

Simulation of succession in a neotropical forest: High selective logging intensities prolong the recovery times of ecosystem functions

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ABSTRACT

There is increasing concern, to what extent production forests in the Neotropics are sustainably managed. The implementation of effective forest management strategies that are ecologically beneficial plays thus a central role to prevent forest degradation. However, to identify effective forest management strategies, there is a need for methods supporting the decision-making process.

The main objective of our study is to analyze the mid- and long-term impacts of different management intensities, such as varying the minimum stem diameter of harvestable commercial trees, on the dynamic and structure of a species-rich tropical lowland forest of French Guiana. Therefore, we have applied the management module of a dynamic forest model and analyzed simulation experiments for undisturbed forest growth and selective logging.

For the first time we were able to quantify the mean recovery times of multiple ecosystem functions and properties (biomass, gross primary production, leaf area index, Shannon diversity, timber volume) after selective logging.

Accordingly, we validated simulation results (biomass, number of trees harvested) of selective logging with forest inventory data from the last 32 years. The forest model reliably reproduces the observed pre-logging biomass, tree-size distribution, and logging intensity (10 trees/ha, 39 m³/ha). In addition, it became clear how strongly management with higher logging intensities influences the forest in the long term: (1) the mean recovery times of the investigated ecosystem functions were significantly extended. With very intensive logging (116 m³/ha), the average recovery time of forest biomass was almost twice as long as in a moderate simulation scenario (t_{int} 138 a, t_{mod} 77 a). Similar patterns were observed for other ecosystem functions, e.g. timber volume (t_{int} 158 a, t_{mod} 62 a). (2) Additionally, the functional composition shifted, as up to 30% pioneer tree species in particular invaded the forest.

This innovative use of forest growth models may help in the development of ecologically reasonable forest management strategies.

1. Introduction

Forest ecosystems bind carbon and thus have a stabilizing effect on the global climate (IPCC, 2014; Pan et al., 2011; Watson et al., 2018). In particular, tropical forests play an important role in the global carbon cycle (Houghton et al., 2015; Malhi and Grace, 2000), as they store about 363 ± 28 Pg of the Earth's terrestrial carbon in their living

biomass (Bonan, 2008; Pan et al., 2013). Logging is widely practiced in tropical regions with about half of all humid tropical forests ($> 4.0 \cdot 10^8$ ha) that can be designated as production forests (Blaser et al., 2011). Depending on choices of management strategies (e.g. stem diameter of cutting threshold, cutting cycles) of a silvicultural treatment (e.g. enrichment planting, liana pruning, and thinning around potential crop trees), there is a risk that large areas of these forests will change their

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carbon storage behavior from sinks to sources (Putz et al., 2008b; Bonan, 2008). Tropical forests are a net carbon source as a result of human-induced forest disturbances (Baccini et al., 2017) and most of the world's remaining tropical forests are logged (Pearson et al., 2017). Against this background, it is of global relevance that efforts are made to reduce carbon emissions from forestry (Houghton et al., 2015), and forest management strategies also have a key role within the frameworks of climate and biodiversity protection (IPCC, 2014; Pan et al., 2013). Currently, two challenges are discussed by the public: (i) Often, logging techniques applied are not sustainable on a long-term, which may result in ecosystem degradation due to overexploitation (Huth et al., 2004; Molina, 2009; Reischl, 2012; Roopsind et al., 2018; Steffen et al., 2015) and (ii) management decisions may suffer from an incomplete understanding of the long-term effects of forest management strategies on the growth or carbon balance of tropical forests (Houghton et al., 2015; Werger et al., 2011).

On an international level, action programs have been implemented to reduce detrimental impacts of logging. Prominent examples are the climate protection instrument REDD+ (Danielsen et al., 2011; Mollicone et al., 2007; Tyukavina et al., 2015; World Bank, 2011) and certification systems, such as FSC or PEFC (Clark and Kozar, 2011; Durst et al., 2006; Rotherham, 2011). Such programs create incentives through compensation payments or certification of timber to initiate a transformation of conventional forestry into sustainable forest management (Long, 2013). If timber and carbon stocks do not recover at healthy harvesting intervals, these managed forests become susceptible to conversion to intensified land use with all the associated carbon emissions (Asner et al., 2006; Roopsind et al., 2018), and the objectives of the action programs may not be achieved. Different challenges arise: On the one hand, it is difficult to quantify the regional biomass distribution and logging rates on a high degree of detail (Gibbs et al., 2007; Malhi and Grace, 2000; Van Breugel et al., 2011), which is important to estimate variations in the global carbon balance. Regarding this, the vegetation status is one of the most uncertain variables in quantifying the carbon cycle (Pan et al., 2013). On the other hand, the long-term effects of the applied management strategies on forest growth need to be studied (Houghton et al., 2015; Piponiot et al., 2016a). Consequently, a successful implementation of such international action programs requires methods and knowledge to assess the impact of forest management options, such as selective logging, on forest growth in the tropics (De Sy et al., 2015; Molina, 2009; Reischl, 2012; Steffen et al., 2015). Forest models can be used to assess the long-term effects of current management actions (Huth et al., 2004; Shugart et al., 2018) and thus contribute to the decision-making process (De Sy et al., 2015). Complex interrelationships between ecosystem functions and management strategies can thus be revealed.

To investigate the effects of selective logging on the regeneration ability of five forest attributes in French Guiana (Paracou), we applied the individual-based forest growth model FORMIND with a newly implemented management module (Fischer et al., 2016; Kammesheidt et al., 2002). One original aspect of the study are the complex analyses in which the recovery times of several forest attributes were taken into account simultaneously. In addition to biomass, model outputs such as gross primary production, the leaf area index, the functional diversity of the species groups, and timber volume could be projected with a high degree of detail. In our study, we defined the recovery of a specific forest attribute as followed: Once an attribute value has reached its mean value of the pre-logging phase after the simulated logging intervention, we considered the remaining forest stands at the Paracou site as recovered.

The Paracou research station is located in the permanent forest estate (PFE) of French Guiana (Piponiot et al., 2016a). When the Paracou experiment was established in 1982, the main research focus was on timber and its sustainable renewal in order to strengthen the development of management rules in the PFE area. Forestry forms the primary economic sector's main part of the country and about 45% of the PFE

areas have been certified according to PEFC (PEFC International, 2017) since 2013. This high proportion demonstrates the importance of forestry for the country and at the same time indicates the interest of the French National Forest Service (ONF) in resource-efficient, modern forestry techniques. The available forest inventory data from Paracou provide an excellent basis for the parameterization of forest models. Cooperation with the ONF helped to further develop model studies, from which other tropical regions can also benefit. The linkage of these precise field data with the individual-based forest growth model FORMIND enabled us for the first time to evaluate the effects of logging on tree growth in a high degree of detail – such as five forest attributes simultaneously, in an annual resolution, for three successional stages – and a qualitatively good reproduction of the observed pre- and post-logging biomass values and tree size distribution. This kind of innovative use of forest growth models can assist in the development of ecologically reasonable forest management strategies.

In this study, we address the following research questions:

1. Is it possible to reproduce the medium-term dynamics of a selectively logged forest with individual-based forest modeling?
2. How do different management intensities (stem diameter of lower cutting threshold) affect the ecosystem functions of the forest (biomass, gross primary production, leaf area index, diversity, timber volume)?
3. How are the recovery rates of the forest's ecosystem functions influenced by logging intensities?

To examine these questions, the FORMIND forest model was parameterized for the Paracou site. Secondly, we compared the simulation results with field data. Then, we analyzed different logging scenarios in simulation experiments. Finally, we analyzed the mean recovery times of diverse forest attributes across logging intensities very detailed from an ecological point of view. For investigating different intensities of selective logging, the model parameter of the minimum stem diameter at breast height of harvestable commercial trees was varied (hereinafter referred to as dbh of lower cutting threshold).

2. Material and methods

2.1. The Paracou test site and forest inventory data

The Paracou test site is located in French Guiana (Location: 5°16'28"N, 52°55'25"W), which belongs to the Guiana Shield, north-eastern of the Amazon Basin. More than 94% of French Guiana's land area is covered with moist lowland *terra firme* rain forest that has a high number of tree species (150–220 species per hectare) and standing biomass (Fauset et al., 2015). The floristic composition is typical of Guianan rainforests with dominant families including Leguminosae, Chrysobalanaceae, Lecythidaceae, Sapotaceae and Burseraceae (Guitet et al., 2014).

In 1984, twelve 6.25 ha plots, each one divided into 4 subplots of 1.56 ha, were established. All trees with a stem greater than 0.1 m diameter breast height (dbh) have been identified, tagged, mapped, and measured in these plots. From 1986 to 1988 different logging treatments were applied to 9 plots (details in Blanc et al., 2009; Héroult and Piponiot, 2018), with 4 plots established as controls (T0). Furthermore, there was one undisturbed 25-hectare-plot that was set up in 1992. In 3 logged plots (T1), selected timbers were extracted, with an average of 10.4 trees (from 5.8 to 15.4 trees) greater than 0.5 m dbh removed per hectare, corresponding to a timber volume average of 32.5 m³/ha (from 15.4 to 51.8 m³/ha). In 8 plots, in which intensive timber stand improvement (TSI) was applied, logging intensity averaged 20.6 trees (from 5.1 to 41.7 trees) greater than 0.5 m dbh removed per hectare, corresponding to a timber volume average of 53.4 m³/ha (from 12.4 to 109.8 m³/ha). Subsequent poison girdling of selected non-commercial species killed an average of 16.6 trees greater than 0.4 m dbh/ha. Skid

trails and logging roads were mapped during the logging operation (Herault et al., 2010). Furthermore, the damage status of the trees was recorded using a categorical code for each type of damage (see Table A4). Complete inventories were conducted annually until 1995, then every two years, with a most recent census in 2016.

In order to parameterize and calibrate the forest model of FORMIND, we used the part of the inventory data set that belongs to the T0-control and biodiversity plots (primary forest totaled 62.5 ha). To parameterize and validate the logging simulations, the plots with treatment T1 were chosen (18.75 ha in total).

2.2. Description of the FORMIND forest model

In this study, we used the individual-based forest gap model FORMIND plus management module (Fischer et al., 2016; Huth et al., 2005, 2004) to point out the mean recovery times of aboveground biomass, gross primary production, leaf area index, diversity and timber volume after selective logging. Forest gap models describe forest succession in small-scale forest patches (patch: $20\text{ m} \times 20\text{ m}$, time step: 1 a). The simulated forest area can range from 1 ha up to several km^2 (in this study 16 ha) being composed of squared patches. The demographic processes considered are tree growth, mortality and recruitment; the trees within a forest patch compete for space and light. Individual tree growth is calculated on a carbon balance, based on eco-physiological processes, such as photosynthesis, respiration, carbon allocation, and litter fall. The relationship between aboveground biomass and carbon can be estimated by multiplying with a factor of 0.47 (IPCC, 2003).

In tropical forests, the high number of tree species is a particular challenge for forest models. In FORMIND, tree species are therefore grouped into plant functional types (pfts) according to species-specific functional traits, such as maximum growth heights, maximum growth rates or light demands. In order to assess the forest dynamics and structure, e.g. tree species composition and tree size distribution can be calculated. The tree shape is simplified and described assuming cylindrical stems and crowns.

The model architecture of FORMIND is modularized. This concept allows extending the forest model by adding a module to simulate different types of forest management, e.g. selective logging. All trees that meet certain criteria will be logged. Simultaneously, surrounding trees can be damaged, depending on the chosen logging strategy, intensity, and dbh of lower cutting threshold. Different logging strategies can be investigated with the management module: (i) reduced impact logging, in which the damage is reduced by directing the felled trees' direction to the closest gap and thus lower damage to the remaining forest stock. Furthermore, damage to potential crop trees are excluded; and (ii) conventional logging, in which a felled tree's direction of fall is randomly chosen and damage to the remaining forest stock is uncontrollable. A detailed model description is provided in Fischer et al. (2016). The FORMIND model's general concept is shown in the supplementary material (Appendix A, Fig. A1).

2.3. Parameterization of the forest model

The forest inventory data of the undisturbed plots (T0-control) were used (i) to parameterize tree allometry (e.g. maximum stem diameter increment, maximum tree height), (ii) to classify tree species into plant functional types (pft), (iii) and to calibrate some remaining uncertain model parameter values. Each tree species has been assigned to one of eight pfts, based on both maximum stem diameter increment and maximum tree height. About 800 tree species (Appendix C) were grouped into three classes of growth rates (successional state) and four height classes (see Fig. A2). Table 1 shows the functional traits assigned for each of the eight pfts. Table 1 also lists the attribute values of mean aboveground biomasses, mean basal area, and mean tree numbers calculated from the undisturbed plots. FORMIND internal allometric

relationships were used for this (see Table A1). Some parameters were numerically calibrated (maximum leaf photosynthesis, global number of seeds, maximum annual stem diameter increment, maximum stem diameter) using an optimization method (dynamically dimensioned search algorithm; Lehmann and Huth, 2015). For model calibration we used the tree size distribution and aboveground biomass of each pft in order to reproduce the forest stand structure as realistically as possible over time (Fig. A3). Following this approach, the model was calibrated against 136 data points originating from the forest inventories (see Appendix A). To compare the simulated results and forest inventory data we visualized both in 1:1 plots and maximized the R^2 (see Fig. A4; Leyer and Wesche, 2007).

Furthermore, an established management module was enabled in order to investigate the effects of selective logging (Huth et al., 2004). The parameters were determined from the forest inventory data of the T1-plots: The number of commercial trees out of all trees per pft were calculated as well as the dbh of lower cutting threshold was averaged to 0.55 m; the parameter dam_1 describes the proportion of damaged trees in the residual forest stand per stem diameter class (dam_{dia}) during a selective logging event. The simulation results of the logging scenario with a dbh of lower cutting threshold of 0.55 m were compared with forest inventory data from the logged plots (T1-plots), such as the stem number and stem volume of the harvested commercial trees (referred to as timber volume) as well as the loss of the mean aboveground forest biomass. For more information about the parameterization, see Appendix A, and C.

2.4. Simulation of selective logging

For the simulation of selective logging we enabled the management module and simulated a single logging event. To simulate different selective logging intensities we varied the dbh of lower cutting threshold between 0.1 m and 1.0 m in 0.1 m-steps. In total, we simulated 11 logging scenarios with varying dbh of lower cutting thresholds. A reference illustrated the undisturbed growth of primary forest in an equilibrium phase, before selective logging took place (pre-logging phase). To simulate undisturbed forest growth, we used the parameter settings conforming to Paracou's undisturbed control plots (T0). Additionally for the logging scenarios, we used parameter settings of the logging event according to Paracou's T1-plots. This referred to the simulation scenario with a lower cutting threshold of dbh equal to 0.55 m (so-called moderate logging scenario: $39\text{ m}^3/\text{ha}$ or 10 trees/ha were harvested), where the fall direction of the felled trees was controlled. In this case, the simulation results were compared with the associated field data (T1) during the post-logging phase. In the other 10 logging scenarios, the falling direction of felled trees was not controlled and potentially crop trees were damaged. One of these scenarios, with a dbh of cutting threshold of 0.1 m, was referred to as an intense logging scenario (yield: $116\text{ m}^3/\text{ha}$ or 306 trees/ha).

The simulation for all scenarios began on a treeless (empty) area of 16 ha. Annual time steps and a total of 750 years were simulated. Simulation results for the spin-up time of 450 years were excluded from further analysis. One single logging event took place after the 500th simulation time step. This was then assigned to the observed logging event in the year 1986. By doing so, we could count years after selective logging (time of logging equals 0). Of the entire model outputs, we analyzed the final 300 years of each simulation scenario. The time interval [1; 250] corresponded to the post-logging phase and the time interval [−50; 0] to the pre-logging phase.

Beyond the analysis of aboveground biomass (AGB) for the three successional states (see Table 1) and the overall forest stand, the forest model was used to extrapolate the development of the entire forest stand's gross primary production (GPP), leaf area index (LAI), normalized Shannon diversity (H'), and timber volume (V_T). We also analyzed the mean recovery times of these five forest attributes for the years after logging. In our study, the mean recovery times for the

Table 1

Grouping of tree species into eight plant function types pfts for the Paracou test site (T0-control plots). Functional traits were assigned to each pft. Besides, attribute values of the mean aboveground biomass, mean basal area, and mean stem number were calculated (averaged over all forest inventory years 1984–2016) using allometric relations (see Appendix Table A1, Fig. A2; ODM: organic dry matter).

pft	Potential tree height [m]	Growth rates	Successional state	Mean stem numbers [1/ha]	Mean biomass [t_{ODM} /ha]	Mean basal area [m^2 /ha]
1	< 16.0	Slow growing	Late	2.11	0.20	0.02
2	16.0–26.5	Slow growing	Late	236.63	59.23	5.05
3	16.0–26.5	Semi-fast growing	Mid	15.07	3.91	0.38
4	16.0–26.5	Fast growing	Early	5.20	1.70	0.19
5	26.5–34.0	Slow growing	Late	154.59	122.86	8.09
6	26.5–34.0	Semi-fast growing	Mid	174.64	184.91	13.25
7	26.5–34.0	Fast growing	Early	16.90	14.32	1.34
8	34.0	Whole range	Mid	15.50	30.68	2.40
Total				620.64	417.81	30.72

simulated forest attributes after logging were determined as follows: For each logging scenario, the simulation results of these attributes were smoothed using local regression models (loess; smoothing span = 0.05). These smoothed curves were then analyzed to identify the point of time during the post-logging phase at which the attribute values, within a given tolerance range, returned to the pre-logging baseline. The tolerance ranges were set to the standard deviations of every simulated mean attribute value (averaged over 16 ha and 150 a). To better interpret mean recovery times of five forest attributes of different logging intensities expressed by changing dbh of lower cutting thresholds, we fitted trend lines of non-linear least squares to logarithmic dbh of lower cutting thresholds. The quality of these trends was given as residuals (see Fig. A6). Moreover, we used the normalized Shannon diversity H' (1) to explain the diversity of tree species groups (pft), taking into account the relative abundance of species groups (Marcon et al., 2014; Spellerberg and Fedor, 2003). A change in H' should illustrate the impact of damage on forest structure in different selective logging scenarios, where p_i is the proportion of individuals belonging to the i th pft and P is the total number of pfts (here 8) in the data set:

$$H' = - \frac{\sum_{i=1}^P p_i \cdot \ln p_i}{\ln P} \quad (1)$$

H' has been normalized and ranges between 0 and 1. The higher the index is, the more homogenous is the distribution of pfts (Huston, 1994). Standard deviations for the total forest stand's aboveground biomass (16 ha simulation area) were given to measure the deviation from the average forest attributes over 1 ha, and to interpret the stability of the ecosystem (Leyer and Wesche, 2007). Detailed information about the software used throughout our analysis, see Appendix B.

3. Results

3.1. Simulated biomass dynamics of a selectively logged forest

First, we analyzed aboveground biomass (Fig. 1a and b) for a moderate and an intense logging scenario (Fig. 1a and b). In the moderate scenario 10 trees/ha with 39 m^3 /ha were harvested and in the intense scenario 116 m^3 /ha and 306 trees/ha. Logging intensity was expressed by the dbh of lower cutting threshold. It can clearly be seen that the first logging event (time equals 0 a) in both scenarios was followed by an immediate decline in aboveground biomass (AGB), accompanied by an increase in productivity in comparison to the reference (mean $\text{AGB}_{\text{ref}} 439 t_{\text{ODM}}$ /ha, mean $\text{sd}_{\text{ref}} \pm 67 t_{\text{ODM}}$ /ha; averaged over 16 ha simulation area). Generally, the decline in aboveground biomass was directly proportional to the intensity of selective logging, but the increase in productivity was indirectly proportional. In the moderate scenario, 10 trees per hectare were harvested with an overall commercial bole volume around 39 m^3 /ha; aboveground biomass decreased by $109 t_{\text{ODM}}$ /ha one year after logging (Fig. 1a). In the intense

scenario, the overall aboveground biomass decline was twice as strong (Fig. 1b). In this scenario, more than 306 commercial trees were harvested per hectare, with a total stem volume of 116 m^3 /ha, so that the overall aboveground biomass decreased by $211 t_{\text{ODM}}$ /ha.

In a second step, we explored the structural development of the forest stand by analyzing species compositions. In the moderate scenario (Fig. 1a) the tree species' group composition shifted slightly during 70–80 years after logging: the aboveground biomass of the pioneer species recovered their initial levels faster than that of the climax or intermediate tree species. After this phase both the forest stand structure and overall biomass returned to the reference values of primary forest growth (pre-logging phase); likewise the timber volume (see also Fig. A7).

A comparison of the simulated and observed aboveground biomass per species group (pfts grouped by successional state) between 1986 and 2016 shows that our model can reproduce the dynamics and species group composition of a selectively logged forest (Fig. 1c). During the post-logging phase the simulated total aboveground biomass corresponded well to the observed values (R^2 0.991, rmse $4.6 t_{\text{ODM}}$ /ha). Slight deviations were visible in the simulated and observed aboveground biomass of the climax species after logging (see also Fig. A5). For the pre-logging phase, the forest model also slightly overestimated the observed total mean aboveground biomass ($418 t_{\text{ODM}}$ /ha) with 5%. The deviations between observed and simulated biomass values were less than the observed standard deviation ($\text{sd}_{\text{obs}} \pm 67 t_{\text{ODM}}$ /ha) (see also Fig. A4).

The intense scenario was characterized by a stronger shift in the species group composition and the aboveground biomass was only slowly recovering (138 a) (Fig. 1b). A rapid increase in the forest stand's overall aboveground biomass was particularly noticeable during about 50 years after logging. In this phase there is a steady increase of fast-growing pioneer species' biomass. The increase of rapid gross primary production directly after logging was followed by a phase (> 130 a after logging), which was characterized by productivity rates around $20 t_{\text{ODM}}$ /ha similar to the baseline (Fig. 1d).

3.2. Effect of different selective logging intensities on ecosystem functions

We investigated the impacts of different logging intensities on the productivity of the remnant forest stand's aboveground biomass in a set of simulation scenarios. Therefore, we varied the dbh of lower cutting threshold stepwise between 0.1 m and 1.0 m in 0.1-m-intervals. Fig. 2 shows the relation between a changing dbh of lower cutting threshold and the remaining forest stand biomass (Fig. 2a) or gross primary production (Fig. 2b) after logging: The fewer trees were harvested (high dbh of lower cutting thresholds), the higher the remaining forest biomass, meaning that with low logging intensity, productivity shows only minor changes. Additionally, it becomes clear that a large part of the stand biomass has already grown back to the level of the baseline after about 60 years. However, complete biomass recovery of the forest

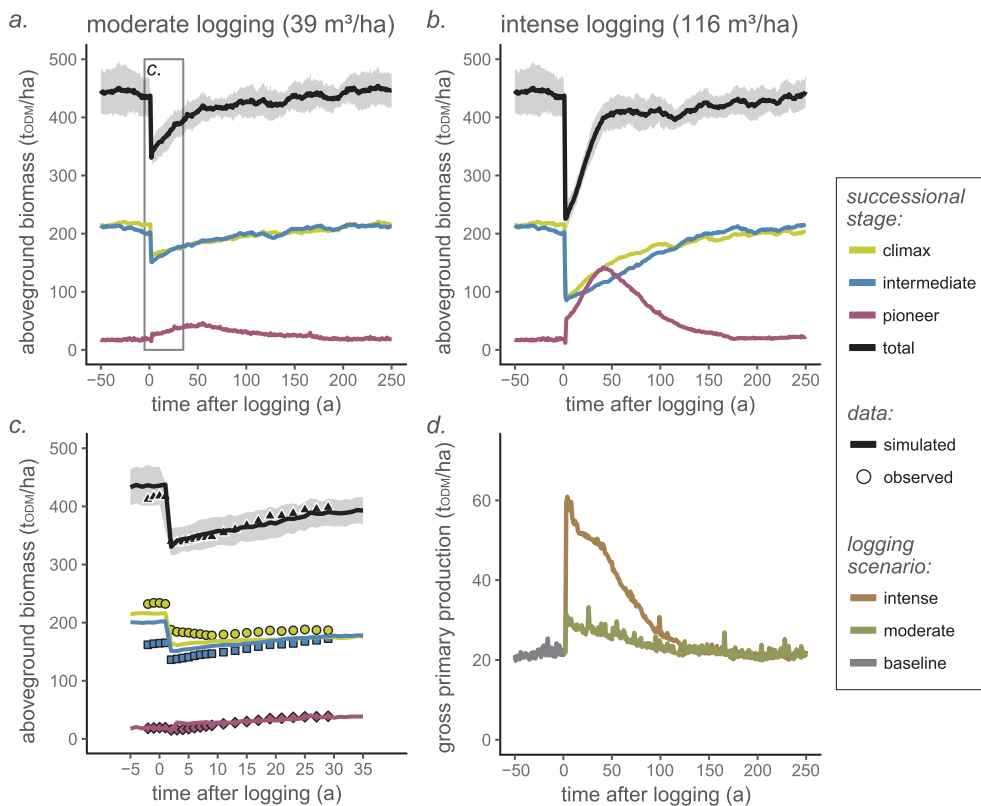


Fig. 1. Comparison of a moderate and intense logging scenario (dbh of lower cutting thresholds 0.55 m; 0.10 m) after a 50-year pre-logging phase reflecting primary forest growth as a reference. Depending on the intensity of the selective logging event the amplitude and elasticity of the mean aboveground biomass plus standard deviation (a., b.) and gross primary production (d.) changed. Model outputs are shown either for the total forest stand or the plant functional types grouped by successional states averaged over 16 ha-simulations. (c.) The dots indicate mean annual aboveground biomass values calculated on basis of Paracou's forest inventory data of the T1-plots. The year of logging (1986) was assigned to simulated time equaled 0.

structure takes almost twice as long (130–140 a), as the functional composition is still strongly shifted (cf. Fig. 1b). In the case of gross primary production, a higher logging intensity resulted in a higher productivity of the logged forest. Fig. 2c represents the relationships between the forest's gross primary productions and forest stand biomass during six decades after selective logging. It can be seen that there is a negative relationship between the two attributes, meaning higher productivity values for forest stands with low biomass. This negative relationship becomes stronger the longer the logging event has passed.

We explored also the average duration that the entire forest stand needed to recover after logging (mean recovery time; Fig. 3) for five specific forest attributes, such as the aboveground biomass, gross primary production, leaf area index, Shannon diversity, and timber volume. We found that timber volume has the longest mean recovery

times in all scenarios, followed by forest biomass, leaf area index and gross primary productivity (Fig. 3a). The Shannon diversity indices have the shortest mean recovery times. Fig. 3b displays the mean recovery times of the moderate and intense logging scenarios. In the intense scenario, the forest stand takes at least twice as long to recover compared to the moderate scenario. This applies to all forest attributes examined. When evaluating different management strategies (Fig. 3a), we found logarithmic relations between the different dbh of lower cutting thresholds and mean recovery time of the forest attributes. For the intense and moderate logging scenarios, the mean recovery times of the attributes under consideration were compared with the official cutting cycle of 65 years in French Guiana (Fig. 3b). For the moderate logging scenario this recovery time of the attributes was sufficient, only the recovery time of the aboveground biomass was about 5–15 years

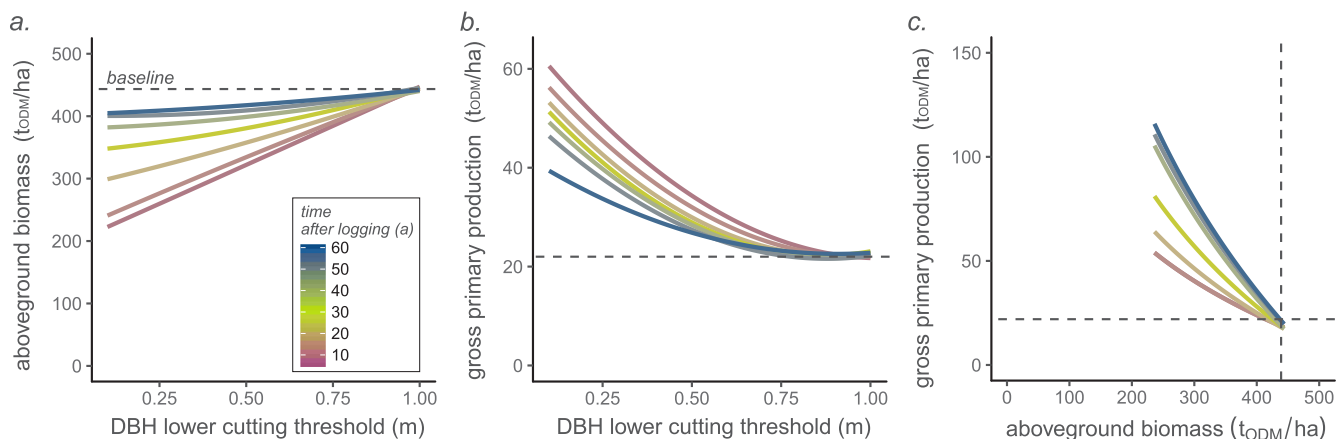


Fig. 2. Interrelationships between aboveground biomass (a.) or gross primary production (b.) and minimum dbh of harvestable commercial trees during six decades after selective logging ($0 \text{ a} < \text{time} \leq 60 \text{ a}$; see Fig. 1). The trend lines were determined using the linear regression of a second-degree polynomial. (c.) Relationships of gross primary productivity to the aboveground biomass also during 60 years after logging. The trend lines were determined using least square regression of a logarithmic biomass. The baselines indicate averaged attribute values of primary forest growth as a reference (averages over 150 years and 16 ha, pre-logging phase).

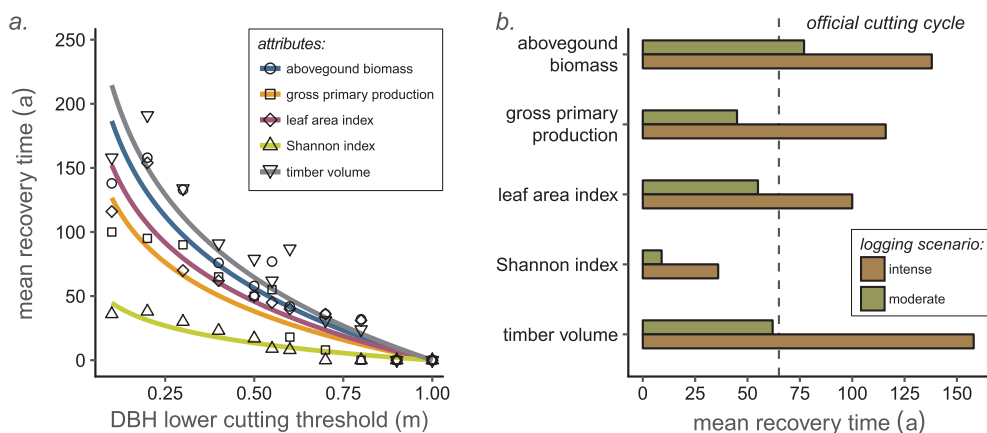


Fig. 3. Evaluation of different management strategies. (a.) Development of the mean recovery time of different forest attributes (aboveground biomass, gross primary productivity, leaf area index, and Shannon index) analyzed in relation to the logging intensity (dbh lower cutting threshold). The dots correspond to the recovery time determined from the simulation scenarios. The trend lines were derived by modeling the nearest least squares of a logarithmic dbh. (b.) Comparison of mean recovery times for the moderate and intense logging scenarios (dbh of lower cutting thresholds 0.55 m, 0.1 m) regarding the same attributes. The dashed line indicates French Guiana's official 65-years cutting cycle.

longer (70–80 a). In contrast, the mean recovery times of the five forest attributes of intensive logging were at least twice as long as the official cutting cycle in French Guiana. The timber volume and forest biomass are particularly remarkable, as they have the longest recovery times compared to LAI, GPP, and Shannon diversity. With increasing dbh of lower cutting threshold the values of the recovery time converge at 1.0 m. From this dbh onwards, there were nearly no commercial trees in the simulated forest stand. The recovery time of the Shannon index was approximately 40 years, which is below French Guiana's official cutting cycle of 65 years.

4. Discussion

4.1. Incorporation of the model approach

One of the main achievements of this simulation study are the detailed findings for the quantitative evaluation of the succession of several forest attributes for the Paracou test site in French Guiana, which have either not yet been recorded extensively in the terrain (e.g. GPP, LAI, Shannon diversity) or are being relevant in public discussions (AGB, timber volume).

With the term “detailed” we mean the resolution of the simulation results (e.g. annually, per pft, and per hectare), and a qualitatively good reproduction of the observed pre- and post-logging biomass values and tree size distribution. Literature research has shown that for the Amazon and adjacent regions most empirical information focus on the recovery of a single forest attribute, e.g. the standing biomass after disturbance, which is important to calculate carbon fluxes (Piponi et al., 2016b; Poorter et al., 2016; Rutishauser et al., 2015). An original aspect of our study are the complex analyses in which the mean recovery times of five forest attributes were taken into account simultaneously. We considered the five attribute values of AGB, GPP, LAI, Shannon diversity, and timber volume to be important to estimate over a longer period of time, as they provide valuable insights into the condition of a production forest for tropical forestry.

The accuracy of the forest model was achieved by linking large-scale, long-term and consistently recorded field data and forest modelling. Most of the model parameter values could be calculated, hence, only three uncertain parameters were numerically calibrated with the inventory data of the undisturbed control plots (T0) of Paracou using the dynamically dimension search (Lehmann and Huth, 2015). As a result, the forest model only slightly overestimated the observed mean aboveground biomass by 5% (AGB_{obs} 418 t_{ODM}/ha , AGB_{sim} 439 t_{ODM}/ha). Rutishauser et al. (2010) obtained values between 388 t_{ODM}/ha and 443 t_{ODM}/ha for the aboveground biomass of the same control plots in 1991 and 2007 (using allometry for wet tropical forests by Chave et al. (2005)), respectively, which confirms our results for allometry used by FORMIND (see Table A1; Fischer et al., 2016).

As a second important step, we validated our simulation results of one of the selective logging scenarios (moderate: 39 m^3/ha or 10 trees/ha) with an independent set of Paracou's forest inventory data (T1-plots). Deviations between simulated and observed aboveground biomass values during 30 years after logging were low (R^2 0.991, $rmse$ 4.6 t_{ODM}/ha), indicating that biomass dynamics and recovery time of logged forests were well represented by the model simulations.

One reason for these reasonably simulation results was the excellent database of the Paracou forest. Indeed, the Paracou database is unique in terms of (i) the frequency of forest inventories every two years, (ii) the spatial extent (120 ha area), (iii) the duration (35 years of inventories) including more than 30 years of post-logging inventories, and (iv) the methodological consistency, with same team of staff from the beginning. This and the close cooperation with French Guiana's National Forest Service (ONF) helped to further develop such model studies, from which other tropical regions can also benefit. With the FORMIND forest model inclusive management module it is possible to estimate the mean recovery times of at least these five forest stand attributes for logged forest at Paracou with a high degree of detail. The model can be easily adapted to simulate further forest management strategies by varying parameters, such as the dbh of lower cutting threshold, the cutting cycle or the number of trees per commercial tree species to be harvested. The model parameterization developed can also be applied to obtain new knowledge on the dynamics of forests or to test novel management strategies, such as the impact of modernized techniques to reduce logging damage (Piponi et al., 2018; Putz et al., 2008a); given that such modern techniques are being used in less than 5% of selectively logged forest areas worldwide (Nasi et al., 2011).

The approach of this study was based on the grouping of over 800 observed tree species into eight pfts. This aggregation is suitable for applications with process-based models (Fischer et al., 2018; Köhler et al., 2000). This was also valid with increasing model complexity (forest model plus management module), as required by this investigation. The advantages of tree species aggregation are that information from all trees recorded was included in the model parameterization. This had a positive effect on the model's accuracy and the robustness of model outcomes; evenly, the parameterization effort was manageable. However, the representation of temporal changes in tree species diversity is limited with the concept of pfts. This may be an explanation for the fast recovery time of the Shannon diversity in this study. Maréchaux and Chave (2017) developed another process-based model in which 139, out of 800, tree species were parameterized one by one for the Paracou site. Compared to the pft approach, a high number of represented species in a forest model allows reproducing trait variability between species in more detail. However, a very detailed functional trait data basis is needed, and the model parameterization is laborious, especially for rare tree species. The latter could mean that only subsets of data on dominant tree species can be considered,

making it difficult to investigate complex interactive processes on the entire forest stand. In addition, transferring the model concept to other locations is challenging. Nevertheless, such a species-specific model approach could be perspective used to evaluate the interactions between logging and the species composition. The FORMIND forest model of the Paracou test site represents the tree species composition in aggregated form, meaning the functional composition of the forest stand is emphasized, which seems reasonable for the long-term evaluation of the effects of logging.

4.2. Long-term effects of logging intensity on forest functions

A major challenge for tropical forestry is the identification of timber harvesting thresholds that are compatible with recovery times of forest attributes that can be used as indicators to ensure stable values of biomass, harvest yield or other ecosystem services (Petrokofsky et al., 2015). Assuming that there are as many indicators as possible to estimate the long-term impact of logging interventions on forest growth, the higher the confidence of the stability or instability of a management strategy can be considered (Duelli and Obrist, 2003; Mace et al., 2012). The recovery times of remaining aboveground biomass vary with the intensity of timber harvest, as discussed in the literature (Huang and Asner, 2010; Roopsind et al., 2018; Rutishauser et al., 2015). Our results support studies who concluded that logging strategies postulating reduced impacts do not necessarily ensure full recovery of forest biomass; at least not within government-specific thresholds of minimum cutting cycles (Huth et al., 2004; Keller et al., 2007; Roopsind et al., 2018; Sist and Ferreira, 2007; Valle et al., 2007; Zarin et al., 2007). This can also be said of the Amazon Basin (Piponiot et al., 2016b), where forest management practices differ between countries (Rutishauser et al., 2015). The minimum cutting cycles are fixed between 30 and 60 years with harvests of 10–30 m³/ha, often too short to restore commercial timber reserves. In particular, in French Guiana, with an official cutting cycle of 65 years and a mean logging intensity of 8–29 m³/ha (averaged over the last 15 years), reduced impact logging-techniques are used in practice (Piponiot et al., 2016a). Our results showed that, under assumptions of our moderate logging conditions (dbh of lower cutting threshold 0.55 m, 39 m³/ha), the recovery for aboveground biomass took about 5–15 years longer than the French Guiana's official cutting cycle is. For instance, if the biomass stock of the moderate scenario is to fully regenerate, we recommend raising the average dbh of lower cutting threshold, over all pfts, to at least 0.6 m, so that the pre-logging value could be reached after 65 years. It can also be assumed that the timber volume will also recover during this period of time (see Fig. 3). In this study, we assumed the same value of dbh of lower cutting threshold for all pfts in each logging scenario. The effects of diversifying this parameter on the recovery time of forest attributes by assuming group-specific parameter values would have to be investigated in future.

Another challenge of this study was that we were able to demonstrate that French Guiana's official cutting cycle of 65 years, under assumptions of the moderate logging scenario, may be sufficient for the restoration of the LAI, and gross primary production at the study site Paracou. Besides, we have also analyzed the average recovery time of functional diversity to give a rudimentary indication that a cutting cycle of 65 years could be sufficient to restore the structural composition of the tree species. We showed, the complete regeneration of multiple forest attributes following a logging intervention can be used as important indicator of ecological stability. However, we would still have to investigate the impact of sequential logging interventions on forest growth and timber volume yields. The expectation is that managed forests will maintain both their ecological and economic value and provide ecosystem services over long periods of time. As long as logging intensities are low, selectively logged forests supply biomass and timber, as long as the regeneration time is shorter than a country's cutting cycle. Roopsind et al. (2018) found that vulnerabilities can

occur as early as the second cutting cycle and start forest degradation, with negative consequences for the carbon balance; however, the biodiversity and ecosystem services of a forest can also be affected (Millennium Ecosystem Assessment, 2005). There is a risk to lose these ecosystem services through opportunity costs that bring financial benefits. Therefore, payments must be made for ecosystem services that require effective decision-making and monitoring structures to initiate improved forest management strategies for carbon sequestration and biodiversity protection.

Another important question to discuss is how forestry interventions may decrease the time to biomass or timber recovery. Our results showed at the example of French Guiana that the forest stand could regenerate completely within the official cutting cycle unless the dbh of the lower cutting threshold was reasonable. It also became clear that the relationship between aboveground biomass and gross primary production is variable: both change as a function of logging intensity and the time passed since logging. This shows that it is crucial to consider the successional state of a forest stand to be logged (Héroult and Piponiot, 2018). One option to shorten the recovery times of ecosystem functions and properties is to reduce damage by using gentle harvesting techniques (Putz et al., 2008a). At the same time, the cutting cycles must be extended and depletion must be prevented (Piponiot et al., 2018). Different forestry practices to increase the growth rates and yields of commercially viable species such as enrichment planting, liana pruning and thinning around potential crop trees are also likely to stop overexploitation of forests. Fundamental problems regarding these techniques are high costs and the acceptance of using toxic chemicals in the environment. Another strategy is diversifying commercial species lists while adapting the timber industry to this diversification. However, the extensive adoption of such practices implies a change in the prevailing approach to forest management (Messier et al., 2013). This means that more sustainable logging strategies can reduce both yield and income. The trade-offs must therefore be balanced between ecological and economic aspects by applying techniques to reduce the impacts of selective logging.

In this study, we looked at the dynamics of forest functions and properties from an ecological point of view. These must be extended by economic aspects in future studies. It is important to develop forest management strategies that reduce damage to forest as well as increase effective harvest volumes. Furthermore, it is needed to evaluate the effects of forest management on biomass dynamics in the context of climatic changes (Fargeon et al., 2016). The question of how ecosystem attribute changes affect recovery of the forest during climate change must be analyzed (Héroult and Piponiot, 2018). For example, the cutting cycle, the minimum dbh of cutting threshold value of commercial tree species or reduced impact logging techniques can be adjusted by changes in forest management regulations (Putz et al., 2008a,b). Besides, it is an open question to what extent climate change influences the biomass or carbon balance of the forest stand (Guimberteau et al., 2016; IPCC, 2014).

5. Conclusions

The key objective of this study was to apply the FORMIND forest model that enables to evaluate the impact of various forest management strategies in controlled simulation experiments to be carried out over long periods of time in scenarios. By linking empirical data from an intensively studied test site and forest modeling, we succeeded in developing a parameterization for the forest model including a management module. Additionally, it was possible to evaluate important functional attributes (gross primary production, leaf area index, and Shannon-diversity, timber volume) whose empirical measurement is challenging or has not yet been carried out. For the first time we were able to analyze and quantify the mean recovery times of complex forest attributes simultaneously with a high degree of detail. We have found that increasing logging intensities, by reducing the dbh of the lower

cutting thresholds of commercial trees, extend the mean recovery times of the investigated ecosystem functions and properties considerably. As an example, based on our simulation results for Paracou in French Guiana, we recommend a dbh of lower cutting threshold for commercial tree species of at least 0.55 m for a cutting cycle of 65 years.

In future, it might be very interesting to discuss the trade-off between maximizing the harvested timber volume and minimizing the damage to the residual forest stand with respect to recovering the amount of timber. In addition to the ecological aspects, on which we are focusing in particular, economic aspects, but also climatic changes, should also be taken into account in future studies.

This methodological approach of forest modeling may allow developing forest management strategies that are more economic and ecological friendly. Knowledge gained through such simulation experiments will support the decision-making processes (e.g. REDD+ and FSC-labeling).

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Conflicts of interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.foreco.2018.08.042>.

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