi)$  (Adler, 1996); a large value of  $\beta$  stretches the range of the competition impulse. The parameter  $\delta$  also has an effect on the range, but it acts conversely to  $\beta$ . Adler (1996) found that  $\alpha$  and  $\beta$  are related to self-thinning processes whilst  $\delta$  has only an auxiliary role. We did comparative calculations by modifying these two range parameters by the same amounts (see again the bottom section of Fig. 2). This revealed that  $\beta$  had indeed a much greater effect on the model outputs than  $\delta$ , which was also noted by Adler (1996). Fig. 2 shows the local competition effect  $p_{j,t}(\xi)$  as a function of the distance from the exerting tree for two diameters.

An increase of the values of the growth parameters  $Av$  and of the range parameter  $\delta$  will lead to increasing  $id_{i,t}$ , while increasing  $\beta$  can decrease  $id_{i,t}$ . The influence of the strength parameter  $\alpha$  on  $id_{i,t}$  is less than that of other competition parameters.

The role of the growth parameters  $k$  and  $p$  is more complex.  $k$  scales the potential diameter increment, and, up to the point where diameter increment is maximum, increasing  $k$  also increases the diameter increment. Beyond that point, increasing values of  $k$  lead to a decrease in diameter increment. Thus an increase of  $k$  means rapid growth for smaller trees and slower growth or smaller increments for larger trees. Parameter  $p$  determining the location of the maximum of the increment curve has the opposite effect: An increase of  $p$  means slow growth for smaller trees and larger increments for larger trees.

Increasing parameter values of  $a$ ,  $b$  and  $c$  lead to increasing mortality.

## 2.3. Parameter estimation

For our analyses, we required realistic model parameters. To this end, we used the parameters estimated from the time series data of three forests, where the locations of all trees were recorded and each tree was repeatedly measured.

All model parameters were estimated separately for each forest. To obtain model parameters  $A$ ,  $k$  and  $p$  for potential diameter increment, we first grouped the trees into 4 cm-diameter classes. For each diameter class, the 95–100% percentiles of tree increment values were selected from the data for fitting Eq. (1), assuming that they represent potential growth under moderate or no inhibiting competition. The annual diameter increments were derived from periodic diameter increments, i.e. the averages of 5–10 years' increment observations. Using these results the parameters  $A$ ,  $k$  and  $p$  were estimated through nonlinear least squares regression in the statistical analysis software SAS (SAS, 2010).

In contrast to traditional competition indices (Biging and Dobbertin, 1992, 1995), the competition parameters  $\alpha$ ,  $\beta$  and  $\delta$  (Eqs.

(3) and (4)) must be estimated simultaneously with the growth parameter  $\nu$  (Eq. (2)). A hybrid quasi-Newton least squares method for the estimation of  $\alpha$ ,  $\beta$ ,  $\delta$  and  $\nu$  was used in this study and implemented in SAS (SAS, 2010).

Finally, the mortality parameters were estimated by means of a simulated annealing method, as described in detail in Murphy and Pommerening (2010). The necessary starting values were found by trial and error.

## 2.4. Description of the three forests

The three tree populations selected represent a wide range of growth conditions to demonstrate the wide applicability of the model. However, the investigation was intentionally limited to predominantly mono-species forests to focus on intra-specific competition at this stage. As noted, no birth processes occurred during the measurement period for any of the three study sites.

The beech (*Fagus sylvatica* L.) spatio-temporal data for plot 41–700 (0.25 ha in size) belongs to a Swiss thinning trial at Embrach (longitude: 8°10'22.13", latitude: 47°22'18.32"). The plot is in an even-aged beech forest which was established between 1891 and 1905 and re-measured every 5–10 years until 1991. However, spatial information is only available from 1940 onwards, with 107 trees in 1940. The plot is located at 590 m a.s.l. with a mean annual temperature of 8.3 °C and a mean annual precipitation of 1030 mm.

The Norway spruce (*Picea abies* (L.) KARST.) spatio-temporal data for plot 31 (0.12 ha in size) is part of a replicated thinning experiment at Karlstift (Austria, longitude: 14°45'59.7", latitude: 48°34'50.8"). The trees have naturally regenerated and the plot is located at 930 m a.s.l. with a mean annual temperature of 4.5 °C and a mean annual precipitation of 950 mm. The plot was established in 1964 in predominantly even-aged Norway spruce and re-measured every five years until 2004. The spatio-temporal measures began in 1994 with 135 trees.

The interior Douglas fir (*Pseudotsuga menziesii* var *glauca* (MIRB.) FRANCO) spatio-temporal data for plot 3 (0.10 ha in size) is part of a larger study in the Alex Fraser Research Forest in British Columbia (Canada, longitude: 52°3', latitude: 121°52') at approximately 1000 m a.s.l. The mean annual temperature is 4.2 °C and the mean annual precipitation is 450 mm. The plot is located in an uneven-aged Douglas fir forest and was established in 1988 and re-measured three times until 2004. This forest site had not been cut for the last 20 years or longer, and is under protection from large scale fires, which otherwise frequently occur in this forest type (LeMay et al., 2009). The initial number of trees in 1988 was 252.

The beech and the Norway spruce forests have a fairly uniform structure and are much more influenced by human disturbances than the Douglas fir forest, which can be considered as a natural forest.

## 2.5. Estimated model parameters

For each forest, all nine model parameters were estimated and presented in Table 1. Because of the differences between these three forests caused by different ecological conditions, the estimated parameters vary considerably. The differences are particularly large for the parameters  $b$  and  $p$  for the beech versus Douglas fir forests.

Table 1 also gives the root mean square error and mean bias for the predicted annual diameter increments using the calibrated model. Fig. 3 shows a comparison between observed and predicted diameters at the end of the observation periods. Also, the empirical and simulated mark variograms were compared, as these play a crucial role in our study. The low biases and root mean square errors, along with good coincidence between actual and predicted

**Table 1**

Site and species-specific parameters of the three spatial time series beech (*Fagus sylvatica* L., Embrach, Switzerland), Norway spruce (*Picea abies* (L.) KARST., Karlstift, Austria) and interior Douglas fir (*Pseudotsuga menziesii* var *glauca* (MIRB.) FRANCO, Alex Fraser Research Forest, British Columbia, Canada). G—tree growth, C—competition and B&D—birth-and-death processes.

Parameter	Description	Beech	Norway spruce	Douglas fir	Estimation		
1	G	$A\nu$	Diameter increment parameter: product of parameter $A$ in the potential diameter increment model (Eq. (1)) and parameter $\nu$ in the diameter increment estimation (Eq. (2)).	46.2678	24.9407	134.4464	Regression
2		$k$	Parameter in the potential diameter increment model (Eq. (1)).	0.0415	0.0658	0.0263	
3		$p$	Parameter in the potential diameter increment model (Eq. (1)).	5.1544	5.5289	0.5470	
4	C	$\alpha$	Shot-noise parameter scaling impulse strength (Eq. (3)).	1.8045	2.3760	0.3548	
5		$\beta$	Shot-noise parameter scaling impulse range (Eq. (3)).	0.7570	0.6599	0.4375	
6		$\delta$	Shot-noise parameter scaling impulse range (Eq. (3)).	6.7249	9.6583	1.7214	
7	B&D	$a$	Mortality parameter in 2nd mortality source (Eq. (9)).	0.0091	0.0322	0.0125	Trial & Error + Simulated Annealing
8		$b$	Mortality parameter in 2nd mortality source (Eq. (9)).	1.9203	0.5791	0.0117	
9		$c$	Critical diameter multiplier threshold for the average of a 5-year period (1st mortality source; Eq. (8)).	6.61	–	3.01	
10		$T$	Observation period of the research site in years.	51	10	16	–
		$RMSE$	Root mean square error of annual diameter increment estimation in cm.	0.12092	0.10649	0.07033	–
		$Bias$	Bias of annual diameter increment estimation in cm.	0.00228	–0.00021	–0.00375	–

mark variograms indicate that the model fits well the different data and that the parameterisation is accurate.

### 3. Sensitivity analyses

#### 3.1. Introduction

This paper uses methods of sensitivity analysis for tracing the contribution of model parameters and of the corresponding processes in spatial pattern formation. The aim of sensitivity analysis in general is to explore for a given model the influence of model parameters  $x_i$  on an output variable  $y$ . The output of the model is a real number, which is a deterministic function of the  $x_i$  (see Saltelli et al., 2000),

$$y = f(x_1, \dots, x_s). \tag{11}$$

The vector  $(x_1, \dots, x_s)$  is considered a point in an  $s$ -dimensional “parameter space”. In local sensitivity analysis, parameters are varied within a neighbourhood centred at some point in the parameter space, which is often called “midpoint” or “origin”. Global methods try to simultaneously explore the model behaviour over the whole parameter space. A question of particular interest is parameter interaction (Saltelli et al., 2000, 2004; Marino et al., 2008). Roughly speaking, this concerns the mutual influence of the  $x_i$  in such a way that, for example, a simultaneous increase of  $x_1$  and  $x_2$  leads to a larger effect on  $y$  than a simple addition of the effects of a separate increase of  $x_1$  and  $x_2$ . (Parameter interaction is a concept quite different to parameter correlation.)

We considered  $s=9$  numerical parameters  $x_1, \dots, x_9$ , following the numbering in Table 1. Only subsets of the whole theoretical 9-dimensional parameter space  $0 \leq x_i \leq x_{i, \max}$  (where  $x_{i, \max}$  is a suitable maximum value of  $x_i$ ) can be used, because many parameter vectors lead to implausible results or do not occur in nature. A common indication of such combinations is the premature death of all trees of the forest. To ensure ecologically sound starting configurations, we decided to use the original model parameters as

estimated from the three times series. We used them as starting points for the sensitivity analyses and then studied the behaviour of the model in the neighbourhood of these “origins”.

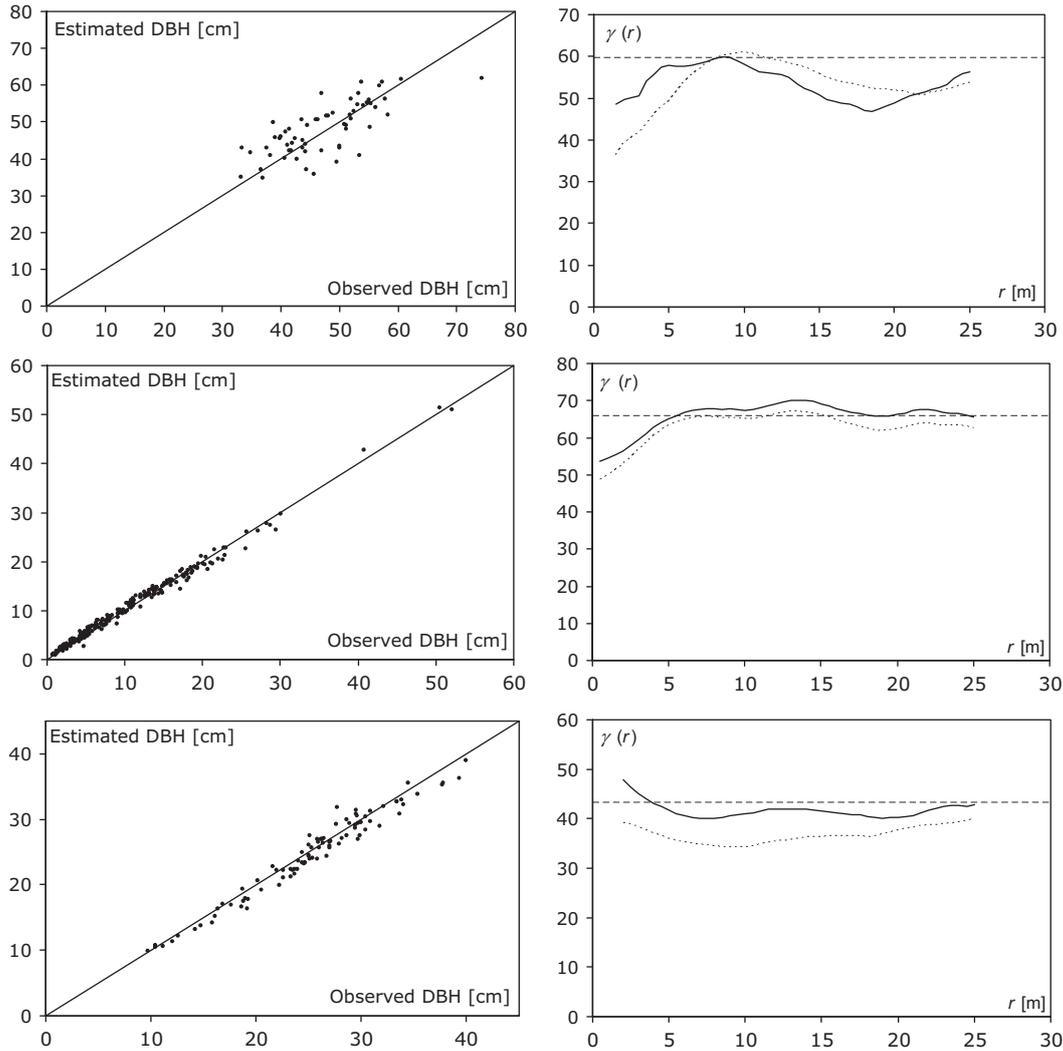
For the beech time series, we also included a shorter observation period of  $T=16$  in addition to the original observation period of  $T=51$ , in order to assess the influence of  $T$  on the results of the sensitivity analyses.

We then ran the model with varied model parameters in the neighbourhood of the estimated parameters given in Table 1.

As output variable we considered for  $y$  in Eq. (11) a second-order characteristic, closely related to the mark variogram. After a number of comparative experiments using different second-order characteristics, we decided to focus on the mark variogram,  $\gamma(r)$ , as this characteristic very clearly represents differences in the resulting point patterns (see for example Kint et al., 2003; Suzuki et al., 2008). This characteristic includes information on the spatial variability of tree locations as well as on tree marks. (If it had been our objective to disentangle mark and location variability, we would have used the ideas in Renshaw et al., 2007). The mark variogram is defined as

$$\gamma(r) = \frac{1}{2} E(m(o) - m(r))^2, \tag{12}$$

i.e. half the mean of the squared mark difference for two points of distance  $r$ , see Illian et al. (2008). The function is set to 0 for  $r$  values smaller than  $r_0$ , the smallest occurring inter-tree distance. Then it has the tendency to increase up to an  $r$  value  $r_1$  referred to as range of correlation. Beyond that point the function fluctuates around a constant value that is equal to the variance of the marks, see, for example, Figure 5.21 on page 349 in Illian et al. (2008). The curve for the Douglas fir forest in Fig. 3 is close to this behaviour, while the other two curves in Fig. 3 show typical deviations. (The beech variogram curve shows a similar pattern to that of the Douglas fir forest for small  $r$ , but exhibits more variation at larger distances. For the Norway spruce forest, the decrease of the curve for small  $r$  indicates short-range tree interactions, i. e. the occurrence of pairs of



**Fig. 3.** Estimated versus observed diameters for: (top left) plot 41–700 (Embrach beech [*Fagus sylvatica* L.] time series) in 1991 after 51 annual simulation periods; (centre left) plot 3 (interior Douglas fir [*Pseudotsuga menziesii* var *glauca* (MIRB.) FRANCO] time series) in 2004 after 16 annual simulation periods; and (bottom left) plot 31 (Norway spruce [*Pseudotsuga menziesii* (L.) KARST.] time series) in 2004 after 10 annual simulation periods. Empirical variogram (solid line) and corresponding variogram of the simulation involving both mortality models (dotted line) for: (top right) observed beech data in 1991; (centre right) Douglas fir data in 2004; and (bottom right) Norway spruce data in 2004. A bandwidth of  $h=4.0$  m was used in all cases for the mark variograms. The horizontal dotted lines correspond to the diameter variance.

dominant and suppressed trees at short distances.) In general, large values of  $\gamma(r)$  result from a high degree of spatial variability of the marks, while the ratio of  $r_1$  to  $r_0$  characterises spatial correlation.

Since the mark variogram is a function of inter-tree distance  $r$  and all values of  $r$  (within an ecologically relevant interval) have to be considered,  $\gamma(r)$  is not a suitable output variable for SA. Therefore a discrepancy number  $\Delta_m$  was used, which is defined as

$$\Delta_m = \int_{r_0}^{r_1} (\gamma_0(r) - \gamma(r))^m dr, \quad (13)$$

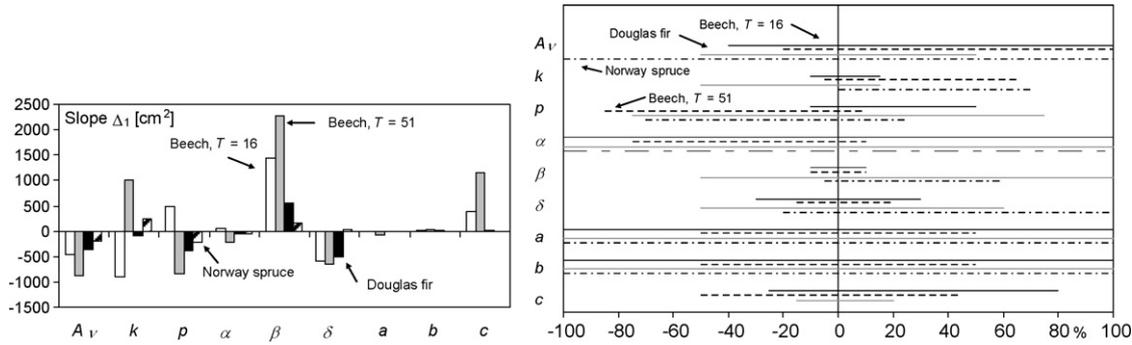
where  $\gamma_0(r)$  is the mark variogram for the forest of interest with the model parameters in Table 1;  $\gamma(r)$  is the mark variogram representing another point in the parameter space, i.e. with the same starting configuration and observation period  $T$  as for  $\gamma_0(r)$ , but with different parameters;  $m$  is an exponent, where the cases  $m=2$  and  $m=1$  are of particular interest. Thus  $\Delta_m$  characterises the deviation of  $\gamma(r)$  from a given “null” mark variogram  $\gamma_0(r)$ .

In the model calculations, we approximated the integral by a sum using a step width of 0.5 m. The lower integral limit,  $r_0$ , corresponds with the hardcore distance (minimum distance between trees) rounded up to the nearest 0.5 m step. We defined the upper limit  $r_1$  in such a way that it corresponded with the correlation

range of the mark variogram  $\gamma_0(r)$  of the original data at the end of the observation period,  $T$ . This decision was made since usually short distances between trees are of particular ecological importance in forest ecosystems, as this is the spatial range where stronger interactions commonly take place. As a result,  $\Delta_m$  was calculated between 1.5 m and 8.5 m for the beech forest (15 summands), between 0.5 m and 5.5 m for the Douglas fir forest (11 summands) and 2.0 m and 7.5 m for the Norway spruce forest (12 summands). All mark variograms  $\gamma(r)$  and  $\gamma_0(r)$  were estimated according to Illian et al. (2008) with a bandwidth of 4.0 m.

With the aim to analyse smooth, locally approximately linear functions, we decided to use  $\Delta_1$ , i.e. the quantity in Eq. (13) with  $m=1$ , which is a signed real variable that is equal to zero when the model parameters used in generating  $\gamma(r)$  and  $\gamma_0(r)$  are the same. (Then in fact we consider the difference of integrated mark variograms. The integral in Eq. (13) then becomes the difference of the integrals  $\int_{r_0}^{r_1} \gamma(r) dr$  and  $\int_{r_0}^{r_1} \gamma_0(r) dr$ ). This decision was made, because

1. We observed undesirable results for alternative definitions of deviation measure,  $\Delta_2$  and  $|\Delta_1|$ , a quantity similar to  $\Delta_1$  but using absolute differences,  $|\gamma_0(r) - \gamma(r)|$ . By definition, the cor-



**Fig. 4.** Behaviour of the model function  $\Delta_1$  for the mark variogram with respect to the nine parameters (OAT analysis). The bars (left) show the corresponding slopes of  $\Delta_1$  in the parameter ranges (right) in which the dependence of  $\Delta_1$  on the parameters is (nearly) linear.

responding integrands are positive and so are the two  $\Delta_m$  characteristics. Thus we obtained a positive deviation measure even if we chose the original parameters of Table 1 for simulating forest development, based on two independent estimates of  $\gamma_0(r)$ .

2. The use of  $\Delta_2$  and  $|\Delta_1|$ , which corresponds to the  $L^1$  and  $L^2$  norms used in functional analysis, leads to functions  $f$  in Eq. (11) which are strictly nonlinear even in the near neighbourhood of the original model parameters.

A disadvantage of our choice of  $\Delta_1$  is that in the integral in Eq. (13) (and in the corresponding sum) positive and negative differences may cancel out, resulting in a value of  $\Delta_1 = 0$  even when  $\gamma(r)$  and  $\gamma_0(r)$  are not equal for all  $r$ . However, in our simulation experiments the corresponding mark variograms showed a behaviour where our deviation measure made sense for nearly all parameters. Thus  $\Delta_1$  constitutes our function  $f$  in Eq. (11).

This may be the appropriate place to comment on our choice of the number of runs,  $N$ , as in the model description of Section 2.1.5. Naturally, the mark variograms obtained from different runs of our model differed even though starting configurations and model parameters were fixed, because of the stochastic component in the mortality sub-model. However, for the sensitivity analyses we required a deterministic function  $f$ . After some experimentation we found that  $N = 500$  runs were sufficient in all cases to obtain reliable mean value results for the output variable  $\Delta_1$ . (If our output had been the mean stem diameter only, a smaller value of  $N$  would be sufficient.)

### 3.2. One-at-a-time analysis

A classical form of sensitivity analysis is one-at-a-time (OAT) analysis (Saltelli et al., 2000). In this analysis, the influence of each model parameter is assessed by varying the parameter but fixing all others (*ceteris paribus*). Mathematically, this yields information about the marginal influence of each model parameter in the neighbourhood of the respective origin  $(x_{1,0}, \dots, x_{9,0})$ , which can be characterised by a partial derivative or slope, assuming that  $f$  is a smooth function of its parameters.

This gives valuable information on the “importance” of each parameter: a parameter  $x_i$  is considered as more important than parameter  $x_j$ , if

$$\left| \frac{\partial f}{\partial x_i} \right| > \left| \frac{\partial f}{\partial x_j} \right|. \quad (14)$$

We calculated  $f(x_{1,0}, \dots, x_{i,0} + d_i, \dots, x_{9,0})$ , where  $d_i$  is the actual deviation of parameter  $x_i$  from the origin value  $x_{i,0}$ . The analysis

proceeded in equidistant steps of  $d_i$  between

0 and  $2x_{i,0}$ , i.e.  $x_{i,0} \pm 100\%$  of  $x_{i,0}$ .

We were particularly interested in an approximately linear behaviour of  $f$  in dependence of  $x_i$  in the neighbourhood of the origin, i.e. in an approximate relationship as

$$f(x_{1,0}, \dots, x_{i,0} + d_i, \dots, x_{9,0}) = f(x_{1,0}, \dots, x_{9,0}) + a_i d_i,$$

where  $a_i = \partial f / \partial x_i$ , since this indicates smoothness around the origin, and is related to the first term of a Taylor expansion.

For all forests and all parameters  $x_i$ , the intervals including  $x_{i,0}$  with a nearly linear behaviour of  $f$  depending on  $x_i$  were determined. They differ between  $(-100\%, 100\%)$  and  $(-10\%, 10\%)$ . Outside of these intervals the behaviour can be strongly nonlinear. The partial derivatives were estimated using a relative scale, such that  $x_{i,0} = 0$  and  $2x_{i,0} = 1$  in the case of the full  $-100\%, 100\%$ -interval. This facilitated comparisons between parameters. The slopes of approximating lines were estimated by linear regression using the values in the linearity intervals and forcing the lines through the known values at the origins. The results for the output variable  $\Delta_1$  are shown in Fig. 4. Note that these slopes can be positive or negative, indicating the direction in which the variables influence spatial variability.

### 3.3. Extended Fourier Amplitude Sensitivity test

As an alternative to simple OAT the extended Fourier Amplitude Sensitivity test, a variance-based global sensitivity method (Saltelli et al., 2000) was applied. The Fourier Amplitude Sensitivity Test (FAST) was first devised in the 1970s by Cukier and others (see Cukier et al., 1978) and further developed by Saltelli et al. (1999) to become the extended FAST method. eFAST is model-independent and is applicable irrespective of the degree of linearity or additivity of the model. The method quantifies the contribution of the individual input parameters to the variance of the output variables. It reveals both parameter main effects on the model output and the sum of the effects due to its higher-order interactions with other parameters (Saltelli et al., 2000; Saloranta and Andersen, 2007).

The model output was analysed based on discrete Fourier transformation using the software package SimLab 2.2 (Simulation environment for uncertainty and sensitivity analysis, Saltelli et al., 2004). Following its specific sampling procedure 30,000 function values for different parameter sets were calculated, i.e. 30,000 times 500 = 15,000,000 replications were made, since every function value is based on 500 runs. This corresponds to parameter values sampled in a wave-like form, so that the amplitude of the particular wave was equal to the parameter's predefined variation range. The sampling covered the whole multidimensional parameter space. We applied this procedure to all parameter sets.

**Table 2**  
Variation percentages around the standard parameter values for the multiple parameter variation of the extended Fourier Amplitude Sensitivity Test (eFAST).

Parameters			Beech, T=16	Beech, T=51	Norway spruce	Douglas fir
1	G	$Av$	±10%	±5%	±90%	±20%
2		$k$	±10%	±5%	±25%	±25%
3		$p$	±10%	±5%	±25%	±25%
4	C	$\alpha$	±10%	±5%	±90%	±40%
5		$\beta$	±10%	±5%	±25%	±30%
6		$\delta$	±10%	±5%	±25%	±30%
7	B&D	$a$	±30%	±10%	±90%	±50%
8		$b$	±30%	±10%	±90%	±50%
9		$c$	±10%	±5%	–	±10%

The eFAST method also allows a grouping of parameters and thus an upscaling of the results for single parameters to those of the three processes. After analysing the individual contribution of each of the model parameters to the output variance, we re-analysed the model behaviour by grouping the model parameters into: growth ( $Av$ ,  $k$ ,  $p$ ), competition ( $\alpha$ ,  $\beta$ ,  $\delta$ ) and birth-and-death ( $a$ ,  $b$ ,  $c$ ) processes. The eFAST group analysis included 20,000 model runs per forest and observation period with 500 runs.

The suitable parameter space was determined in preliminary investigations as a sub-set of the whole nine-dimensional parallel epipedon  $0 \leq x_i \leq x_{i,max}$ , which was taken as a smaller parallel epipedon. Each variable varied in an interval defined by two variation percentages around the respective origin between minimum and maximum ranges, see Table 2. The percentages were determined so that no nine-dimensional point within the smaller epipedon led to a very extreme result (e.g. with too many trees dying before the end of the observation period). This criterion resulted in different variation percentages for the parameters, which even differed for the two beech simulations with different observation periods  $T$ .

It is interesting to compare the percentages (i.e. the sizes of the parallel epipedons) for the Norway spruce and Douglas fir data with those for the beech data. Because of the longevity of the observation period for the beech forest, any parameter variation was expected to have a larger impact on the resulting spatial patterns, while for the other two forests smaller impacts were expected. Indeed, the variation percentages for the beech forest are clearly smaller than for the spruces and firs. It is also interesting to compare the linearity intervals found in the OAT analysis with the percentage intervals used in the eFAST analysis. We found that for all model parameters, the linearity intervals were often much smaller than the full (–100%, 100%)-sensitivity-analysis interval. However, the percentage intervals of the eFAST analysis were always even smaller and completely within the linearity intervals.

In the eFAST analysis we assumed uniform distributions of all model parameters within the minimum – maximum ranges, which is standard practice (Saltelli et al., 2000).

## 4. Results

### 4.1. Single model parameters

The results of the OAT and eFAST analyses are very similar and are therefore presented together in one section. The ecological interpretation will follow in Section 5. Throughout Section 4 we will discuss the influence of the model parameters on the output variable  $\Delta_1$  based on Figs. 4 and 5.

**Beech forest:** The three parameters of main influence are  $\beta$ ,  $k$  and  $c$ , the latter is more important in the case of  $T=51$  (Figs. 4 and 5). Considering the comparatively slow growth of beech, competition, in particular the range of competition, is apparently most important followed by growth represented by parameter  $k$ . Mortality, as expressed by parameter  $c$ , has for  $T=16$  little influence but becomes more important with the longer observation period.

**Douglas fir forest:** Competition parameters play a major role, again the range parameters  $\beta$  and  $\delta$ . Additionally, the growth parameters  $Av$  and  $p$  are important.

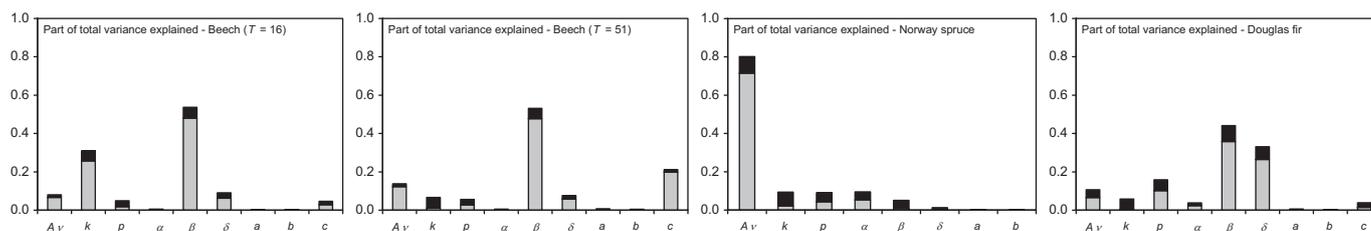
**Norway spruce forest:** The three growth parameters and the competition range parameter  $\beta$  are the most important ones. However, competition is less prominent in this forest than in the other two.

Parameter interaction characterised by its portion of the total variance in the eFAST analysis is less than 30% in the majority of cases, as shown in Fig. 5.

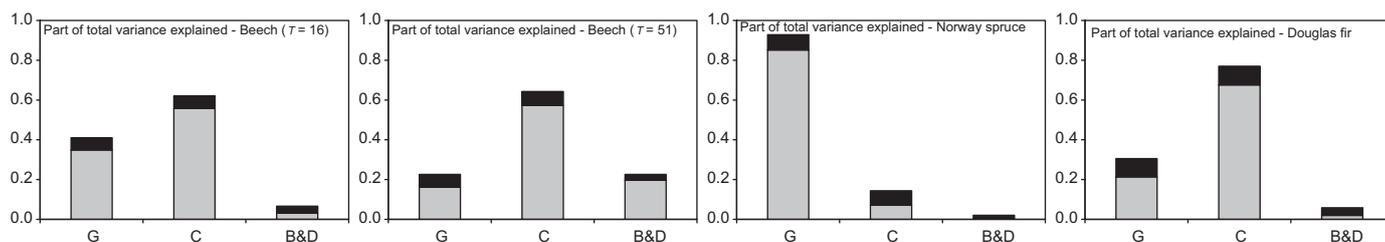
In summary, the competition range parameter  $\beta$ , is most influential followed by the growth parameter  $k$ . An increase of parameter  $\beta$  leads to increased variability in all four cases; the role of  $k$  is less clear, probably because of the complex role of  $k$  in the growth model.

### 4.2. eFAST group analysis

The results of the eFAST group analysis are presented in Fig. 6. They characterise the joint behaviour of the parameters corresponding to the three processes G, C and B&D. Since no births occurred in our time series data as explained in Sections 1 and 2, B&D only reflects mortality in our study.



**Fig. 5.** Proportions of the total variance explained by nine model parameters (Table 1) with regard to the model function,  $\Delta_1$ , analysed by the extended Fourier amplitude sensitivity test (eFAST) method. The grey area (main effect) denotes the portion of total variance explained by the particular parameter alone and the black area (interactions) similarly the part explained by all parameter interactions where the particular parameter is included.



**Fig. 6.** Proportions of the total variance explained by groups of model parameters (Table 1) with regard to the model function,  $\Delta_1$ , analysed by the extended Fourier amplitude sensitivity test (eFAST) method. The grey area (main effect) denotes the portion of total variance explained by the particular parameter alone and the black area (interactions) similarly the part explained by all parameter interactions where the particular parameter is included.

In the beech and Douglas fir forest, the competition parameters contribute most prominently to the total variance of spatial variability characteristic  $\Delta_1$ . By contrast, in the Norway spruce forest, the dominating process is G. Interpreting the heights of the bars of the main effects in Fig. 6, for the beech forest and  $T=51$ , C is three times “more important” than G, i. e. the competition parameters explain three times more variance than the growth parameters. In the case of the longer observation period, B&D is two times more influential than in the case of  $T=16$  on the expense of G. In the Norway spruce forest, G is more than four times more important than competition, whilst B&D plays a minor role. The results of the Douglas fir forest show a pattern similar to that of the beech forest, i.e. C is more than three times more influential than G and B&D plays again an insignificant role.

As with the analysis of single model parameters, parameter interactions are in all cases not particularly strong.

In summary, competition processes mainly influence the spatial variability characteristic  $\Delta_1$ .

## 5. Discussion and conclusions

We developed an explanatory model that enabled us to study the influence of parameters associated with the processes growth (G), inter-plant competition (C) and birth-and-death (B&D) on the spatial variability variable  $\Delta_1$  for three quite different forests. Thus a model-based approach provided a means of examining the influence of ecological processes for larger spatial and longer temporal extents, which hardly can be gained through field experiments. Sensitivity analyses were used to investigate the importance of particular aspects, characterised by model parameters, of the ecological processes G, C and B&D.

The results obtained can be well explained ecologically. It is easy to understand that competition plays a major role in the beech forest and that for the longer observation period mortality is more important than for the shorter. However, it is perhaps surprising that the range of correlation, expressed by parameter  $\beta$ , turned out to be so influential. Increasing  $\beta$  increases the range and strength of competition and thus increases the size differences between dominating and suppressed trees. Therefore it is ecologically plausible that increasing values of  $\beta$  increase spatial variability expressed by  $\Delta_1$ .

We observed the same trend also for the Douglas fir forest. This is a natural forest with a complex structure. Human interventions have been absent from this site for the last 16 years. It is usually assumed that competition processes are of greater importance the more unaffected by human management and the more structurally complex a forest is (Davies and Pommerening, 2008; Pretzsch, 2009). Also, fierce competition for soil water appears to be a serious issue, since the site is located in the interior, dryer parts of British Columbia (LeMay et al., 2009).

The results were different for the Norway spruce forest. Here competition was expected to be less important because the structure of the forest is simple and regular thinnings take place, which

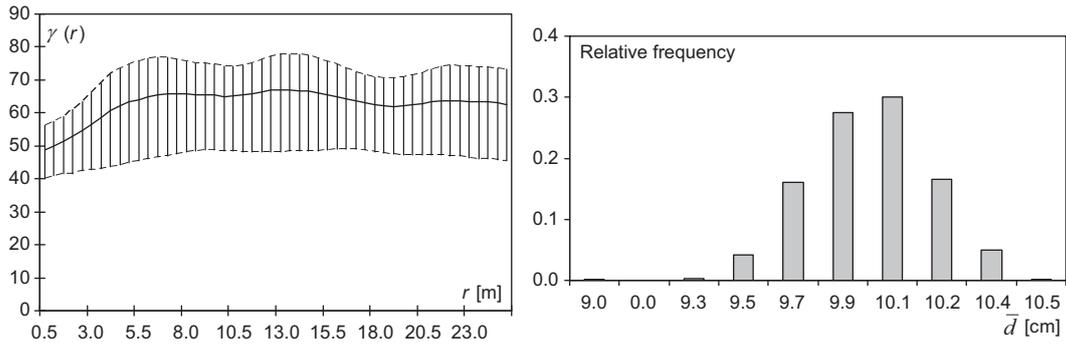
reduce competition. Furthermore, the Norway spruce forest is comparatively young and according to the growth dynamics of this species growth is the most important process at this age. This behaviour was indeed observed, and the short observation period of  $T=10$  may partly explain why mortality is less important.

We applied two methods, the basic one-at-a-time and the more complex eFAST, and obtained similar results. This double-checked our results. OAT provided a simple way of finding the directions in which the parameters influence variability.

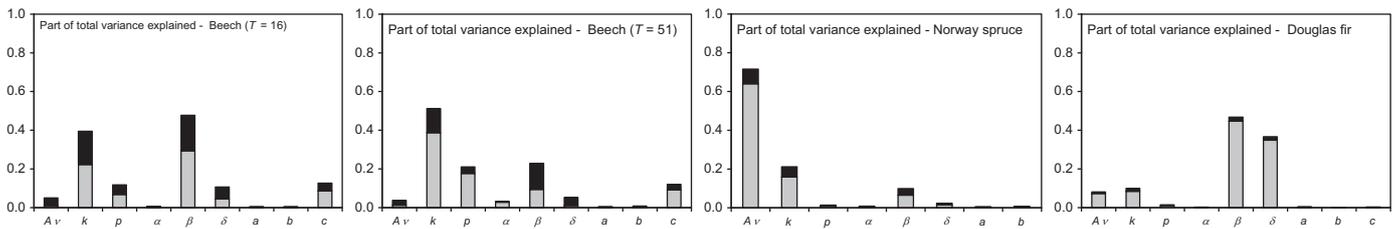
The aim of our study was to understand the influence of ecological process parameters on spatial variability. For this purpose,  $\Delta_1$  was a suitable output variable. For other questions, other output variables may be of value. If the focus of a study is for example on the spatial variability of tree locations only,  $\Delta_1$  may be replaced by a characteristic using the difference of  $K$  functions  $K_0(r)$  and  $K(r)$  in the integral in Eq. (13). And if stem diameters are of primary interest, the difference of diameter distribution functions may play the role of the integral over the difference of mark variograms. (The cumulative nature of the  $K$  function and of the distribution function avoids the integral.)

Our study shows that the initial structure of a forest plays an important role as well as the length of the observation period  $T$ . The former reflects the forest development stage in the beginning, for example stand initiation, stem exclusion, understory reinitiation and old growth stage as defined by Oliver and Larson (1996); depending on the development stage, different processes dominate. For small  $T$ , even large changes of the parameters will cause only small changes in the pattern at the end of the period, while for large  $T$  even small parameter variations can cause great changes. In particular the comparison of the two different observation periods  $T=16$  and  $T=51$  for the beech forest shows that the growth parameter  $k$  is more important for short-term effects on spatial tree patterns, whilst the mortality parameter  $c$  is more influential when long-term effects are studied. As  $k$  scales the growth rate, see Eq. (1), this parameter naturally has a major influence on the diameter growth as shown in the sensitivity analyses; however its role is more complex than that of  $\beta$ , there is no unique reaction to increasing  $k$ .

The results also emphasised the importance of time as a crucial factor in assessing the relative weight of different processes. While growth and competition are continuous processes that take place in every time step, death processes are discrete. They can occur in smaller or larger numbers at one particular point in time and fail to occur for many years afterwards. This may explain why mortality parameters can only assume some importance if a spatial pattern is investigated which is the result of processes of many years, where discrete mortality events accumulate. The study by Ruger et al. (2007) involving observation periods of up to 1000 years supports this view. The reader should note that mortality heavily influences the mark variogram as disappearing trees lead to the isolation of others and potentially to large size differences of neighbouring trees.



**Fig. 7.** The variability of the model results demonstrated for the interior Douglas fir [*Pseudotsuga menziesii* var *glauca* (MIRB.) FRANCO] time series in 2004 after 16 annual simulation periods ( $T=16$ ). Five hundred model runs with the original model parameters from Table 1 were used. *Left:* The mark variograms  $\gamma_0(r)$  (solid line—mean of 500 runs, dashed lines—minima and maxima of 500 runs, bars—mean values  $\pm$  standard deviation). *Right:* Empirical distribution of the mean tree diameter  $\bar{d}$  from 500 runs.



**Fig. 8.** Proportions of the total variance explained by *nine* model parameters (Table 1) with regard to mean diameter,  $\bar{d}$ , analysed by the extended Fourier amplitude sensitivity test (eFAST) method. The grey area (main effect) denotes the portion of total variance explained by the particular parameter alone and the black area (interactions) similarly the part explained by all parameter interactions where the particular parameter is included.

The length of the time interval  $T$  also has an influence on parameter interaction. The results for beech in Figs. 5 and 6 indicated that, in many cases, parameter interactions decrease with increasing  $T$ .

When testing the model behaviour we also explored the variability of the model output and were surprised by its large extent, although the only stochastic element in our IBM was that of the second mortality component (Eq. (9)). Since stochasticity is an important feature of IBMs, our observation should be noted by potential users; such effects have been infrequently reported in other papers on IBMs. As mentioned in Section 3, the authors had to use 500 runs per model run in both sensitivity analysis methods to obtain reliable mean value results for the output variable  $\Delta_1$  (see Fig. 7).

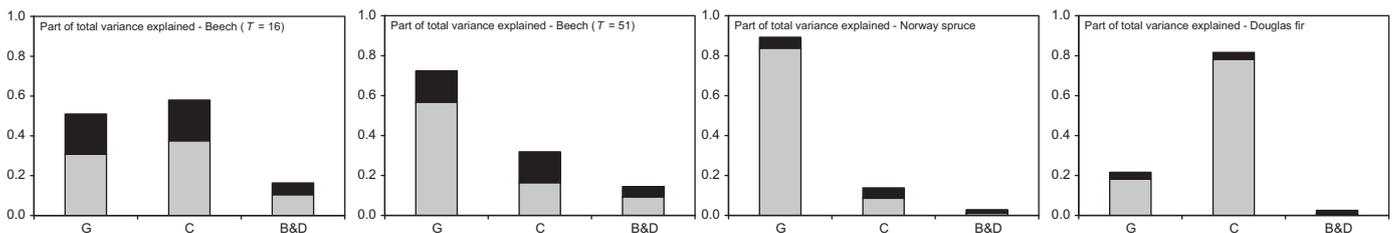
The study results indicate a number of general trends which may be of interest for future investigations. Both the OAT and eFAST analyses identified the range parameter  $\beta$  and the growth parameter  $k$  as the most important model parameters; competition has proved to be an important variability-generating process in all three forests. Since the mark variogram was used, this statement includes both the variability of tree locations and diameters and is supported by other studies such as Davies and Pommerening (2008) and Gray and He (2009). Depending on the development stage of the forest under study, the eFAST analysis highlighted that

competition can be 3–4 times more important than growth and 3–8 times more influential than mortality. These quantitative relations between the three processes can help to better link spatial patterns to development stages (Christensen et al., 2007), since they are likely to take characteristic values in different development stages.

Within the quantification of competition, the range of tree interaction, characterised by our model parameter  $\beta$ , is of particular importance. That the identification and modelling of tree interaction ranges merits attention is an interesting and important message.

In this paper, birth processes were not considered, but with suitable data the same methods could be applied to parameters relating to this process. Two to three more parameters would probably suffice, perhaps one parameter describing the intensity of tree seedlings and another one controlling the degree of clustering (see for example Batista and Maguire, 1998; Nanos et al., 2010).

Finally, the authors also investigated tree density,  $\lambda$ , and mean tree diameter,  $\bar{d}$ , as output variables in addition to  $\Delta_1$ . Both variables do not represent spatial variability. Nevertheless, some of the results of SA are similar to those associated with  $\Delta_1$ .  $\lambda$  is largely influenced by  $\beta$  and  $k$ . The eFAST results for  $\bar{d}$  are shown in Figs. 8 and 9. Again, also for the mean diameter  $\beta$  and  $k$  are the



**Fig. 9.** Proportions of the total variance explained by *groups* of model parameters (Table 1) with regard to mean diameter,  $\bar{d}$ , analysed by the extended Fourier amplitude sensitivity test (eFAST) method. The grey area (main effect) denotes the portion of total variance explained by the particular parameter alone and the black area (interactions) similarly the part explained by all parameter interactions where the particular parameter is included.

most important model parameters in the case of the beech forest, while for the Norway spruce forest the growth parameters  $\lambda$  and  $k$  are dominant and for the Douglas fir forest again the range parameters  $\beta$  and  $\delta$ . The eFAST group analysis (Fig. 9) highlights that  $G$  and  $C$  are almost equally important in the beech forest for  $T=16$ , whilst for  $T=51$  in the same forest  $G$  is three times more important than  $C$ . This again reflects the decisive influence of the observation period, but shows an interesting difference to the behaviour of spatial variability expressed by  $\Delta_1$ . In the Norway spruce forest  $G$  has also by far the greatest influence on  $\bar{d}$ , whilst  $C$  is dominating in the Douglas fir forest. This can be explained by the fact that the Norway spruce forest is in a development stage and age class, where growth processes clearly prevail. By contrast, the Douglas firs (especially the smaller trees) are exposed to fierce competition as mentioned above and this has a marked influence on tree diameters.

Another question, which was beyond the remit of this paper, is the question of parameter correlation. If we considered different forests, we would find, of course, different model parameters as a result of fitting our model. Statistical analysis may show that some of the parameters are correlated. So far we only analysed three forests with the model approach used, therefore it was not possible to carry out a reliable correlation analysis. Therefore we assumed parameter independence in the sensitivity analyses. However, preliminary results of a follow-up investigation suggest that there are strong positive correlations between  $\alpha$  and  $\delta$  while the range parameter  $\beta$  is only weakly correlated with the two other competition parameters. More studies with other forest types are, of course, required to confirm these preliminary results.

This study points to an area of quantitative ecology which deserves more attention and further systematic investigations. The use of an IBM coupled with parameter sensitivity analyses can give insights into ecological processes and their effect on spatial point patterns in forests, but may also provide insights for other plant communities.

## Acknowledgements

The authors thank the Research Committee of the School of the Environment, Natural Resources and Geography (Bangor University, Wales, UK) for the funding of three research visits to Bangor and Freiberg which helped to develop the idea for this paper. A SUTROFOR fellowship funded Valerie LeMay's term at Bangor University in summer 2008. Andreas Zingg (Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland) kindly provided *beech* time series data. Dr Markus Neumann (Austrian Federal Research and Training Centre for Forests, Natural Hazards and Landscape, Vienna, Austria) contributed the *Norway spruce* time series data to this study for which the authors are very grateful. Professor Peter Marshall (University of British Columbia, Vancouver, Canada) kindly made his interior Douglas fir data available for this work. Professor Uta Berger (Dresden Technical University, Germany) supported the study with comments based on her experience with the KiWi growth model and Dr. Volker Grimm (UFZ Centre for Environmental Research Leipzig-Halle, Germany) with comments on the ODD protocol. Dr Nadja Rüger (Dresden Technical University, Germany) and Dr Stefano Tarantola (Joint Research Centre of the European Commission, Ispra, Italy) provided helpful guidance for the use of the SimLab software. Professor Hans Pretzsch offered valuable advice on Eq. (1). Mikey West (Bangor University) has greatly contributed to this study through hardware and network support. We are also very grateful for the valuable and constructive comments of three anonymous reviewers.

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