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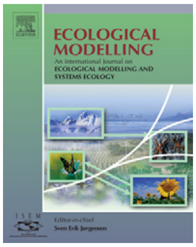

Impact of uncertainty in tree mortality on the predictions of a tropical forest dynamics model

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ABSTRACT

A sensitivity analysis on the impact of uncertainty in tree mortality on the predictions of an individual-based spatially explicit forest dynamics model (SELVA) was performed. The model was developed to investigate the impact of felling (logging) on the demography and structure of tree populations in tropical forests (French Guiana). This study addressed questions about (1) the relative impact on model predictions of uncertainty in mortality processes at different stages of tree development; (2) the interactions between the mortality processes and different felling regimes; and (3) the impact of different felling regimes on the demography and structure of tree populations, taking account of answers to (1) and (2). A global approach of sensitivity analysis based on the decomposition of the output variance was applied. Based on prior knowledge about model uncertainties, mortality processes at the stages germinated seed, standing juvenile, standing adult, and tree-fall were focused as input factors. The input factors were multivariate mortality sub-models involving several parameters with no explicit biological meaning. Thus, an approach based on confidence ellipses of parameter estimates was used to vary input factors homogenously, so that the impact of different input factors on a given model output could be compared. As outputs, the numbers of living, dead and recruited trees, and the tree diameter structure were analysed over 336 years of simulation. An additional local sensitivity analysis provided deeper insights into the relationships between model input and output. The results showed that standing juvenile mortality was the largest source of uncertainty, ahead of standing adult mortality, germinated seed mortality and tree-fall. Moreover, mainly standing juvenile mortality interacted with the felling regime, resulting in changes of the diameter structure of the studied tree population (*Dicorynia guianensis* Amshoff, *Caesalpiniaceae*). Felling all trees $\geq$60 cm diameter of that population every 42 or 84 years was found not sustainable in the long term. But enhancing the description of standing juvenile mortality may alter these predictions. As major conclusions, (i) standing mortality at the juvenile stage should be modelled thoroughly to ensure reliable long-term predictions, and (ii) the interaction of standing juvenile mortality and the felling regime may be an important relationship to be considered in the evaluation of the sustainability of felling regimes.

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1. Introduction

Forest dynamics models are developed to study and predict the evolution of forest ecosystems, or parts of them, under natural or managed conditions (e.g. van Gardingen et al., 2003, 2006; Gourlet-Fleury et al., 2005; Huth et al., 2005; Degen et al., 2006; Köhler and Huth, 2007). Many forest dynamics models aim at addressing complex relationships, such as the temporal and spatial interaction of tree growth, mortality and regeneration processes. Therefore, they integrate a high number of ecological processes that are usually described by just as many sub-models (we refer to the functions or algorithms of one particular process as sub-model). However, some processes such as mortality are modelled under considerable uncertainties: due to the long life-cycle of trees, tree mortality is a rare event (e.g. 1–3% of the living trees, each year, in tropical forests; Condit et al., 1995), and its accurate description requires the regular survey of a huge number of trees. Usually, available samples of dead trees are small (Favrichon, 1998; Alder and Silva, 2000; Phillips et al., 2003; Gourlet-Fleury et al., 2005). Moreover, samples of seed and juvenile mortality are scarce as common forest inventories do not include tree regeneration stages. Thus, a crucial issue is to assess how and to what extent uncertainty in tree mortality at different stages of tree development affects the model output. Moreover, the interaction between tree mortality and human impact, through felling, is an important issue concerning sustainable forest management, particularly in tropical forests (Gourlet-Fleury et al., 2004).

The issue of uncertainty in mortality modelling was addressed for different types of dynamics models for tropical forest stands: matrix models (Picard et al., 2008), cohort models (Alder and Silva, 2000), gap models (Huth and Ditzer, 2000; Kammesheidt et al., 2001) and individual-based spatially explicit models (Phillips et al., 2003). However, to our knowledge, no comprehensive quantitative study focussing on both mortality over a large range of stages of tree development (germinated seed, juvenile, adult) and interaction effects with felling has been reported so far in the literature.

To study this issue, gap models and individual-based spatially explicit models appear more suitable than the other model types, as they rely on a detailed representation of ecological processes and forest structure. Usually, gap models describe growth as an ecophysiological process (Bossel and Krieger, 1994; Köhler and Huth, 1998; Ditzer et al., 2000; Huth and Ditzer, 2000, 2001; Pinard and Cropper, 2000; Kammesheidt et al., 2001; Köhler et al., 2001; Glauner et al., 2003). In contrast, many individual-based spatially explicit models rely on the description of phenomena (e.g. diameter growth) based on observed data (e.g. longitudinal diameter measurements) and theoretical knowledge (e.g. about potential growth and its modification through competition), rather than describing the underlying ecophysiological processes (Gourlet-Fleury, 1997; Moravie et al., 1997; Gourlet-Fleury and Houllier, 2000; Phillips et al., 2003, 2004; Robert, 2003; Gourlet-Fleury et al., 2005; Valle et al., 2007). However, a similarity between the latter models and many gap models is mortality description on the basis of phenomena (e.g. mortality rate or probability based on diameter growth or tree crowding); scientific understanding and data are lacking to describe mortality as an ecophysiological process in gap models (Keane et al., 2001). As a difference, in gap models mortality usually affects the number of trees per gap subunit (canopy layer or tree cohort); in individual-based spatially explicit models mortality usually affects trees more specifically, according to their individual characteristics and environment. Thus, the latter models appear most suitable to study the issue of uncertainty in mortality modelling.

We used the individual-based spatially explicit model of forest dynamics in French Guiana, SELVA (Gourlet-Fleury, 1997; Gourlet-Fleury and Houllier, 2000; Gourlet-Fleury et al., 2005). SELVA allows analysing mortality processes over a large range of stages of tree development unlike other models of the same type. But the results should be of interest also for other forest dynamics models, which rely on a similar basis for mortality description (i.e. phenomena).

How model input uncertainties propagate on the output was investigated using methods of sensitivity analysis, aiming at establishing the relative importance of input factors (Cariboni et al., 2007). We present an approach to deal with the following problem. In sensitivity analysis, input factors, mostly model parameters, are usually varied within a certain range. Parameter ranges may be determined based on the literature and physical boundaries (Huth and Ditzer, 2000; Kammesheidt et al., 2001), or as fixed percentages of default values (Battaglia and Sands, 1998; Paul et al., 2003). This is possible if parameters have an explicit biological meaning such as a mortality rate. However, in SELVA the mortality probability of an individual tree is related to variables charactering the tree and its environment in multivariate (logistic regression) sub-models. Thus, parameters have only implicitly a biological meaning, and another approach to determine parameter ranges is needed.

The results of our study should address the following questions: (Q1) what is the relative impact of mortality processes at different stages of tree development on the predictions of demography and diameter structure of tree populations? Implicitly, the question also asks for the processes to be focused for model enhancement. (Q2) What are the interactions between the mortality processes and different felling regimes? Based on answers to Q1 and Q2, one should be able to better interpret model results with respect to the overall question the model is intended to answer: (Q3) what is the impact of different felling regimes on the demography and structure of tree populations in French Guiana?

2. Materials

2.1. *Model description*

SELVA is implemented in the generic software platform CAPSIS 4.0 (de Coligny, 2008). The construction and functioning of SELVA is described in detail by Gourlet-Fleury (1997), Gourlet-Fleury and Houllier (2000), and Gourlet-Fleury et al. (2005). Model functions and parameters are given in Appendix A.

SELVA simulates the life-cycles of tree species spatialised in a forest stand, including processes of regeneration and

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recruitment, growth and mortality. Any recruited focal tree interacts with its neighbours located within a 30-m radius through competition, described by competition indices. Forest dynamics is simulated using a time step of three years. The tree populations of *Dicorynia guianensis* Amshoff (*Caesalpiniaceae*), the most valuable timber species in French Guiana, and of any other tree species pooled together are distinguished.

Simulation of the life-cycle of *D. guianensis* includes a detailed description of the regeneration and juvenile phases (Fig. 1). Each tree ≥1 cm diameter at breast height (dbh) is given Cartesian coordinates (*x* and *y*). Below this dbh, cohorts of trees within a grid of 10 m × 10 m cells are simulated.

The regeneration phase starts with seed production and dispersal by trees ≥25 cm dbh. Seeds die due to random mortality (fungal rotting and insect predation) and due to distance-dependent mortality (predation by granivorous mammals). Overlapping of seed shadows of neighbouring trees creates crowding places where density-dependent mortality of germinated seeds occurs. The transition of germinated seeds to the juvenile stage includes the stages seedling, sapling (0.5–1 cm dbh) and pre-recruited juvenile (1 cm dbh). Juvenile growth up to the adult stage (increment from 1 to 10 cm dbh) is related to the dbh at the beginning of a three year time step, including stochastic variation. Slower growing juveniles or juveniles occurring in locally denser stand areas suffer increased standing mortality. Additionally, juveniles can be broken by falling neighbours. Starting from 10 cm dbh, the average growth of the adult *D. guianensis* trees is related to the dbh at the beginning of a time step and modified by competition, including stochastic variation. Slower growing or bigger adults suffer increased standing mortality (i.e. adults die standing as opposed to adult tree-fall described below).

The life-cycles of any other species than *D. guianensis* are described for adult trees only (dbh ≥10 cm; Fig. 1). Each tree is given Cartesian coordinates. Recruitment, i.e. the number of new trees, is related to local stand density. Average growth is related to the dbh at the beginning of a time step and modified by competition, including stochastic variation. Slower growing trees suffer increased standing mortality.

Tree-fall deaths of *D. guianensis* and of any other species rely on the same processes. There are three scenarios of tree-fall implemented in SELVA: a focal adult tree can fall alone (primary tree-fall), it can be broken or uprooted by the fall of a neighbouring tree (secondary tree-fall), or it can fall over at the margin of newly created gaps (complex tree-fall). Tree-falls are related to dbh, local stand density or relative position of trees.

The tree populations of *D. guianensis* and of any other species can roughly be characterised by the number of adult trees per ha: about 9 and 610 trees, respectively (figures of year 1999 taken from experimental data specified in Section 2.2).

2.2. Model calibration

SELVA was calibrated based on experimental data from the Paracou field station (5°18′N; 52°53′W) near Sinnamary in French Guiana (Gourlet-Fleury et al., 2004). It has been examined in detail (Gourlet-Fleury, 1997; Gourlet-Fleury and Houllier, 2000; Gourlet-Fleury et al., 2005) concerning logical and biological consistency, statistical properties and error characteristics of model components (evaluation criteria of forest growth models by Vanclay and Skovsgaard, 1997).

However, there are four processes for which few data were available. Parameter values of the corresponding sub-models were empirically adjusted, i.e. chosen or tuned to correctly render ecological knowledge and hypotheses (Gourlet-Fleury et al., 2005). The processes are the density-dependent mortality of germinated *D. guianensis* seeds, the standing mortality of *D. guianensis* juveniles, the standing mortality of *D. guianensis* adults and complex tree-fall (for all species).

2.3. Uncertain mortality processes

The four mortality processes described by empirically adjusted sub-models were supposed a priori to be the most uncertain input factors of SELVA (Fig. 1). Based on these processes, we studied how uncertainty in mortality at different stages of tree development (germinated seed, juvenile and adult) affects model predictions. The equations of the mortality processes (Gourlet-Fleury et al., 2005) are for the density-dependent mortality of germinated *D. guianensis* seeds:

$$m_{\mathrm{gseed}} = \frac{1}{1+\exp^{(a_3\,dens+b_3)}}; \tag{1}$$

the standing mortality of *D. guianensis* juveniles:

$$m_{\mathrm{juv}} = \frac{1}{1+\exp^{(a_6+b_6\,\Delta D+c_6\,G_{30})}}; \tag{2}$$

the standing mortality of *D. guianensis* adults:

$$m_{\mathrm{Dgstanding}} = \frac{1}{1+\exp^{(a_8+b_8\,\Delta D+c_8\,D^{d_8})}}; \text{ and} \tag{3}$$

the complex tree-fall for adults of all species:

$$m_{\mathrm{fall3}} = \frac{1}{1+\exp^{(a_{11}+b_{11}\,G_{30})}}. \tag{4}$$

When a tree ≥40 cm dbh falls, e.g. due to primary tree-fall, the sub-model of complex tree-fall (Eq. (4)) gives, for each neighbouring tree of the falling tree, its probability to fall over as well. The explanatory variables in Eqs. (1)–(4) are: *dens* = number of germinated seeds per 10 m × 10 m cell, ΔD = mean annual dbh increment (cm/year) during the previous three year time step, G_{30} = local basal area, i.e. total cross-sectional area (m^2/ha) at 1.3 m height of trees ≥10 cm dbh located ≤30 m from the focal tree, and D = dbh (cm) at the beginning of a time step. The parameters are a_3, b_3, a_6, b_6, c_6, a_8, b_8, c_8, d_8, a_{11} and b_{11} (Table 1 and Appendix A). Notations are the same as in Gourlet-Fleury et al. (2005).

2.4. Felling regime

Felling focused on *D. guianensis* as the most valuable timber species in French Guiana. The parameters of the felling regime

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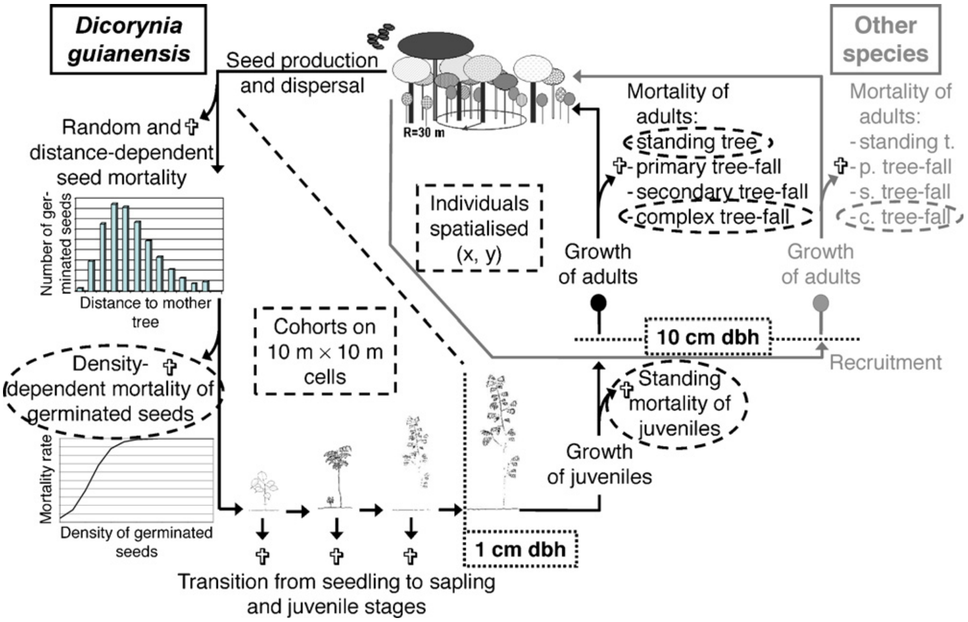

Fig. 1 – Outline of the sequence of ecological processes in SELVA describing the life-cycles (regeneration starting from seed production, recruitment, growth and mortality) of *D. guianensis* (black arrows and notations) and of any other species pooled together (grey arrows and notations). Tree-falls of both *D. guianensis* and any other species rely on the same processes while all other processes are specific either to *D. guianensis* or to any other species. *D. guianensis* trees are simulated as cohorts on 10 m × 10 m cells below 1 cm diameter at breast height (dbh), and as spatialised individuals above. Trees of any other species are simulated above 10 cm dbh as spatialised individuals. Individuals of *D. guianensis* and/or of any other species interact with each other through competition. Competition is exerted upon a focal tree by neighbours located within a 30-m radius. Dashed loops indicate the most uncertain mortality processes.

are the minimum diameter cutting limit (*DCL*) and the duration of felling cycles (*FC*). At a given point in time t after the beginning t_0 of a simulation run, either felling ($F = 1$) or no felling ($F = 0$) occurs according to the following algorithm:

$$F = \begin{cases} 1 & \text{if } t = t_0 + kFC, \quad k \in N - \{0\} \\ 0 & \text{otherwise} \end{cases} . \tag{5}$$

In the case of felling ($F = 1$), all *D. guianensis* trees $\geq DCL$ are removed.

3. Methods

3.1. *Scope of sensitivity analysis*

SELVA includes several deterministic, stochastic and non-linear sub-models (Appendix A). For a given model parameterisation, simulation runs must be repeated to account for the variability generated by the stochastic components of the sub-models. Hence, a global approach of sensitivity analysis was required that was free from linearity, additivity and monotonicity assumptions of the model (Cariboni et al., 2007). As a definition, global approaches assess the effect, on a given

Table 1 – Parameter values of the settings “high mortality”, “low mortality” and “default mortality” for the sub-models of the processes germinated seed mortality, standing juvenile mortality, standing adult mortality and complex tree-fall

Process	High mortality	Low mortality	Default mortality
Germinated seed mortality	$a_3 = -0.03$ $b_3 = 2.25$	$a_3 = -0.02$ $b_3 = 3.75$	$a_3 = -0.025$ $b_3 = 3$
Standing juvenile mortality	$a_6 = 2.35$ $b_6 = 6.5$ $c_6 = -0.12$	$a_6 = 2.75$ $b_6 = 17.5$ $c_6 = -0.08$	$a_6 = 2.55$ $b_6 = 12$ $c_6 = -0.1$
Standing adult mortality	$c_8 = -0.0044$ $d_8 = 1.49$	$c_8 = -0.0024$ $d_8 = 1.33$	$c_8 = -0.0034$ $d_8 = 1.41$
Complex tree-fall	$a_{11} = 2.251$ $b_{11} = 0.093$	$a_{11} = 3.517$ $b_{11} = 0.271$	$a_{11} = 2.884$ $b_{11} = 0.182$

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model output, of an input factor when all the other input factors are varying. By contrast, in local approaches the effect of the variation of one single input factor is assessed while the other input factors are fixed to their default values (Cariboni et al., 2007). Global approaches enable to quantify interactions between input factors, which was necessary to answer question Q2.

3.2. *Global sensitivity measures*

To quantify the impact of one or several input factors on the variability of a given model output, we used sensitivity measures based on the decomposition of the output variance. Let $Y = f(X_1, X_2, X_3, X_4, X_5)$ be the model function that relates the five studied input factors X_1, X_2, X_3, X_4 and X_5 (i.e. the five sub-models: four uncertain mortality processes and felling regime) to an output Y. Referring to Saltelli et al. (2004) and Jacques (2005), the impact of an input factor X_i on the variance of Y can be evaluated as the decrease of the variance of Y if X_i is fixed to a given value x_i^* (i.e. if the parameters of a sub-model are fixed to given values): $V(Y|X_i = x_i^*)$. Given the problem of choosing the value of x_i^*, the expectation for all possible values of x_i^* is calculated: $E[V(Y|X_i)]$. The higher $E[V(Y|X_i)]$, the lower is the impact of X_i on Y. Considering the theorem of the total variance $V(Y) = V[E(Y|X_i)] + E[V(Y|X_i)]$, the term $V[E(Y|X_i)]$, instead of $E[V(Y|X_i)]$, is preferred as an indicator of the sensitivity of Y to X_i, since the higher the impact of X_i, the higher is the value of the indicator. Finally, the measure of sensitivity of Y to X_i is defined by normalising this indicator by the total output variance $V(Y)$:

$$S_i = \frac{V[E(Y|X_i)]}{V(Y)} \tag{6}$$

This measure corresponds to the first-order sensitivity index by Sobol' (1990). Referring to Saltelli et al. (2004), the impact of the interaction between two orthogonal input factors on the output Y can be defined in terms of conditional variances as well, and the conditional variances can be considered in the context of the general variance decomposition scheme proposed by Sobol' (1990). Hence, in the present study second and third order measures S_{ij} and S_{ijm} were calculated to evaluate the interaction of two input factors X_i, X_j and three input factors X_i, X_j, X_m on the output Y, respectively:

$$S_{ij} = \frac{V_{ij}}{V(Y)} \tag{7}$$

and

$$S_{ijm} = \frac{V_{ijm}}{V(Y)}, \tag{8}$$

where

$$V_i = V[E(Y|X_i)], \tag{9}$$

$$V_{ij} = V[E(Y|X_i, X_j)] - V_i - V_j, \tag{10}$$

and

$$V_{ijm} = V[E(Y|X_i, X_j, X_m)] - V_{ij} - V_{im} - V_{jm} - V_i - V_j - V_m. \tag{11}$$

In the case of repeated simulation of a given model parameter setting, the inner means (approximation of E) were calculated separately for each repetition, and the outer variance V was calculated based on the inner means of all repetitions. Input factors were considered to have an important impact if their sensitivity measures (S_i, S_{ij}, S_{ijm}) were higher than an arbitrarily fixed threshold of 0.10.

3.3. *Additional local sensitivity analysis*

For a given input factor with considerable impact on an output variable ($S_i > 0.10$), the evolution of the output variable over time was plotted for the different values of the input factor. All other input factors had the default values (local sensitivity analysis; Section 3.1).

3.4. *Variation of input factors*

As an explicit biological meaning could not be assigned to the individual parameters of the mortality sub-models (Section 1), we defined for each sub-model (Eqs. (1)–(4)) three settings of parameter values: the default values (called "default mortality"), parameter values implementing a higher mortality than the default values ("high mortality") and parameter values implementing a lower mortality than the default values ("low mortality"). In this way, the impact of the mortality processes could be interpreted easily from an ecological point of view.

However, there was the risk to bias the comparison between the processes through the choice of the parameter values for each setting. For instance, for a relatively large range between "high mortality" and "low mortality" for standing adult mortality, and a relatively small range for standing juvenile mortality, one may obtain a higher impact of standing adult mortality than of standing juvenile mortality, and vice versa. Thus, to be able to compare the impact of different processes, parameter ranges (Table 1) had to be determined in a homogenous manner. This applied both to parameters of different processes and to different parameters of a single process. We dealt with this problem as described hereafter.

3.4.1. *Germinated seed mortality*

The rate of density-dependent mortality of germinated seeds (m_{gseed}, Eq. (1)) was plotted versus simulated values of the number of germinated seeds per 10 m × 10 m cell (*dens*; Fig. 2). Starting from the curve of "default mortality", parameter values were varied to obtain the curves of "high mortality" and "low mortality". As a backing, the ratio of the partial derivates of the parameters a_3 and b_3 ($(\partial m_{\text{gseed}}/\partial a_3)/(\partial m_{\text{gseed}}/\partial b_3)$) was taken into account. For instance, starting from a chosen variation of b_3, the ratio was used to assess the order of magnitude for varying a_3. In general, for the four mortality processes analysed, parameter values of "high mortality" and "low mortality" were determined in such a way to maintain the meaning of each processes, e.g. an increase of m_{gseed} with *dens* in the case of germinated seed mortality.

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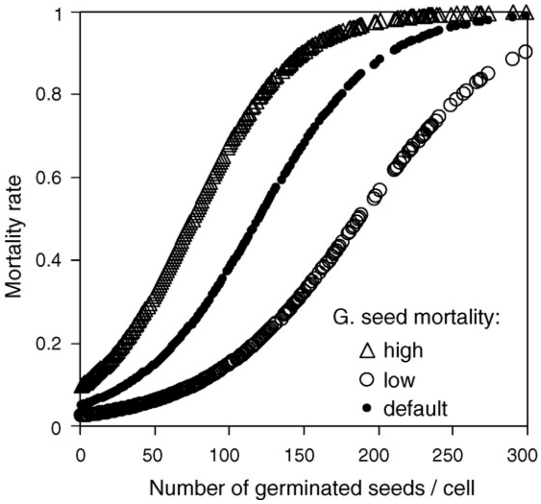

Fig. 2 – Plot of the rate of density-dependent mortality of germinated *D. guianensis* seeds versus simulated values of the number of germinated seeds per 10 m × 10 m cell (m_{gseed} versus *dens*; Eq. (1)) for the parameter settings "high mortality", "low mortality" and "default mortality".

3.4.2. *Standing juvenile and adult mortalities*

In contrast to germinated seed mortality, which was a deterministic sub-model, standing juvenile and adult mortalities were stochastic sub-models. Hence, data could be simulated to estimate confidence intervals of default parameter values, and thus to determine the parameter values of "high mortality" and "low mortality" as the bounds of the confidence intervals.

For the standing mortality of *D. guianensis* adults (Eq. (3)), only the parameters c_8 and d_8 were varied while the parameters a_8 and b_8 were fixed to their default values. This was done as c_8 and d_8 were adjusted empirically while a_8 and b_8 were based on experimental data (Gourlet-Fleury et al., 2005).

To estimate confidence intervals of default values of the parameters of standing juvenile mortality (Eq. (2); a_6, b_6, c_6) and standing adult mortality (Eq. (3); c_8, d_8), 70 simulation runs with the default parameter settings were performed. For each juvenile and adult tree, the explanatory variables of m_{juv} and $m_{\text{Dgstanding}}$ (Eqs. (2) and (3)) were recorded at the beginning of a time step, respectively. At the end of the step, the status (living or dead) of each tree was recorded (the data was recorded after the model outputs had stabilised; Section 3.6). Based on this data, 70 estimates were obtained a posteriori for each of the parameters a_6, b_6, c_6 and c_8, d_8 of Eqs. (2) and (3), using maximum likelihood estimation in the SAS 9.1 (SAS Institute, Cary, USA) and R 2.4.1 (R Development Core Team, 2006) software packages, respectively. Out of the 70 estimates, 64 and 50 estimates of each of the parameters of Eqs. (2) and (3) were used in subsequent analyses after elimination of non-plausible values, respectively. Finally, confidence ellipses (at the 10% level) were plotted for the parameters of each sub-model. Each ellipse was centred on the default parameter values and its shape was given by the covariance of the parameter estimates.

For standing adult mortality (Eq. (3)), the intervals of $c_8 = [-0.0044, -0.0024]$ and $d_8 = [1.33, 1.49]$ were determined by projecting the intersection points of the minor axis of the ellipse on the abscissa and ordinate axes, respectively (Fig. 3). The intersection points of the minor axis of the ellipse were chosen since their projections lead to reasonable parameter intervals. This was assessed by plotting predicted probabilities for "high mortality" and "low mortality" using the bounds of the intervals of c_8 and d_8 as parameter values (Fig. 3).

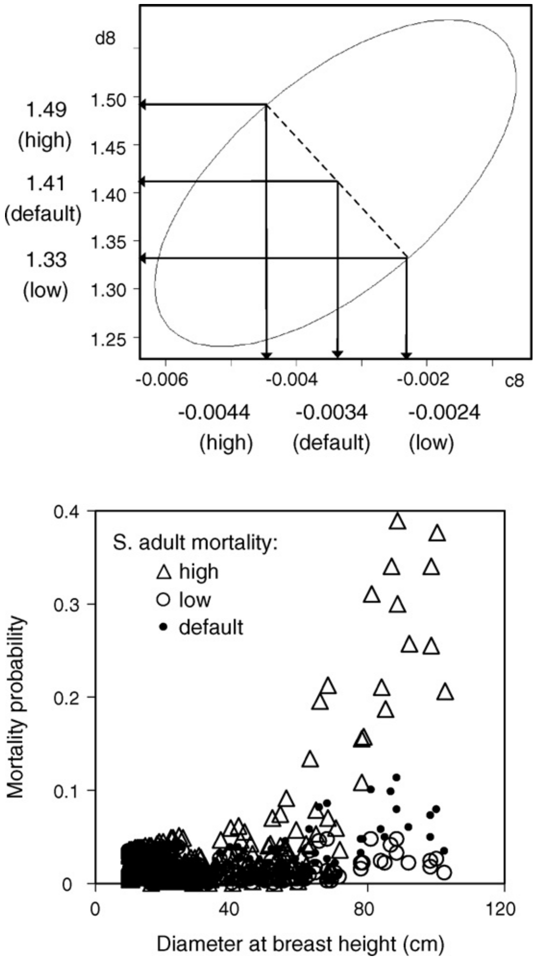

Fig. 3 – Plot above: confidence ellipse (at the 10% level) of parameters d_8 versus c_8 of the standing mortality of *D. guianensis* adults. The ellipse was centred on the default values of c_8 and d_8, and the shape of the ellipse was given by the covariance of 50 estimates of both c_8 and d_8. The values of c_8 and d_8 for "high mortality" and "low mortality" were determined by projecting the intersection points between the ellipse and its minor axis (dashed line) on the abscissa and ordinate axes. Plot below: probability of standing mortality of *D. guianensis* adults versus diameter at breast height ($m_{\text{Dgstanding}}$ versus *D*; Eq. (3)) for the parameter settings "high mortality" and "low mortality" as determined in the plot above, and for the default parameter setting.

For standing juvenile mortality (Eq. (2)), confidence ellipses were plotted for each couple of parameters: c_6 versus a_6, b_6 ver-

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sus a_6 and c_6 versus b_6. Starting from the ellipse of c_6 versus a_6, as it was strongly oval and elongated (i.e. the parameters were clearly correlated) unlike the other ellipses, the intervals of a_6 and c_6 were determined in the same way as for standing adult mortality, i.e. by referring to the minor axis of the ellipse. Then, the bounds of the intervals of a_6 and c_6 were projected on each of the other ellipses, and the intersection points on each ellipse were projected on the axis of b_6. In this way, two intervals for b_6 were obtained: [6.0, 18.0] and [6.5, 17.5]. As they were very similar, one of them could be chosen arbitrarily: $b_6 = [6.5, 17.5]$. Alternatively, an ellipsoid could have been plotted, but we preferred the two-dimensional approach as it was simpler and clearer.

Ranges of parameter values of standing juvenile and adult mortalities were determined in a homogenous manner based on the minor axes of confidence ellipses.

3.4.3. *Complex tree-fall*

The sub-model of complex tree-fall (Eq. (4)) was a part of the sub-model of primary tree-fall (Gourlet-Fleury, 1997). That is, both sub-models had the same default parameter values for a_{11} and b_{11}, but the sub-model of primary tree-fall had additional parameters. For the sub-model of primary tree-fall, parameters a_{11} and b_{11} were estimated based on experimental data, and the standard deviations of the parameter estimates were known (Gourlet-Fleury, 1997). Based on this, confidence intervals (at the 10% level) of the parameter estimates were calculated assuming a normal distribution of parameter estimates. The bounds of the confidence intervals were chosen as parameter values of the parameter settings “high mortality” and “low mortality”.

3.4.4. *Felling regime*

The parameter *DCL* (Eq. (5)) was fixed at 60 cm in accordance with current forestry practice in French Guiana. Felling is currently planned every 60 years. Considering this, parameter values $FC = 42$ years and $FC = 84$ years were chosen as settings for more frequent felling and less frequent felling, respectively. As a reference (default parameter setting), no felling was performed.

3.5. *Output variables*

Germinated seed, standing juvenile and standing adult mortalities (Eqs. (1)–(3)) were specific to the *D. guianensis* population, while complex tree-fall (Eq. (4)) applied to both the *D. guianensis* population and the population of any other species (Sections 2.1 and 2.3). We chose output variables to characterise both populations (Table 2).

3.6. *Simulation runs*

Simulation runs were based on a 36.36-ha study area, the so-called Southern Block of the Paracou field station. In this area, extensive forest inventory data was gathered in 1999. Starting simulation from this data, the curves of the output variables $N10_{Dg}$ and $N60_{Dg}$ (Table 2) over time firstly oscillate, but then stabilise after several hundreds of years (Gourlet-Fleury et al., 2005). Considering this, all simulation runs of the sensitivity analysis started after the stabilisation period, 999 years after 1999, from the same forest stand simulated with the default parameter settings. The starting year after stabilisation was set to $t_0 = 0$ year and simulation time was 336 years.

3.6.1. *Complete factorial design*

First we applied a complete factorial design: five input factors with three parameter settings each, leading to 243 combinations. Each of the 243 combinations was simulated three times to account for the stochasticity of SELVA, resulting in 729 simulation runs. Sensitivity measures (Section 3.2) were calculated at regular time intervals: $t_0 + 81$ years, $t_0 + 165$ years, $t_0 + 249$ years and $t_0 + 333$ years. These dates corresponded to the years just before felling (84-years cycles) and just before every second felling (42-years cycles) when the population recovery after felling reached its maximum.

3.6.2. *Fractional factorial design*

Based on the results of the complete factorial design, we selected a reduced number of the most important combinations of parameter settings. Each of these combinations was simulated 20 times to obtain more robust results. In this fractional factorial design only those input factors were included whose sensitivity measures (S_i, S_{ij} or S_{ijm} at $t_0 + 81$ years, $t_0 + 165$ years, $t_0 + 249$ years or $t_0 + 333$ years) were higher than the threshold of 0.10 (Section 3.2). Applying this criterion (to the results of the complete factorial design given in Table 3 of Section 4), germinated seed mortality was not included in the fractional factorial design. Moreover, the fractional factorial design could be limited to the analysis of the impacts of standing juvenile mortality, standing adult mortality and felling regime on the output variables for the *D. guianensis* population, and of the impact of complex tree-fall on the output variables for the population of any other species (Table 2). Hence, all possible combinations of parameter settings of standing juvenile mortality, standing adult mortality and felling regime were simulated: three input factors with three parameter settings each, leading to 27 combinations. It was necessary to simulate all possible combinations of parameter settings to be able to correctly calculate the sensitivity measures. For complex tree-fall, sensitivity measures were not calculated since it was the only input factor having an impact on the output variables for the population of any other species (Table 3). Instead, two combinations were simulated: the parameter settings “high mortality” and “low mortality”, where the parameter settings of all other input factors were set to their default values. Note that a combination with the default parameter settings of both complex tree-fall and all other input factors was already included in the combinations of parameter settings of standing juvenile mortality, standing adult mortality and felling regime. This was done to perform an additional local sensitivity analysis (Section 3.3) of complex tree-fall, but also of standing juvenile mortality, standing adult mortality and felling regime. In total, the fractional factorial design included 29 combinations, each of which was simulated 20 times, resulting in 580 simulation runs.

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Table 2 – Output variables for the *D. guianensis* population and the population of any other species

Population	Output variable	Definition
D. guianensis	$N10_{Dg}$	Number of trees ≥10 cm dbh per ha
	$N60_{Dg}$	Number of trees ≥60 cm dbh per ha
	$M10_{Dg}$	Mean number of trees per ha and year that died during a three year simulation time step (trees ≥10 cm dbh)
	$R10_{Dg}$	Mean number of trees per ha and year that were recruited during a three year simulation time step (trees ≥10 cm dbh)
	χ^2_{Dg}	Dbh structure in year *t* after the starting year t_0 of a simulation run, characterised by the Chi-square statistic comparing the dbh structures in years *t* and t_0. Dbh classes: 1–5 cm, 5–10 cm,. . ., 65–70 cm, ≥70 cm
Other species	$N10_{OS}$	Number of trees ≥10 cm dbh per ha
	$N60_{OS}$	Number of trees ≥60 cm dbh per ha

dbh = diameter at breast height.

Table 3 – Global sensitivity measures of first order effects (S_i) of the input factors germinated seed mortality (gsm), standing juvenile mortality (sjm), standing adult mortality (sam), complex tree-fall (ct) and felling regime (fr) on all output variables

Output variable	Year t_0+	Sensitivity measures S_i with i = input factor					
		i = gsm	i = sjm	i = sam	i = ct	i = fr	Total
$N10_{Dg}$	81	0.01	**0.87**	0.03	0.05	0.01	0.99
	165	0.06	**0.65**	0.06	0.04	0.04	0.99
	249	0.06	**0.57**	0.06	0.04	0.06	0.99
	333	0.07	**0.52**	0.06	0.04	0.05	0.99
$N60_{Dg}$	81	0.00	0.00	**0.50**	0.02	**0.25**	0.94
	165	0.00	0.01	**0.45**	0.10	**0.20**	0.95
	249	0.02	**0.32**	**0.23**	0.08	**0.12**	0.97
	333	0.04	**0.27**	**0.14**	0.05	0.10	0.98
$M10_{Dg}$	81	0.01	**0.60**	0.01	0.01	0.01	0.82
	165	0.07	**0.63**	0.02	0.01	0.04	0.91
	249	0.08	**0.60**	0.03	0.01	0.05	0.94
	333	0.07	**0.59**	0.04	0.02	0.05	0.97
$R10_{Dg}$	81	0.07	**0.76**	0.01	0.01	0.00	0.97
	165	0.06	**0.55**	0.04	0.01	0.07	0.95
	249	0.06	**0.57**	0.04	0.02	0.07	0.96
	333	0.07	**0.54**	0.04	0.02	0.06	0.97
χ^2_{Dg}	81	0.04	**0.58**	0.01	0.02	0.04	0.94
	165	0.01	**0.60**	0.02	0.04	0.01	0.94
	249	0.03	**0.13**	0.05	0.03	0.05	0.86
	333	0.01	0.08	0.02	0.02	0.05	0.71
$N10_{OS}$	81	0.01	0.08	0.03	**0.25**	0.02	0.71
	165	0.01	0.03	0.01	**0.79**	0.02	0.93
	249	0.01	0.04	0.01	**0.85**	0.02	0.97
	333	0.01	0.06	0.01	**0.79**	0.03	0.97
$N60_{OS}$	81	0.00	0.00	0.00	**0.86**	0.00	0.93
	165	0.00	0.00	0.00	**0.94**	0.00	0.97
	249	0.00	0.00	0.00	**0.95**	0.01	0.98
	333	0.00	0.00	0.00	**0.94**	0.01	0.98

Second (S_{ij}) and third (S_{ijm}) order effects are not given as all but one of them were not above the threshold of 0.10 for important impact. The second order effect above the threshold was $S_{i=sjm,\, j=fr} = 0.11$ for χ^2_{Dg} in year 249. Total is the sum of all first, second and third order effects. Definitions of output variables: Table 2. The results are based on 243 combinations of parameter settings of the sub-models for germinated seed mortality, standing juvenile mortality, standing adult mortality, complex tree-fall and felling regime. Each combination was simulated three times. Simulation time was 336 years, sensitivity measures are given for years 81, 165, 249 and 333. Sensitivity measures >0.10 are indicated in bold.

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4. Results

4.1. *Complete factorial design*

Global sensitivity measures of germinated seed mortality were below the threshold of 0.10 (Section 3.2) for all output variables (Table 3); sensitivity measures of standing juvenile mortality, standing adult mortality and felling regime were above this threshold for at least one of the output variables for the *D. guianensis* population, but for none of the output variables for the population of any other species; and sensitivity measures of complex tree-fall were above this threshold for the output variables of the population of any other species only. Thus, germinated seed mortality was excluded from the fractional factorial design of the most important combinations of parameter settings (Section 3.6). The final results based on the latter design are described hereafter.

4.2. *Fractional factorial design*

4.2.1. *D. guianensis population*

Regarding the relative importance of input factors, the results of the complete factorial design (Table 3) were basically confirmed by those of the fractional factorial design (Table 4).

Out of standing juvenile mortality, standing adult mortality and felling regime, standing juvenile mortality had a considerable impact on all of the output variables for the *D. guianensis* population (first order effects $S_{i=\text{sjm}} > 0.10$ for $N10_{Dg}$, $N60_{Dg}$, $M10_{Dg}$, $R10_{Dg}$ and χ^2_{Dg}; Table 4). Also, the highest values of global sensitivity measures were found for standing juvenile mortality. Furthermore, standing adult mortality and felling regime had a clear impact on $N60_{Dg}$ (first order effects $S_{i=\text{sam}}$ and $S_{i=\text{fr}}$). The felling regime had also an impact on χ^2_{Dg}. Interaction effects were clearly lower than first order effects for most output variables, with few exceptions including in particular χ^2_{Dg}: there was a joint impact of standing juvenile and adult mortalities on χ^2_{Dg} (second order effect $S_{i=\text{sjm},j=\text{sam}}$), of standing juvenile mortality and felling regime on χ^2_{Dg} ($S_{i=\text{sjm},j=\text{fr}}$), of standing adult mortality and felling regime on $N60_{Dg}$ ($S_{i=\text{sam},j=\text{fr}}$), and of standing juvenile mortality, standing adult mortality and felling regime on $M10_{Dg}$ and χ^2_{Dg} (third order effect $S_{i=\text{sjm},j=\text{sam},m=\text{fr}}$). A closer look at these relationships is provided hereafter.

4.2.1.1. *Number of trees ≥10 cm dbh per ha ($N10_{Dg}$).* The first order effects of standing juvenile mortality ($S_{i=\text{sjm}}$) on $N10_{Dg}$ decreased systematically from year 81 to 249, and they were the same in years 249 and 333 (Table 4). However, in year 333 uncertainty in standing juvenile mortality still accounted for $S_{i=\text{sjm}} = 0.75$ of the total variance of $N10_{Dg}$. The local sensitivity analysis (Section 3.3) showed for the setting "high mortality" of standing juvenile mortality a decrease of $N10_{Dg}$ over time (Fig. 4). But the curve of $N10_{Dg}$ flattened after about year 200, and reached values close to 0 at the end of the simulation time (year 336). For the setting "low mortality", the curve of $N10_{Dg}$ increased without flattening.

4.2.1.2. *Number of trees ≥60 cm dbh per ha ($N60_{Dg}$).* Standing juvenile mortality had almost no impact on $N60_{Dg}$ in years 81 and 165, but the highest impact on $N60_{Dg}$ in years 249 and 333 out of all input factors (first order effects $S_{i=\text{sjm}}$; Table 4). In contrast, first order effects of standing adult mortality and felling regime on $N60_{Dg}$ were higher in years 81 and 165 compared with years 249 and 333. Besides, standing adult mortality and felling regime had a low joint impact on $N60_{Dg}$ in years 81 and 165 ($S_{i=\text{sam},j=\text{fr}} = 0.12$ and $S_{i=\text{sam},j=\text{fr}} = 0.11$, respectively; Table 4). Overall, the parameter settings "high mortality" of both standing juvenile mortality and standing adult mortality resulted in a decrease of $N60_{Dg}$, and the settings "low mortality" in an increase of $N60_{Dg}$ over time (Fig. 5). However, the curves of $N60_{Dg}$ flattened after about 60 and 200 years for the settings "high mortality" and "low mortality" of standing adult mortality, respectively. Moreover, the impact of standing adult mortality on $N60_{Dg}$ was immediate while the impact of standing juvenile mortality was delayed. The delay corresponded to the time for the growth of juveniles, which survived after the application of standing juvenile mortality, until the dbh threshold of 60 cm ($N60_{Dg}$ = number of adult trees ≥60 cm dbh per ha). In contrast, standing adult mortality had an impact on $N60_{Dg}$ immediately after year 0. The same explanation applies to the differences in first order effects between years 81–165 and 249–333 highlighted above. About the felling regime (Fig. 5), the *D. guianensis* population ≥60 cm dbh ($N60_{Dg}$) did not completely recover within the felling cycles of 42 and 84 years, resulting both in a stepwise decrease of $N60_{Dg}$ over time. However, higher levels of $N60_{Dg}$ were maintained at the ends of 84-years cycles than at the ends of 42-years cycles.

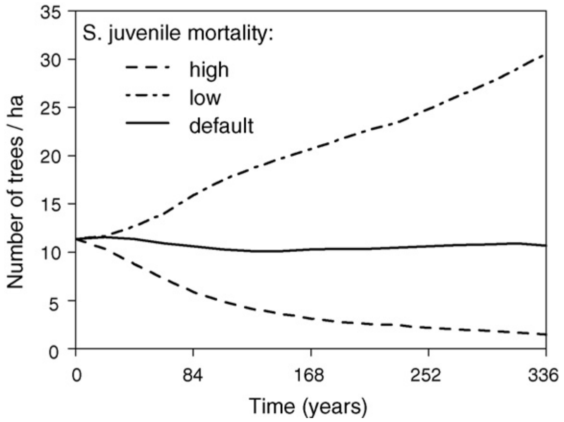

Fig. 4 – Evolution of the number of *D. guianensis* trees ≥10 cm dbh per ha (*$N10_{Dg}$*) over time for the parameter settings "high mortality", "low mortality" and "default mortality" of the standing mortality of *D. guianensis* juveniles. The parameters of the other sub-models of SELVA were fixed to their default values. Values of *$N10_{Dg}$* are means of 20 repetitions outputted every 21 years. Interpolation between mean values is linear.

4.2.1.3. *Number of dead trees per ha and year ($M10_{Dg}$) and number of recruited trees per ha and year ($R10_{Dg}$).* First order effects of standing juvenile mortality on $M10_{Dg}$ and $R10_{Dg}$ for years 81–333 accounted for $S_{i=\text{sjm}} \approx 0.7$ of the total variances of each of the output variables. Differences in $S_{i=\text{sjm}}$ occurred

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Table 4 – Global sensitivity measures of first (S_i), second (S_{ij}) and third (S_{ijm}) order effects of the input factors standing juvenile mortality (sjm), standing adult mortality (sam) and felling regime (fr) on the output variables for the *D. guianensis* population

Output variable	Year t_0+	Sensitivity measures S_i, S_{ij}, S_{ijm} with i, j, m = input factor							
		i = sjm	i = sam	i = fr	i = sjm, j = sam	i = sjm, j = fr	i = sam, j = fr	i = sjm, j = sam, m = fr	Total
$N10_{Dg}$	81	**0.94**	0.03	0.01	0.00	0.00	0.00	0.01	1.00
	165	**0.82**	0.07	0.05	0.03	0.02	0.01	0.01	1.00
	249	**0.75**	0.08	0.07	0.04	0.04	0.01	0.01	1.00
	333	**0.75**	0.07	0.07	0.05	0.04	0.01	0.01	1.00
$N60_{Dg}$	81	0.02	**0.53**	**0.26**	0.02	0.02	**0.12**	0.05	1.00
	165	0.04	**0.53**	**0.24**	0.02	0.02	**0.11**	0.05	1.00
	249	**0.40**	**0.28**	**0.14**	0.05	0.02	0.08	0.03	1.00
	333	**0.38**	**0.18**	**0.14**	0.10	0.08	0.07	0.04	1.00
$M10_{Dg}$	81	**0.64**	0.04	0.04	0.05	0.04	0.05	**0.14**	1.00
	165	**0.73**	0.03	0.06	0.04	0.03	0.03	0.07	1.00
	249	**0.73**	0.05	0.07	0.03	0.05	0.02	0.05	1.00
	333	**0.75**	0.05	0.07	0.03	0.04	0.02	0.03	1.00
$R10_{Dg}$	81	**0.89**	0.02	0.01	0.02	0.01	0.02	0.04	1.00
	165	**0.65**	0.06	0.10	0.04	0.07	0.03	0.05	1.00
	249	**0.73**	0.06	0.08	0.04	0.04	0.02	0.04	1.00
	333	**0.72**	0.06	0.07	0.04	0.05	0.02	0.03	1.00
χ^2_{Dg}	81	**0.64**	0.03	0.09	0.07	**0.12**	0.02	0.05	1.00
	165	**0.68**	0.04	0.02	0.09	0.08	0.03	0.06	1.00
	249	**0.23**	0.08	**0.11**	**0.15**	**0.20**	0.07	**0.14**	1.00
	333	**0.16**	0.09	**0.15**	**0.16**	**0.15**	0.09	**0.20**	1.00

Definitions of output variables: Table 2. The results are based on 27 combinations of parameter settings of the sub-models for standing juvenile mortality, standing adult mortality and felling regime (parameters of the sub-models for germinated seed mortality and complex tree-fall were fixed to their default values). Each combination was simulated 20 times. Simulation time was 336 years, sensitivity measures are given for years 81, 165, 249 and 333. Sensitivity measures >0.10 are indicated in bold.

mainly between years 81 and 165–333 (Table 4). Also, there was a low joint impact of standing juvenile mortality, standing adult mortality and felling regime on $M10_{Dg}$ in year 81. For the parameter setting "high mortality", both $M10_{Dg}$ and $R10_{Dg}$ decreased with increasing simulation time; the curves of $M10_{Dg}$ and $R10_{Dg}$ flattened after about 200 and 60 years, respectively; and it was $M10_{Dg} > R10_{Dg}$ at a given point in time, especially between years 0 and 200 (Fig. 6). The latter was related to the decrease of $N10_{Dg}$ (Fig. 4) for the same setting ("high mortality"), since $N10_{Dg}$ in year t resulted from $N10_{Dg}$ in year $t-3$ minus the number of dead trees ($M10_{Dg}$) plus the number of new trees ($R10_{Dg}$). For the parameter setting "low mortality", $M10_{Dg}$ and $R10_{Dg}$ increased about continuously over time without flattening; it was $M10_{Dg} < R10_{Dg}$; the latter was related to the increase of $N10_{Dg}$ (Fig. 4). Moreover, for a given parameter setting, changes (increase or decrease) in $M10_{Dg}$ and $R10_{Dg}$ over time were similar, and they were related to the change in the number of living trees ($N10_{Dg}$) as explained above. To highlight this, the mortality rate (ratio of $M10_{Dg}$ in year t and $N10_{Dg}$ in year $t-3$) and the recruitment rate (ratio of $R10_{Dg}$ in year t and $N10_{Dg}$ in year $t-3$) were additionally plotted (Fig. 6). In contrast to $M10_{Dg}$ and $R10_{Dg}$, mortality and recruitment rates showed no clear tendency over time for the different parameter settings of standing juvenile mortality.

4.2.1.4. *Dbh structure* (χ^2_{Dg}). First order effects of standing juvenile mortality ($S_{i=sjm}$; Table 4) on χ^2_{Dg} slightly increased from year 81 to 165, followed by a clear decrease until year 333. Moreover, there were interactions, mainly in years 249 and 333, of standing juvenile mortality with standing adult mortality and/or felling regime ($S_{i=sjm,j=sam}$, $S_{i=sjm,j=fr}$, $S_{i=sjm,j=sam,m=fr}$). For the parameter setting "low mortality", the evolution of χ^2_{Dg} over time was very similar to that for the default parameter setting (Fig. 7). For the parameter setting "high mortality", the dbh structure (χ^2_{Dg}) firstly departed but then re-converged towards the initial dbh structure, reaching values close to the curve of the default parameter setting in year 333. However, at this point in time the established adult population ($N10_{Dg}$) was rather small (Fig. 4), so that the respective dbh structure was less meaningful to characterise the population.

4.2.2. *Population of any other species*

The evolutions of $N10_{OS}$ and $N60_{OS}$ (Table 2) over time showed rather small differences between "low mortality" and "default mortality" (also, $N10_{OS}$ stabilised on a lower level than observed in 1999 considered acceptable; Fig. 8). In contrast, for the setting "high mortality", the values of $N60_{OS}$ firstly decreased, but then stabilised (or maybe increased) about after year 250. The values of $N10_{OS}$ firstly decreased as well but then, about after year 90, reached values above those obtained for the default parameter setting, and stabilised about after year 250. This suggests that SELVA counteracted the loss of big trees $\geq$60 cm dbh ($N60_{OS}$) by higher recruitment of new trees, resulting in an increase of $N10_{OS}$.

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5. Discussion

5.1. *Methodology*

Similar to the method used in this study, ANOVA may be applied as global method of sensitivity analysis based on variance decomposition and a limited number of input factor values (Ginot et al., 2006). However, the use of ANOVA requires that its assumptions (normality of residuals, nullity of residuals' expectation, homogeneity of residual variance) are fulfilled or can be fulfilled through data transformation. In the present study, this was difficult to ensure given the complex structure of SELVA.

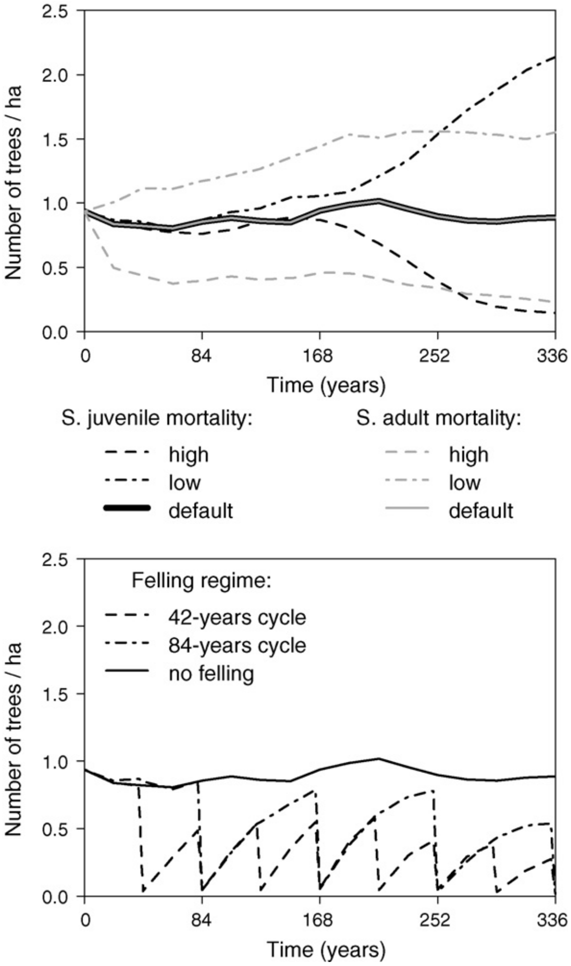

Fig. 5 – Evolution of the number of *D. guianensis* trees ≥60 cm dbh per ha ($N60_{Dg}$) over time for the parameter settings "high mortality", "low mortality" and "default mortality" of the standing mortalities of *D. guianensis* juveniles and adults (plot above), and for the parameter settings "42-years cycle", "84-years cycle" and "no felling" of the felling regime (plot below). In each case (standing juvenile mortality, standing adult mortality and felling regime), the parameters of the other sub-models of SELVA were fixed to their default values. Values of $N60_{Dg}$ are means of 20 repetitions outputted every 21 years, and additionally three years (one simulation time step) before felling in the plot below. Interpolation between mean values is linear.

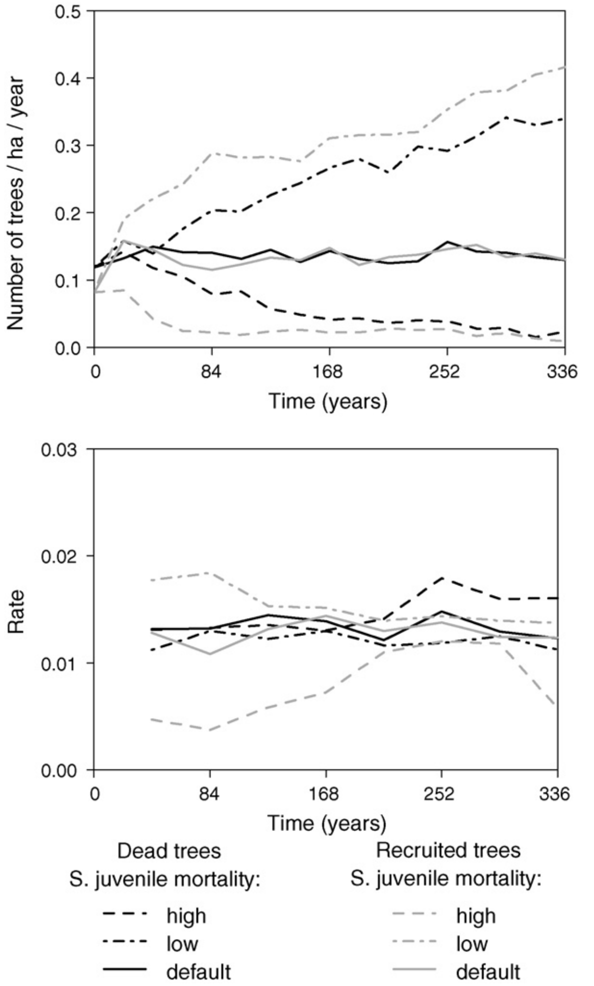

Fig. 6 – Dead and recruited *D. guianensis* trees ≥10 cm dbh that were predicted using the parameter settings "high mortality", "low mortality" and "default mortality" of the standing mortality of *D. guianensis* juveniles. The parameters of the other sub-models of SELVA were fixed to their default values. Plot above: evolution of the number of dead ($M10_{Dg}$) and recruited ($R10_{Dg}$) trees per ha and year over time. Values of $M10_{Dg}$ and $R10_{Dg}$ are means of 20 repetitions outputted every 21 years. Interpolation between mean values is linear. Plot below: evolution of the mortality rate (ratio of $M10_{Dg}$ in year *t* and $N10_{Dg}$ in year *t*−3) and of the recruitment rate (ratio of $R10_{Dg}$ in year *t* and $N10_{Dg}$ in year *t*−3) over time. Values of mortality and recruitment rates are means of 20 repetitions outputted every 42 years (i.e. *t* = 42, *t* = 84, . . ., *t* = 336). Interpolation between mean values is linear.

To compute sensitivity measures based on variance decomposition, such as the indices by Sobol' (1990), Saltelli et al. (2000) describe space-filling sampling schemes. Applying such schemes would have been computationally expensive. Thus, only a limited number of values (parameters) of each input factor (sub-model/process) was used in this study. However, we paid special attention to determine parameter ranges in a homogenous manner.

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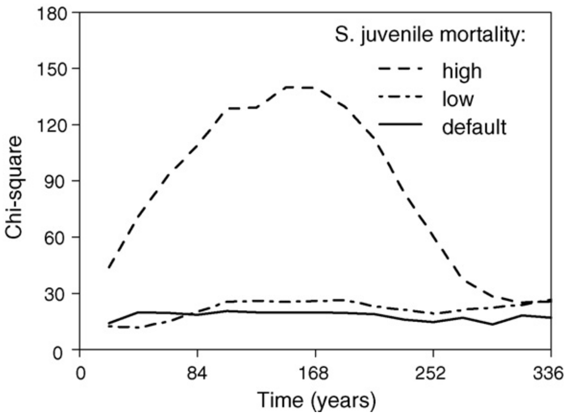

Fig. 7 – Evolution of the dbh structure of the *D. guianensis* population (χ^2_{Dg}; Chi-square between the dbh structure at a given point in time and the dbh structure at the beginning of the simulation) over time for the parameter settings "high mortality", "low mortality" and "default mortality" of the standing mortality of *D. guianensis* juveniles. The parameters of the other sub-models of SELVA were fixed to their default values. Values of Chi-square are means of 20 repetitions outputted every 21 years. Interpolation between mean values is linear.

The approach based on confidence ellipses used to determine parameter ranges complied with model specifications, such as parameters of multivariate sub-models having no explicit biological meaning and being empirically adjusted (Section 3.4). In this study, it could be applied to standing juvenile and adult mortalities, but not to germinated seed mortality and complex tree-fall. Thus, we feel less confident in the results of the sensitivity analysis that involve germinated seed mortality and complex tree-fall, concerning the comparison between processes in particular.

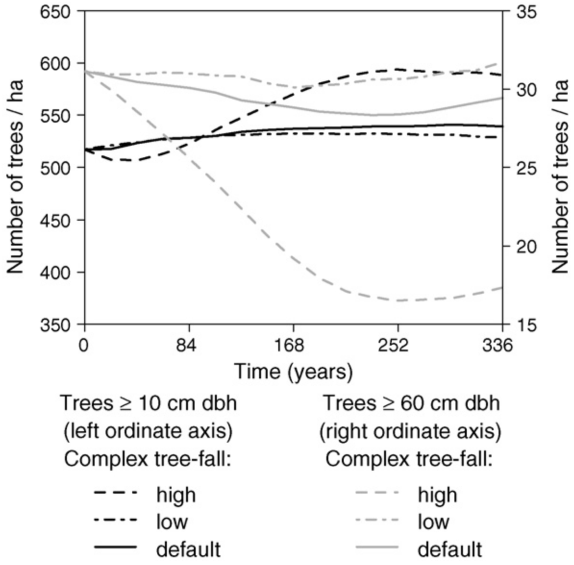

Fig. 8 – Evolution of the number of trees of any other species ≥10 cm dbh (*N10*$_{OS}$; ordinate axis on the left) and ≥60 cm dbh (*N60*$_{OS}$; ordinate axis on the right) per ha over time for the parameter settings "high mortality", "low mortality" and "default mortality" of complex tree-fall. The parameters of the other sub-models of SELVA were fixed to their default values. Values of *N10*$_{OS}$ and *N60*$_{OS}$ are means of 20 repetitions outputted every 21 years. Interpolation between mean values is linear.

In this study, interaction effects and the time course of sensitivity measures were analysed, while other sensitivity analyses of complex tropical forest dynamics models focus on first order effects and the end of the simulation period, respectively (but analyse more input factors; Huth and Ditzer, 2000; Kammesheidt et al., 2001). van Gardingen et al. (2003) stress the importance of analysing simulation results about forest management treatment statistically, including interactions. Ginot et al. (2006) stress that time course analysis of sensitivity measures gives an interesting comparison of the behaviours of parameters, which was underlined by our findings. However, concerning some results of the present study (e.g. the impacts of standing juvenile mortality on *N60*$_{Dg}$; Fig. 5, and of complex tree-fall on *N60*$_{OS}$; Fig. 8), it would have been interesting to get further insights beyond the chosen simulation period of 336 years. As a drawback, this would have increased computation time considerably.

5.2. *Impact of mortality and felling*

5.2.1. *Question Q1*

Our first question (Q1) addressed the relative impact on model predictions of mortality processes at different stages of tree development. At first glance, the results (Tables 3 and 4) suggest considerable impacts of standing juvenile mortality, standing adult mortality and complex tree-fall, but not of germinated seed mortality. However, germinated seed mortality was included into SELVA to emulate observed spatial patterns of *D. guianensis* juvenile and adult distributions (Gourlet-Fleury et al., 2005). Since output variables for spatial patterns were not included in the sensitivity analysis, germinated seed mortality could still play a considerable role in the performance of SELVA that was not reflected by the results of this study. Complex tree-fall had a high impact only on the population of any other species (*N10*$_{OS}$ and *N60*$_{OS}$; Table 3), which was not directly affected by the other mortality processes. Thus, complex tree-fall appears less important as an uncertain process than standing juvenile and adult mortalities. Compared to standing adult mortality, standing juvenile mortality was clearly the most uncertain input factor (Tables 3 and 4). But the impact of standing adult mortality on *N60*$_{Dg}$ (Tables 3 and 4) is particularly important from a forestry perspective, since it gives the number of trees that can potentially be logged above the diameter cutting limit of 60 cm currently used in French Guiana (so-called exploitable stock). Moreover, standing juvenile and adult mortalities had a joint impact on χ^2_{Dg} (Table 4), suggesting that both processes were important sources of uncertainty.

In summary, to answer question Q1, standing mortality at the juvenile stage and, in the second place, standing mortality at the adult stage were the largest sources of uncertainty in model predictions. Similarly, standing mortality of adults

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showed significant systematic effects on predictions of tree population demography (number of trees, basal area) from another individual-based spatially explicit model, whereas tree-fall did not (Phillips et al., 2003). However, in the latter model tree-fall is the probability of a dying tree falling over and complex tree-fall is not described. Moreover, only adult trees (dbh ≥10 cm) are represented so that standing juvenile mortality is not taken into account. Also, Kammesheidt et al. (2001) found predictions of tree population demography from an individual-oriented gap model more sensitive to basic mortality rates than to tree-fall, or seed mortality. Juvenile (dbh ≥1 cm) and adult trees are represented in the latter model, but mortality rates reported in the sensitivity analysis make it difficult to distinguish impacts of juvenile and adult mortalities. Finally, unlike these results other gap models are reported rather insensitive to mortality (Bossel and Krieger, 1994; Huth and Ditzer, 2000). A comparative sensitivity analysis of different model types may provide further insights into uncertainty in mortality modelling.

5.2.2. *Question Q2*

Question Q2 addressed possible interactions between the mortality processes at different stages of tree development and different felling regimes. Natural mortality can hinder the evolution of the remaining population after felling, so that lengthening felling cycles does not guarantee complete population recovery (Gourlet-Fleury et al., 2004). In this respect, standing adult mortality may play a certain role for the population of big trees (joint impact with felling regime on $N60_{Dg}$ in years 81–165; Table 4). However, in the long term, the first order effect of standing juvenile mortality on $N60_{Dg}$ became predominant in the simulations (years 249–333; Table 4). Thus, in the long term, the interaction effects found for the dbh structure appear more important (χ^2_{Dg} in years 249–333; Table 4). The dbh structure represented both the juvenile and adult populations. The juvenile population originated from the population of reproductive adult trees, where the former population was affected directly by standing juvenile mortality, and the latter population by both standing adult mortality and the felling of big, reproductive trees. Hence, the dbh structure was affected jointly by standing juvenile mortality and the felling regime (second order effect; Table 4), as well as by standing juvenile mortality and both standing adult mortality and the felling regime (third order effect). However, further analyses should evaluate these relationships as simulations runs with high standing juvenile mortality highly reduced the number of trees characterising the dbh structure (Section 4.2.1.4).

In summary, as an answer to question Q2 one may say that particularly standing juvenile mortality interacted with the felling regime, resulting in changes of the dbh structure of the *D. guianensis* population. To our knowledge, this question has hardly been tackled in sensitivity analysis of tropical forest dynamics models so far.

5.2.3. *Question Q3*

Question Q3 addressed the impact of different felling regimes on the demography and structure of tree population s in French Guiana, taking account of the answers to questions Q1 and Q2. On the one hand, there was a clear uncertainty in the results concerning Q3 due to the higher impact of standing juvenile and adult mortalities on $N60_{Dg}$ in comparison with the felling regime (Table 4). On the other hand, the little interaction between these input factors for most of the output variables (all but χ^2_{Dg}) enhances the respective results of the local sensitivity analysis (Figs. 4–6). The latter results showed plausible responses of SELVA to changes in input factors, at least qualitatively. This was shown for the relationships between $N10_{Dg}$, $M10_{Dg}$ and $R10_{Dg}$ (Section 4.2.1). It can also be seen from the results that $N60_{Dg}$ stabilised on a higher than the default level if standing adult mortality was reduced, and vice versa (Fig. 5), meaning that driftage of the population of big trees through changes in standing adult mortality was counteracted by the other ecological processes. However, driftage of the population ($N10_{Dg}$ and $N60_{Dg}$) through changes in standing juvenile mortality was hardly counteracted, at least not within the simulation period (Figs. 4 and 5); this underlines the high impact of standing juvenile mortality. But overall, the plausible responses of SELVA to changes in input factors show its performance, and the precision and relevance of its predictions could increase considerably by improving standing juvenile and adult mortalities.

In contrast to the results of this study (Fig. 5), Degen et al. (2006) found *D. guianensis* to recover completely under 65-years felling cycles (460 years simulation time; 60 cm diameter cutting limit) with their model ECO-GENE. They suggest that, in ECO-GENE, populations simulated are more resilient than is probably the case in reality. Based on a comparison between SELVA and ECO-GENE, Degen et al. (2006) suggest that the differences between the predictions come from the different ways demography is described. Our results suggest focussing model enhancement on standing juvenile mortality; in the case of SELVA this may include describing more explicitly the stimulation of juvenile survival in canopy openings. For this reason, populations simulated in SELVA could be less resilient than in reality. Finally, the results of this study underline the importance of including well-founded mortality sub-models into tropical forest dynamics models, in order to obtain reliable long-term predictions of tree population dynamics.

6. Conclusions

- Sensitivity analysis based on variance decomposition appears suitable for complex ecological models, for which a small number of processes (here: four mortality processes) are modelled under considerable uncertainties while the others are rather well-founded. The approach allows quantifying the relative impact of different processes, and their interactions, on a given model output.
- For processes described by multivariate sub-models involving several parameters that have no explicit biological meaning (here: parameters of logistic regression sub-models) and are not based on experimental data, an approach to determine parameter ranges for sensitivity analysis is to compute confidence ellipses of parameter estimates from simulated data. Thus, parameter settings

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can be defined allowing comparison between processes and ecological interpretation. The approach may be of general interest for sensitivity analysis of models relying on similar process description.

- Especially standing juvenile mortality, and in the second place standing adult mortality, should be modelled thoroughly to ensure reliable long-term predictions of tree population dynamics in tropical forests.
- Interaction between standing juvenile mortality and the felling regime may be an important relationship for the evaluation of the sustainability of felling regimes, which should be further analysed.
- For the studied tree population (*D. guianensis*), felling all trees $\geq$60 cm dbh every 42 or 84 years was found not sustainable in the long term. But enhancing the description of standing juvenile mortality may alter these predictions.

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Appendix A. Model functions and parameters of SELVA used in this study

A.1. *Specific functions for D. guianensis*

Process	Sub-model	Parameter values
Regeneration and recruitment (cohorts on 10 m × 10 m cells)		
Seed production by trees $\geq$25 cm dbh	$N_{\text{seed}} = freq\, n_{\text{seed}}$ $n_{\text{seed}} = a_1\, s_{\text{crown}} - b_1$ $s_{\text{crown}} = c_1\, D^{d_1}$ where N_{seed} = number of seeds produced by a tree during a three year time step; $freq$ = average number of seeding events per time step, which varies with tree dbh class; n_{seed} = number of seeds produced during a seeding event; s_{crown} = tree crown area (m^2); D = dbh (cm)	$a_1 = 136.33$, $b_1 = 11691$, $c_1 = 0.1699$, $d_1 = 1.7082$
Mortality of seeds	$m_{\text{seed}} = a_2$ where m_{seed} = global mortality rate of dispersed seeds; surviving seeds are germinating. They are dispersed around the mother tree and split on 10 m × 10 m cells using the function (gamma law): $\Gamma_{b_2,c_2}(dist) = \frac{c_2^{b_2}\, dist^{b_2-1}\, \exp^{-dist/c_2}}{\Gamma(b_2)}$ where $dist$ = distance to mother tree (m)	$a_2 = 0.97$, $b_2 = 4.28$, $c_2 = 2.91$
Mortality of germinated seeds	Eq. (1)	Table 1
Transition including the stages seedlings, saplings (0.5–1 cm dbh) and pre-recruited juveniles (1 cm dbh)	$N_{c+1} = A\, N_c + R_c$ with $A = \begin{bmatrix} 1-b_{41} & 0 & 0 \\ m_{41} & 1-b_{42}-m_{42} & 0 \\ 0 & m_{42} & 1-b_{43}-m_{43} \end{bmatrix}$ where the matrix operates on each 10 m × 10 m cell; N_c = vector of the number of individuals in each stage at time step c; A = matrix of transition parameters; R_c = vector of recruited seedlings (one non-null value, equal to the number of survivors to the mortality of germinated seeds)	$b_{41} = 0.44$, $b_{42} = 0.008$, $b_{43} = 1$, $m_{41} = 0.56$, $m_{42} = 0.56$, $m_{43} = 0.14$,

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Appendix A.1. (*Continued*)

Process	Sub-model	Parameter values
Growth (spatialised individuals)		
Juveniles (1–10 cm dbh)	$\log(\Delta D+1)=a_5+b_5\,D+\varepsilon_5$ where ΔD = mean annual dbh increment (cm/year) over a three year time step; D = dbh (cm) at the beginning of the time step	$a_5=0.0214$, $b_5=0.0233$, $\varepsilon_5 \sim N(\mu;\sigma)$ ($\mu=0$, $\sigma=0.067$; auto-correlated Gaussian random number)
Adults (≥10 cm dbh)	$\log(\Delta D+0.2)=\log(D)+\log[\log(K_7)-\log(D)]+a_7\,NBD+b_7\,\Delta NBD+c_7+\varepsilon_7$ where ΔD = mean annual dbh increment (cm/year) over a three year time step; D = dbh (cm) at the beginning of the time step; NBD = number of trees located ≤30 m and larger in dbh than the focal tree; ΔNBD = variation of NBD during previous time step	$a_7=-0.0033$, $b_7=-0.015$, $c_7=-4.37$, $K_7=135.2$, $\varepsilon_7 \sim N(\mu;\sigma)$ ($\mu=0$, $\sigma=0.375$; auto-correlated Gaussian random number)
Standing mortality (spatialised individuals)		
Juveniles	Eq. (2)	Table 1
Adults	Eq. (3)	$a_8=3.42$, $b_8=4.96$, c_8, d_8 in Table 1

A.2. *Specific functions for any other species*

Process	Sub-model	Parameter values
Recruitment of adults (≥10 cm dbh; spatialised individuals)	$P(R=0)=1-\frac{1}{1+\exp^{(a_{12}+b_{12}\,G_{30\times30})}}$ $P(R\le r)=1-\frac{1}{1+\exp^{(a_{12r}+b_{12}\,G_{30\times30})}}$ $P(R\le 5)=1$ where P = probability of R new trees on a 10 m × 10 m cell during a three year time step; $G_{30\times30}$ = total basal area (m^2/ha) of trees ≥10 cm dbh located on a 30 m × 30 m cell centred on the focal 10 m × 10 m cell	$a_{12}=-0.364$; $a_{12r}=1.456$ for r = 1; $a_{12r}=3.184$ for r = 2; $a_{12r}=4.54$ for r = 3; $a_{12r}=5.642$ for r = 4; $b_{12}=0.665$
Growth of adults	$\log(\Delta D+0.287)=a_{13}+\left[\log(m_{13})+\log(D)+\left(1+\frac{1}{m_{13}}\right)\log\left[\log(K_{13})-\log(D)\right]\right]+\left[b_{13}\,NBD^{1/2}+c_{13}\,\Delta NBD+d_{13}\,\Delta NBD^2\right]+\varepsilon_{13}$ where ΔD = mean annual dbh increment (cm/year) over a three year time step; D = dbh (cm) at the beginning of the time step; NBD = number of trees located ≤30 m and larger in dbh than the focal tree; ΔNBD = variation of NBD during previous time step	$a_{13}=-6.77$, $b_{13}=-0.031$, $c_{13}=-0.018$, $d_{13}=-1.3\times10^{-4}$, $m_{13}=0.51$, $K_{13}=692.65$, $\varepsilon_{13}\sim N(\mu;\sigma)$ ($\mu=0$, $\sigma=0.447$; auto-correlated Gaussian random number)
Standing adult mortality	$m_{\mathrm{OSstanding}}=\frac{1}{1+\exp^{(a_{14}+b_{14}\,\Delta D)}}$ where $m_{\mathrm{OSstanding}}$ = probability of a tree to die standing; ΔD = mean annual dbh increment (cm/year) during the previous three year time step	$a_{14}=3.42$, $b_{14}=4.957$

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A.3. *Functions for both D. guianensis and any other species*

Process	Sub-model	Parameter values
Primary tree-fall	$m_{\text{fall1}} = \frac{1}{1+\exp^{(a_9+b_9 D+c_9 G_{30})}}$ where m_{fall1} = probability of a tree to fall alone; D = dbh (cm) at the beginning of a three year time step; G_{30} = total basal area (m^2/ha) of trees ≥10 cm dbh located ≤30 m from the focal tree	$a_9 = 2.884$, $b_9 = -0.01$, $c_9 = 0.182$
Secondary tree-fall	m_{fall2} = probability of a tree to be broken or up-rooted by the fall of a neighbouring tree. Secondary tree-falls are mechanistically created depending on their relative position and dbh according to primary tree-fall tree	
Complex tree-fall	Eq. (4)	Table 1

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