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# Climate change alters the ability of neotropical forests to provide timber and sequester carbon

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## Abstract

Logging is widespread in tropical regions with ca. 50% of all humid tropical forests ( $1.73 \cdot 10^9$  ha) are regarded as production forests. To maintain the ecosystem functions carbon sequestration and timber supply in tropical production forests over a long term, forest management must be sustainable under changing climate conditions. Individual-based forest models are useful tools to enhance our understanding about the long-term effects of harvest and climate change on forest dynamics because they link empirical field data with simulations of ecological processes.

The objective of this study is to analyze the combined effects of selective logging and climate change on biomass stocks and timber harvest in a tropical forest in French Guiana. By applying a forest model, we simulated natural forest dynamics under current climate conditions and compared the results with scenarios of selective logging under climate change. The analyses revealed how strongly forest dynamics alter under different scenarios of climate change compared to the baseline scenario of current climate conditions: (1) Repeated logging within recovery times led to a decrease of forest attributes including biomass and timber harvest irrespective of the intensity of climate change. (2) With moderate climate change (RCP 2.6) the average biomass remained constant compared to the baseline scenario over the 21<sup>st</sup> century (-1%); likewise, with intensive climate change (RCP 8.5), the average biomass was reduced by 12%. (3) Through combination of

selective logging and climate change, the likelihood of changes in forest dynamics increased, driven mainly by rising temperatures. Assuming RCP 8.5, the averaged timber harvest almost halved regardless of the applied logging rotation cycle.

An application-oriented use of forest models will help to identify possibilities to reduce the effects of unwanted ecosystem changes in a changing environment. To ensure that ecosystem functions in production forests are maintained under climate change conditions, this will help to develop appropriate forest management strategies.

**Keywords:** *aboveground biomass, timber harvest, climate change mitigation, forest degradation, individual-based forest modeling, forest management, tropical forestry, French Guiana, Paracou*

## **Introduction**

Tropical forests play an especially essential role in the global carbon cycle (Houghton et al., 2015; Malhi and Grace, 2000) as they store about half of the Earth's forest carbon in their living biomass ( $471 \pm 93$  Pg C) (Bonan, 2008; Pan et al., 2013) and thus have a stabilizing effect on the global climate (Friedlingstein et al., 2019; IPCC, 2014a; Pan et al., 2011; Watson et al., 2018). Under the influence of climate change and logging, however, forest dynamics are changing. Often, forest stand biomass is characterized as aboveground woody dry biomass of living trees (hereinafter: biomass; Anderson-Teixeira et al., 2016).

Drought, increasing temperature trends, and logging influence the life cycle of trees by altering physiological processes including productivity and mortality (McDowell et al., 2018). According to climate change scenarios provided by the 5<sup>th</sup> IPCC Assessment Report (i.e., representative concentration pathways (RCPs)), average global annual surface temperatures may continuously increase by 1.5–4.0 °C by the end of the 21<sup>st</sup> century (IPCC, 2014a, 2014b). Most regions covered by lowland rainforests will very likely be at least 2–4 °C warmer by 2100 under the assumptions of all RCP scenarios except RCP 2.6 (IPCC, 2014a, 2014b). Warming influences the water balance of trees, which plants often compensate by a reduction in the production and transpiration (Will et al., 2013). In addition, spatial patterns of precipitation will change, leading to more frequently occurring droughts especially in tropical regions (IPCC, 2014a, 2014b). Hence, water limitation may reduce the potential for cooling by transpiration and drought-induced defoliation can increase the temperatures

below the canopy. This has consequences for leaf demography, and thus, for photosynthesis patterns, thereby affecting biomass distributions and forest dynamics. Climate change affects a forest's productivity, depending on tree species composition, water availability, temperature, atmospheric carbon concentration, and geographic location (Hanberry and Larsen, 2014; Morin et al., 2018), by determining rates of photosynthesis, respiration, defoliation, or tree mortality (Aubry-Kientz et al., 2015; Bonan, 2008; Hiltner et al., 2016; McDowell et al., 2018b; Phillips and Lewis, 2014; Strobl et al., 2011).

In addition to climate change, forest management also plays a crucial role in changing tropical forest dynamics. Selective logging events cause abrupt changes in a forest's carbon budget (Hiltner et al., 2018). Thus, repeated logging of commercial tree species within recovery times of important attributes including biomass and commercial timber volume may lead to a degradation of corresponding ecosystem functions (Knoke, 2016). To prevent this, sustainable logging techniques with reduced impacts are favored (Ellis et al., 2019; Putz et al., 2008; Roopsind et al., 2018). Introducing selective logging in a primary forest stand usually results in a decrease in stand biomass and harvestable timber volume after the first cut (Knoke, 2016; Putz et al., 2012). In this context, sustainability means that the volume of timber remains constant during subsequent cuts, which depends largely on the rotation cycle (Knoke, 2016). A shorter rotation cycle leads to a stronger reduction of forest biomass.

However, the impacts of forest management on the future development of tropical production forests are unknown under climate change conditions. A challenge is to understand the combined effects of different climate drivers (e.g., temperature increase) and repeated harvesting with different logging rotation cycles on forest dynamics (Houghton et al., 2015; Werger et al., 2011). Since forest dynamics are quite slow (e.g., decades to centuries), it requires long time until they adapt to climatic changes (Sakschewski et al., 2016). Therefore, besides empirical field studies, scientific methods are needed that can provide robust estimates of long-term forest management and climate change impacts.

The aim of this study is to explore the impacts of climate change and selective logging on forest dynamics. By using dynamic, individual-based forest modeling, it is possible to simulate the impacts of different logging rotation cycles under climate change conditions over longer periods of time (Fischer et al., 2016; Gutiérrez et

al., 2009; Hiltner et al., 2018; Shugart et al., 2018). Furthermore, changes in forest structure (i.e., tree size distribution) and the dynamics of forest attributes influencing important ecosystem functions (i.e., timber supply and carbon sequestration in living biomass) can be analyzed. We addressed the following research questions in detail:

1. How do different rates of temperature and precipitation changes affect the long-term aboveground biomass dynamics of neotropical forests?

2. What are the combined impacts of selective logging and climate change on forest attributes?

Here, we applied the individual-based forest growth model FORMIND including a management module and newly implemented soil water and temperature modules (Fischer et al., 2016; Hiltner et al., 2018) to a neotropical lowland forest north of the Amazon Basin. We investigated the combined effects of climate change (i.e., the effects of temperature and precipitation) and selective logging on the long-term trajectories of several forest attributes, including aboveground biomass, timber harvest, and quadratic mean stem diameter.

## Methods

### The Study area

Paracou is located in French Guiana (location: 5°16'28''N, 52°55'25''W) north of the Amazon Basin. The forests are humid lowland Terra Firme rainforests on Acrisols of sandy clay (Gourlet-Fleury et al., 2004; Hammond, 2005). The climate of French Guiana is equatorial, with an average annual precipitation of  $3,102 \pm 70$  mm and an average annual temperature of  $25.7 \pm 0.1$  °C (2004–2014) (Aguilos et al., 2018). The IPCC AR5 model (IPCC, 2014b, 2014a) and a study of Magrin et al. (2014) predicted an overall increase in mean annual temperatures and a slight decrease in annual precipitation sums, accompanied by more frequently occurring heavy rainfall events, in the surroundings of the Paracou site for most RCPs (see Appendix A, Figure A1). These climatic changes will be accompanied by an increase in extreme weather events such as storms, floods, and droughts until 2100 (IPCC, 2014b, 2014a; Magrin et al., 2014).

Paracou is directly adjacent to a permanent forest estate, which extends over  $2.4 \cdot 10^6$  ha in French Guiana and is mainly managed by the National Forest Service. National Forest Service's management strategies follow

selective logging techniques that require intensive pre-planning. In French Guiana, an official 65-year logging rotation cycle applies, and commercially exploitable trees (see Appendix C, Tab. C1) with a minimum stem diameter at breast height between 50–60 cm are harvested at a cutting rate of up to 25 m<sup>3</sup> ha<sup>-1</sup> or 3–5 trees ha<sup>-1</sup>.

## **The forest model FORMIND**

### **Model description**

In this study, we used the forest model FORMIND in combination with other submodules including soil water, temperature, and management modules (Fischer et al., 2016; Hiltner et al., 2018) to analyze the forest dynamics at Paracou under selective logging and climate change conditions. FORMIND is a process- and individual-based gap model designed to simulate species-rich forests. It describes the vertical and horizontal forest structure and forest dynamics in 20 m x 20 m patches (Fischer et al., 2016). The simulation area can vary from one hectare to multiple km<sup>2</sup> (here: 16 ha) and consists of multiple patches interacting by tree falling.

In each simulated time step, the core processes of growth, mortality, establishment and competition are calculated on tree level and then summed up on ecosystem level. Light irradiation, temperature, and soil water content affects a tree's biomass increase (eq. 4). The distribution of seeds takes place stochastically throughout the forest floor of a patch. If the light conditions at the forest floor are suitable, new seedlings can establish. Competition between the trees of a patch occurs for light due to shading effects and for space due to crown expansion. Tree mortality increases when the space for crown expansion is limited (self-thinning by crowding), when tree growth is reduced (growth-dependent), and when large trees die damaging surrounding trees (gap formation). In addition, each tree is subject to a stochastic basic mortality. The simulated time steps are one year for forest development and one day for temperature and soil water modules.

The tree species are grouped into plant functional types (PFTs) depending on species-specific properties, such as maximum growth rates, mean wood densities, and maximum tree heights (Hiltner et al., 2018). In this study we simulated the behavior of 8 PFTs grouped into three classes of successional types: light-demanding pioneer species, species of intermediate light demand, and shade-tolerant climax species (see Table A4). The geometry of a tree is simplified assuming cylindrical stems and canopies. The allometric relationships are PFT-specific and depend on the current diameter at breast height (dbh) (see Table A5).

### Implementation of selective logging

To simulate selective logging, we implemented a forest management module in which all trees meeting certain criteria are removed from the simulation area (Hiltner et al., 2018; Huth et al., 2004; Kammesheidt et al., 2002, 2001; Köhler and Huth, 2004; Rüger et al., 2007). Depending on a minimum dbh of the lower cutting threshold of commercial trees ( $dbh_{min}$ ), all exploitable trees meeting the  $dbh_{min}$  of at least 55 cm are felled. The intensity of a logging scenario is set through the rotation cycle. Trees of the remnant forest stand can be damaged by tree falling as well as by the construction of skid trails. Skid trails cover a specific proportion of the forest area and they remain ungrown until a defined number of years after each logging event (here: proportion of total area = 5%, ungrown = 10 a). New skid trails were created for each logging event. The management module is fully described in (Hiltner et al., 2018; Huth et al., 2004).

### Impacts of soil water availability and temperature on tree growth

In the forest model, the precipitation level controls the soil water content in the upper soil layer (here: 2.5 m depth). As a function of the soil water content, the drought-stress-induced reduction factor reduces the photosynthesis rate (i.e., gross primary production, GPP) of the trees (eq. 1; Fischer et al., 2014).

$$RF_W = \begin{cases} 0 & : SW < SW_{pwp} \\ \frac{SW - SW_{pwp}}{SW_{msw} - SW_{pwp}} & : SW_{pwp} < SW < SW_{msw} \\ 1 & : SW > SW_{msw} \end{cases} \quad (1),$$

where  $RF_W$  is the reduction factor of tree photosynthesis due to soil water limitation ( $SW$ ), with  $SW_{pwp}$  as the potential wilting point, and  $SW_{msw}$  as the minimum soil water content for potential GPP of each tree.

The temperature dependencies of tree photosynthesis and maintenance respiration were adapted from the LPJ-model (Rödig et al., 2017; Sitch et al., 2003) and calibrated with eddy covariance data (see Appendix A, data sources and calibration of submodules). A temperature-dependent reduction factor negatively affects the assimilation (eq. 2) and maintenance respiration of trees (eq. 3) if the given temperature differs from the optimum temperature (here:  $T_{opt} = 26.5$  °C) for the potential GPP.

$$RF_T = e^{-\left(\frac{T-T_{opt}}{T_{sig}}\right)^2} \quad (2),$$

with  $RF_T$  as reduction factor for temperature  $T$  with  $opt$  for optimum temperature for potential GPP, and  $sig$  for temperature variance.

$$F_M = Q_{10}^{\frac{T-T_{ref}}{10}} \quad (3),$$

where  $F_M$  is the factor for maintenance respiration,  $Q_{10}$  a constant for temperature-dependent respiration, and  $T_{ref}$  the reference temperature (here: mean annual temperature at Paracou). Thus, the increment of the aboveground biomass of a tree  $t$  ( $\Delta B_t$  [t<sub>ODM</sub> ha<sup>-1</sup>]; ODM: organic dry matter) is:

$$\Delta B_t = (1 - R_{g,t}) \cdot (GPP_t \cdot (L) \cdot RF_{W,t} \cdot RF_{T,t} - R_{m,t} \cdot F_{M,t}) \quad (4),$$

where  $GPP$  [t<sub>ODM</sub> ha<sup>-1</sup>] is the gross primary production,  $L$  is the light climate for a tree  $t$ ,  $R_g$  [0; 1] is the proportion of growth respiration, and  $R_m$  [0; 1] is the proportion of maintenance respiration of a tree. The increment of forest stand biomass  $\Delta B$  is the sum of changes in tree biomass  $\Delta B_t$ :

$$\Delta B = \sum_{t=1}^{t=n} \Delta B_t \quad (5).$$

Biomass increment of a tree  $\Delta B_t$  is translated into stem diameter increment using allometric relationships (Table A5). Stem diameter  $D$  [m] is estimated using a relationship between aboveground biomass and stem volume:

$$B_t = \frac{\pi}{4} \cdot D_t^2 \cdot H_t \cdot F_t \cdot \frac{\rho_t}{\sigma_t} \quad (6),$$

where  $H$  is the tree height [m],  $F$  the form factor [-],  $\rho$  the wood density [t<sub>ODM</sub> m<sup>-3</sup>], and  $\sigma$  the fraction of aboveground biomass attributed to the stem [-]. The stem diameter  $D$  is used to calculate the species-specific tree geometry (e.g., tree height, crown extension; see Hiltner et al. (2018)).

Establishment of seedlings is not directly dependent on precipitation and temperature variability but results from forest dynamics and changes in competition between trees within a forest stand. If the biomass gain of a tree is reduced due to temperature variations, the growth-dependent mortality increases. Higher tree mortality also leads to a more open forest, which promotes the establishment of light-demanding pioneer tree species. Parameter descriptions, values, and references of the temperature and soil water modules are listed in Table

A1. For a full model description, please, see Fischer et al., (2016); for the download of FORMIND, please, see [www.formind.org](http://www.formind.org).

### **Model parameterization approach**

The parameterization of the forest model including the management module for the Paracou site is fully based on Hiltner et al. (2018). In this study, we implemented the soil water and temperature modules. The parameterization of the soil water module relied on information from literature concerning the physical properties of the dominant soil type at the Paracou site, which are Acrisols of sandy clay (Fischer et al., 2014; Gourlet-Fleury et al., 2004; Larcher, 1994; Maidment, 1993). The parameterization of the temperature module was derived from measurements of the microclimate along with eddy covariance data from Paracou between the years 2004–2015. A baseline climate scenario was also derived from this data set. For detailed descriptions of all data sources as well as the determined model parameters and their derived values see Appendix A: Data sources, Calibration of the submodules, Tables A1, A2, and A3.

### **The simulation settings**

The simulation of forest dynamics began on a treeless (empty) area of 16 ha. A period of 1,400 years was simulated with an annual time step for the model output. Simulation results for the spin-up time of 449 years were excluded from further analysis. Logging events with different logging rotation cycles took place from the 500<sup>th</sup> simulation year on. This first logging event was then assigned to the year 2000, in which the simulation of climate change began.

We analyzed three different climatic phases: (i) The time interval [450; 500] corresponded to the pre-climate-change phase and the pre-logging phase (assigned to years 1950–2000). This interval reflected a baseline scenario of a mature forest stand in equilibrium without logging. (ii) The time interval [501; 600] represented the phase of climate change (assigned to years 2001–2100), from which periodically recurring logging events with varying rotation cycles were simulated. (iii) The time interval [601; 1,400] represented a hypothetical phase after climate change, for which we assumed constant climate conditions and continued logging.

In total, three different types of simulation experiments were undertaken: (E1. “climate change”) Simulations of four future climate change scenarios were compared with one simulation under current climate conditions

at the Paracou site. (E2. “Climate change + selective logging”) Eleven scenarios of selective logging with varying logging rotation cycles were simulated under the aforementioned five climate scenarios (Table 1). (E3. “general climate sensitivity”) The general influence of changes in temperature and precipitation on the biomass dynamics at the Paracou site were investigated in a sensitivity analysis using six scenarios per climate variable. The implementation of these three types of simulation experiments will be described in the following subsections:

### **E1: The climate change scenarios**

We implemented climate change scenarios on the basis of four RCP scenarios (RCP 2.6, 4.5, 6.0, 8.5; data source see Table A3) described in the IPCC AR5 (IPCC, 2014a, 2014b) and a baseline scenario called RCP 0.0.

For RCP 0.0, we repeated 10 years of daily recorded (2004–2014) climate data 140 times to get a time series over 1,400 years. Averaged over the entire simulation time, the annual temperature is  $25.7 \pm 0.1$  °C and the annual precipitation is  $3,102 \pm 70$  mm a<sup>-1</sup>. In order to construct RCP-based climate change scenarios (containing 1,400 years of daily values), we used daily values of temperature and precipitation of the RCPs for the 21<sup>st</sup> century (see Figure A1) and extended them according to the following procedures:

- For the pre-climate-change phase (simulated years 0–500), data from ten years (2004–2014) of daily meteorological measurement series for temperature and precipitation from the Paracou site were repeated 50 times.
- For the climate-change phase spanning the years 2001–2100, the RCP (2.6, 4.5, 6.0, and 8.5) data followed (simulated years 501–600).
- To model the hypothetical post-climate change phase, temperature and precipitation values of the last two years of the RCP data were repeated 400 times (simulated years 601–1,400) assuming the climate at the end of the 21<sup>st</sup> century was continued.

Please note that our approach to implementing climate change (RCP 2.6–RCP 8.5) considers extreme events and long-term climate trends in the pre-climate-change phase as well as in the climate-change phase. But in the post-climate-change phase, extreme weather events (e.g., heavy rainfall, seasonality) were

smoothed. Depending on the RCP, temperatures will increase by about 0.6–3 °C for the investigated study region; annual precipitation will decrease by approximately 0–10% while contrasts between dry and rainy seasons will intensify (see Figure A1; IPCC, 2014a).

## **E2: The selective logging scenarios**

We simulated different logging scenarios where the rotation cycles were varied between 10–100 years, in 10 year-steps (Table 1). In this set of logging scenarios, the direction of fall of logged trees was assumed to be random and new skid trails were created for each logging operation. All selective logging scenarios (Table 1) were simulated across the five climate scenarios as described above.

We defined an additional scenario called “moderate logging” which corresponds to the official rotation cycle of French Guiana, where logging is repeated every 65 years. This scenario represents the treatment of Paracou’s T1-plots where 36 m<sup>3</sup> ha<sup>-1</sup> (or 10 trees ha<sup>-1</sup>) were felled during a logging operation.

## **E3. Scenarios for the general climate sensitivity analyses**

To analyze the general sensitivity of forest dynamics to climate variables, we developed two sets of climate scenarios (Set T and Set P), each based on the baseline climate scenario RCP 0.0 (see E1). The amount of variation in temperature in Set T and precipitation in Set P were added or subtracted from the daily values of the RCP 0.0 climate scenario (Table 2), which means that each variable value was equally influenced throughout the time series. These climate scenarios were used to simulate both natural forest dynamics without logging and the moderate logging scenario. We then compared the averaged biomass, GPP, respiration, and mortality of the simulated years 601–1,400.

## **Analysis of the simulation scenarios**

In order to assess the quality of the model, we compared the simulation results of the moderate logging scenario with that derived from the forest inventory data of Paracou’s logged plots (T1-plots). We compared stem numbers and timber volumes of the harvested trees as well as the loss of the mean aboveground forest biomass. For each climate scenario, we evaluated the biomass of the overall forest stand, of the PFTs grouped by successional type (see Table A4), as well as the development of the means and cumulative sums of harvested-timber volumes. We also analyzed the quadratic mean stem diameter (QMD [m]) both for all trees of the forest

stand and of a subset of the total stand. The subset contained only the large, potentially harvestable trees with a  $\text{dbh} \geq 0.55$  m. The development of the standing timber volume of the total forest stand was quantified for the post-climate-change phase. The timber volume (TV [m<sup>3</sup>]) refers to the usable stem volume of the commercial tree species of the Paracou Forest. A cylindrical stem multiplied by a form factor  $f$  is assumed, indicating that a tree's stem is not exactly cylindrical.  $TV$  was calculated as follows:

$$TV = \sum_{i=1}^n \pi/4 \cdot D^2 \cdot h(D) \cdot f(D) \quad (7),$$

where  $D$  is the dbh [m] of the  $i^{\text{th}}$  tree per simulated hectare and  $h$  is the tree height [m] (see Table A5). Software used for analysis of this study is listed in Appendix B.

## Results

### Forest dynamics before and after a moderate logging event

We compared the simulated and observed biomass per functional species group (Figure 1). The model can reproduce the dynamics and species composition of a logged forest. Simulated total biomass matches well with the observed values before and after logging ( $R^2 = 0.82$ ,  $\text{RMSE} = 8.92 \text{ t}_{\text{ODM}} \text{ ha}^{-1}$ ; ODM: organic dry matter) and also the number of commercial trees was consistent (simulated:  $10 \text{ trees ha}^{-1}$ ,  $36 \text{ m}^3 \text{ ha}^{-1}$ , observed:  $10 \text{ trees ha}^{-1}$ ,  $33 \text{ m}^3 \text{ ha}^{-1}$ ). Minor deviations were found between the simulated and observed biomass of climax species and species with intermediate light requirements before felling. For the simulations of forest dynamics after the logging event, the model slightly underestimated the forest biomass development (up to  $38 \text{ t}_{\text{ODM}} \text{ ha}^{-1}$ ), which seems to be mainly due to pioneer species. Overall, the deviations between observed and simulated biomass values were smaller than the observed standard deviation ( $\text{sd}_{\text{obs}} = 67 \text{ t}_{\text{ODM}} \text{ ha}^{-1}$ ).

### Sensitivity of stand biomass to climate variables

Under current climate conditions the simulated forest had a biomass of  $418 \text{ t}_{\text{ODM}} \text{ ha}^{-1}$  (baseline scenario). Results of the sensitivity analyses of temperature and precipitation (experiment E3 “general climate sensitivity”) show different responses to the forest (Figure 2). We found a unimodal curve with its maximum at a temperature of  $26.5^\circ \text{C}$  (Figure 2.a), and an ascending curve when precipitation was below  $2,300 \text{ mm a}^{-1}$  (Figure 2.b). The reduction of biomass occurred due to a decline in GPP and an increase in respiration (see Figure A3). Our results showed that under current climatic conditions, the forest has already reached the maximum of biomass.

For moderate logging we obtained the same general patterns, but with lower biomass values compared to the scenario without logging (Set P =  $-46 \text{ t}_{\text{ODM}} \text{ ha}^{-1}$  and Set T =  $-62 \text{ t}_{\text{ODM}} \text{ ha}^{-1}$ ). Further results on the sensitivity of forest attributes (i.e., maintenance respiration, GPP, and mortality) to climatic drivers can be found in Figure A3.

### **Impacts of climate change on biomass dynamics**

When simulating impacts of climate change (E1 “climate change”), the biomass dynamics changed just a little (Figure 3.a). The development of forest biomass was rather similar in the baseline (RCP 0.0: no climate change) and the RCP 2.6 scenarios (mean  $\text{biomass}_{\text{RCP2.6}} = \text{biomass}_{\text{RCP0.0}} + 5 \text{ t}_{\text{ODM}} \text{ ha}^{-1}$ ; Figure 3.a). Only in the RCP 8.5 scenario, the forest biomass decreased by  $50 \text{ t}_{\text{ODM}} \text{ ha}^{-1}$  after 2100 compared to the baseline value of RCP 0.0 (Figure 3.a). After 2100, it took another 100 years for the forest stand to reach a new biomass equilibrium, but at a lower level. Main driver of this biomass depletion was the temperature increase, which was on average  $3^\circ\text{C}$  warmer per year after 2100 (see Figure A1). This caused changes in the biomass distribution across tree size classes of the forest (Figure A4, unlogged). The aboveground biomass of trees with dbh between 0.2 m–0.9 m decreased due to a decline in GPP and an increase in maintenance respiration; and also, slightly more small pioneer species (dbh < 0.2 m) became recruited (Figures A2, A4).

### **Impacts of selective logging under climate change on forest dynamics**

Here, we evaluate the simultaneous influences of different levels of climatic changes and selective logging on biomass, timber provision, and forest structure in Paracou’s forests (experiment E2 “climate change + selective logging”). In the moderate logging scenario and no climate change (RCP 0.0), all commercial trees were harvested (Figure 3.b), which resulted in a logged stem volume of on average  $36 \text{ m}^3 \text{ ha}^{-1}$  during the first logging (Figure A7), however, it averaged  $27 \text{ m}^3 \text{ ha}^{-1}$  spanning the years after 2100. Our results show that under intensive climate change as represented in RCP 8.5 scenario, biomass degrades more rapidly when timber is felled. The forest stand biomass did not recover after the first logging event at a rotation cycle of 65 a (Figure 3.b). However, the extent of the biomass change depended on the climate scenario: For RCP 8.5, the stand biomass recovered faster after the first logging due to a stronger ingrowth of pioneer species and tree species of intermediate shade-tolerance, whereas the biomass decreased by an average of about  $103 \text{ t}_{\text{ODM}} \text{ ha}^{-1}$  after 2100 compared to the baseline from before 2000 (Figure 3.b). In RCP 2.6, biomass decreased by  $43 \text{ t}_{\text{ODM}} \text{ ha}^{-1}$

compared to the baseline (Figure 3.b); However, biomass increased slightly in RCP 2.6 after 2000 compared to the baseline (Figure 3.b). The results for RCP 4.5 and RCP 6.0 can be found in Figures A2, A4, A5, and A6.

### **Timber provision**

Overall, the harvest volumes at repeated logging under RCP 0.0 and RCP 2.6 are similar (Figures 4.b, 4.c). Mean timber volumes per harvest rises with increasing length of the logging rotation cycle (Figure 4.b). For rotation cycles longer than 70 years, harvested timber volumes came to saturation. At a rotation cycle of 70 years, an average timber volume of  $25 \text{ m}^3 \text{ ha}^{-1}$  or 8 trees  $\text{ha}^{-1}$  per event could be harvested in the long term. Regarding the cumulative timber harvest volume, rotation cycles at 50–60 years provided an optimum total timber harvest volume (Figure 4.c). In the climate change scenarios RCP 0.0 and RCP 2.6, the shorter the rotation cycles were, the slightly higher the harvest. The official rotation cycle of 65 years is therefore sustainable under these climate scenarios (Figure A7: RCP 0.0 and RCP 2.6).

Compared to the climate scenarios RCP 0.0 and RCP 2.6, the average volume of timber per harvest decreased by 40% under RCP 8.5 (Figure 4.b;  $\text{TV}_{\text{RCP2.6}} = 25.5 \text{ m}^3 \text{ ha}^{-1}$  or 8.23 trees  $\text{ha}^{-1}$ ,  $\text{TV}_{\text{RCP8.5}} = 15.2 \text{ m}^3 \text{ ha}^{-1}$  or 5.18 trees  $\text{ha}^{-1}$ ). In this case, the official rotation cycle of French Guiana of 65 years caused a reduction of timber volume, whereas a logging rotation cycle of 100 years is sustainable (Figure 4.a). Harvest failures occurred for some logging events in a 10-year rotation cycle (Figure 4.a). For RCP 8.5, cumulative timber volume was maximized at logging rotation cycles between 50 and 60 years (Figure 4.c).

### **Forest structure and harvest potential**

In this study, we used the quadratic mean stem diameter (QMD) to evaluate the forest structure, i.e., the distribution of tree sizes in the forest across different logging and climate scenarios. QMD increases with longer logging rotation cycles, while stronger changes in climate led to lower values. Compared to the baseline scenario ( $\text{QMD}_{\text{BL}} = 21.2 \text{ cm}$ , no logging), the QMD for short logging rotation cycles dropped to 18.3 cm and 17.2 cm for RCP 2.6 and RCP 8.5, respectively (Figure 5.a). The stand biomass (Figure 5.b) and the biomass of commercially exploitable trees in the stand (Figure 5.c) decreased consistently with stronger climate change and linearly with shorter rotation cycles. The effects of logging damages in the remaining stand reduced the biomass stocks of potential crop trees (Figure 5.c).

## Discussion

### Impacts of climate change on forest dynamics and forest structure

We simulated the forest dynamics of the Paracou forest for the 21<sup>st</sup> century using an individual-based forest model in which demographic processes are explicit and tree species diversity is described using functional species groups (PFTs). For the RCP 8.5 scenario, biomass production decreased compared to the baseline. Our analyses of the model sensitivity identified rising temperatures as strong climate drivers of this behavior.

It is likely that temperatures will rise in the future in many tropical regions (IPCC, 2014a), exposing rainforests to novel temperature regimes. In particular, the Amazon Basin has already been affected by a warming trend of 0.63 °C over the 20<sup>th</sup> century (Victoria et al., 1998). Under climate change conditions, precipitation in the Amazon varied more strongly regionally and seasonally (IPCC, 2014a; Marengo et al., 2009). The period 1950–1970 was wet in the northern Amazon but since 1977 this region has become drier (IPCC, 2014a; Marengo et al., 2009). General circulation models project a regional temperature increase of 2–4 °C by 2100 and a decrease in precipitation specifically during dry seasons (IPCC, 2014a; 2014b). The IPCC's special report (IPCC, 2018) assumed that functions of different terrestrial ecosystems are likely to show only minor changes if the global average temperature increase remains below 1.5 °C. This holds true for simulation results of Paracou's forests for the RCP 2.6 scenario, in which the forest biomass remained rather stable until 2100. Even under assumptions of the RCP 8.5 climate scenario (+ 3.0 °C), the forests of Paracou were able to buffer changes in temperature and precipitation without occurrence of tipping points. The forest stand biomass decreased by 25%, as warming caused reductions in the trees' GPP as well as an increase in respiration and growth-dependent tree mortality. Aubry-Kientz et al. (2019) simulated the effects of climate change on forest growth at Paracou. They estimated a decline in the forests' average stem diameter growth rates of 36% (RCP 8.5) until 2100. A reduction of biomass production would have negative long-term effects on carbon sequestration and timber supply (de Groot et al., 2002).

Mean annual precipitation in French Guiana is expected to change only slightly until 2100. Thus, variations of mean annual precipitation levels are less relevant for forest dynamics than those of temperature. In our study, species composition was negatively affected in RCP 8.5, resulting in a decline in the gross primary production

of shade-tolerant slow-growing species. Large commercial trees with a dbh greater than 0.9 m will be largely replaced by small and fast-growing tree species. The shift in species composition is caused by a change in the competitive situation within the forest. Pioneer species establish more quickly in forest gaps. Cheesman and Winter (2013) studied the negative effects of strong warming (e.g., RCP 8.5) on the growth of juvenile plants in tropical forests. While non-pioneer species showed a significant decrease in growth rates under intense warming, the growth of pioneer species was only slightly reduced. Moreover, pioneer species were able to adapt to thermal conditions faster than non-pioneer species.

The strength of the present study is that climate effects (at daily resolutions) were modeled at the individual tree level and then analyzed at the ecosystem level. We focused on long-term consequences of climate change and logging. This is a major advantage of forest modeling approaches compared to empirical experiments, which can explore only short time periods (Fischer et al., 2016).

### **Impacts of selective logging under climate change**

Climate change poses challenges for management pre-planning, as it will affect the dynamics and structures of tropical forests. When pre-planning logging, it can become important to consider long-term climate change effects to facilitate sustainable forest management. Our study suggests that the combination of two forcing factors (logging and climate change) had stronger negative impacts on biomass stocks, standing timber supply, and timber harvest than the individual factors alone (logging or climate change). Carbon sequestration in living biomass of forests depends strongly on management parameters such as the cutting rate, damage to the remaining stand, and rotation cycles (Hiltner et al., 2018; Knoke, 2016). Another study on Paracou's forests showed that in once-felled forests, about 78% of the biomass can remain in the stand and biomass recovered to pre-harvest values after ca. 80 years (Hiltner et al., 2018). In our study, we demonstrated a negative effect of repeated harvesting during the recovery time on stand biomass, QMD, and timber volume. A reduction of harvest volumes after the first logging has been discussed with regard to sustainable timber production (Knoke, 2016; Putz et al., 2012; Roopsind et al., 2018). Harvest reduction depends on details of the applied forest management strategy, such as the logging rotation cycle, cutting rate, damage to the remaining stand, and overexploitation of a particular commercial tree species (Huth and Ditzer, 2001; Knoke, 2016; Putz et al., 2012; Roopsind et al., 2018).

Repeated logging may also affect the abundance of commercial tree species. If, for example, the same tree species is harvested in a second logging as in the first harvest, the yield can be reduced by as much as 60% (for a 40-year rotation cycle; Knoke, 2016; Putz et al., 2012). In our moderate logging scenario, the harvested timber volume after the first logging remained stable for rotation cycles longer than 65 years for RCP 2.6. Under the RCP 8.5 scenario, the rotation cycle needed to be expanded to 100 years to avoid timber volume degradation. Tropical forest management is currently confronted with developing diversification strategies for commercially used species (Knoke, 2016). This requires more flexibility in species selection, i.e., harvesting from a larger pool of tree species rather than targeting the same species at each logging event (Knoke, 2016; Putz et al., 2012). In French Guiana, logging mainly concentrated on only four commercial species (Piponiot et al., 2016) (*Dicorynia guianensis*: 67%, *Qualea rosea*, *Ruitzenaria albiflora*: 12%, *Sextonia rubra*: 9%) despite of a much larger pool of economically viable species (e.g., 74 tree species at Paracou; see our Appendix C). Hence, the relative abundance of these commercial species for the next logging event is inevitably lower (Piponiot et al., 2018) and after a few harvest cycles their proportion maybe turn so small that their use would not be economically viable anymore. The smaller the pool of commercial species, the greater the depletion (Piponiot et al., 2019). We showed that the regenerative capacity of the forest will decline under climate change conditions. Thus, diversifying the pool of harvested species can reduce the pressure on the currently limited pool of target species.

### **Limitations and perspectives of the approach**

Our results show that even in the RCP 8.5 scenario, the forest was able to buffer the consequences with no tipping points. Please note that we do not consider disturbance events caused by climate change in this study. Extreme, abrupt disturbance events such as flooding, or storms, could cause also larger changes in forest dynamics and are prevalent natural stressors in the Amazon Basin (Barlow et al., 2003; Espírito-Santo et al., 2010; Esquivel-Muelbert et al., 2020; Magnabosco Marra et al., 2018; Negrón-Juárez et al., 2018, 2010; Rowland et al., 2015). This holds also for Paracou, where the number of fallen trees is higher in the wettest years (Aubry-Kientz et al., 2015). The trees uproot more easily when the soil is saturated with water. Therefore, the total stand biomass had decreased after such events, mainly because of tree mortality (Aubry-Kientz et al., 2015).

In our model, existing ecological consequences of climate change on the growth of trees were taken into account via different reduction factors (eq. 1). This approach involves some limitations due to simplified assumptions. For example, we consider a simplified approach to determine at which specific temperature the CO<sub>2</sub> assimilation of trees stops when temperatures deviate strongly from the optimal temperature for photosynthesis. Beside the CO<sub>2</sub> assimilation, also tree respiration depends on temperature. Based on the Q10-law, we can reproduce well the dependence of maintenance respiration on temperature (Bohn et al., 2014; Prentice et al., 1993). Moreover, CO<sub>2</sub> assimilation of trees in the model is limited by water scarcity (Fischer et al., 2014). So far, the effects of soil water supersaturation are not included. We aim to integrate these effects into our future work.

Individual-based forest models have the advantage that the simulation results can be compared one-to-one with data from forest inventories. Simulation results can be analyzed at the ecosystem level, which is crucial for projecting the long-term ecological impacts of climate change and forest management on the growth variability of tropical forest stands. The results from such model simulations can be used to determine whether current forest management activities will be sustainable even under future climate change conditions (Aubry-Kientz et al., 2019; Huth and Ditzer, 2000; Piponiot et al., 2019; Sist and Ferreira, 2007). In this context, forest models offer excellent possibilities, as they allow a comprehensive assessment and complement empirical analyses. Furthermore, their methodology is generic enough to be transferred to other forest locations as climate change scenarios for new locations can be extracted from available global climate models. Furthermore, different forest management strategies can be directly integrated into the model, such as conventional logging, reduced-impact logging, and thinning of potential crop trees. In future, more and more forest inventories and remote sensing data will become available that can be used for the parameterization of dynamic forest models and the validation of their simulation results (Hansen et al., 2013; Knapp et al., 2018; Lausch et al., 2018b, 2018a; Piponiot et al., 2019, 2018). This will help to enhance forest models.

Internationally, action programs have been established to reduce the negative impacts of deforestation on forests. The climate change mitigation program REDD+ (Danielsen et al., 2011; Dourdain and Hérault, 2015) and certification schemes such as FSC and PEFC (Clark and Kozar, 2011) are exemplary. Programs like these

create incentives encouraging forest transformation through compensation payments or certification of sustainably produced timber products (Long, 2013). If timber and carbon stocks do not recover from damage through harvesting within sufficiently extended rotation cycles, tropical production forests may degrade. To develop sustainable strategies for tropical forest management, simulation studies are a useful tool. The advantage of simulation studies is the investigation of the long-term effects of timber use under different climatic conditions; such investigations are not possible with empirical studies. By combining empirical data, climate change projections and forest models, we can derive recommendations on whether proposed strategies are sustainable in terms of carbon sequestration and timber supply. With moderate logging and moderate climate change conditions, we recommend keeping the official rotation cycle of 65 years for the forests around Paracou (for maintaining a sustainable harvest). The rotation cycle would have to be extended to 100 years under severe climate change conditions. This extended cycle ensures the regrowth of commercial trees and thus sustainable use.

## Conclusions

Main goal of this study was to assess the impacts of climate change on a neotropical forest in combination with forest management. We were able to (i) develop a parameterization for a forest model including management as well as soil water and temperature modules, and (ii) to evaluate important forest attributes (i.e., biomass, timber volume, and QMD) with a high degree of detail.

Our simulation results support the conclusions of the IPCC for the specific case of a forest in French Guiana (IPCC, 2018). With moderate climate change (RCP 2.6: null anthropogenic CO<sub>2</sub>-emissions until 2100), the biomass and harvested timber volume remained almost constant compared to current climate conditions. Under current climate or RCP 2.6, we recommend limiting logging intensity to 3–5 commercial trees ha<sup>-1</sup>, with a minimum cutting threshold of at least 55 cm dbh and a minimum logging rotation cycle of 65 years. Such a strategy would help to prevent forest degradation in the long term (i.e., over several centuries). Moreover, we were successful in demonstrating the extent to which the volume of timber dropped from the second harvest onwards. Assuming intensive climate change (RCP 8.5), timber harvests decreased by approximately 40% on average over the next centuries, irrespective of the rotation cycle. For the RCP 8.5 scenario, we were not able

to identify a strategy to prevent the long-term degradation of biomass and timber harvests. Forest degradation was even accelerated when short logging rotation cycles were assumed. This implies, logging damages should generally be reduced as much as possible in order to maintain the carbon storage capacities of forests.

The forests studied here are characteristic of the Guiana Shield (Guitet et al., 2018), an ancient geological formation in the northern part of South America. These are often dense and grow on very poor soils (Grau et al., 2017). This results in low tree growth, mortality, and recruitment rates (Piponiot et al., 2016). Simulation studies like this may help to facilitate decision-making processes, for instance, for REDD+ or certification systems. Thus, the innovative use of forest models will contribute to the development of economically and ecologically feasible forest management strategies in the context of climate change.

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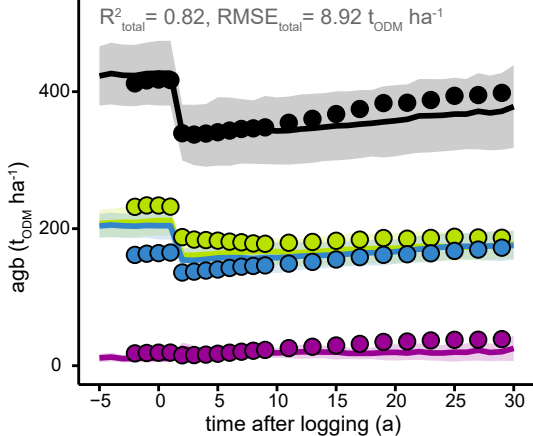
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 789 8137(CAT)FEATUREISSUES(VI)DROUGHTINDUCEDFORESTMORTALITY  
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Figure 16, 1 column 16 stems  $\text{m}^{-3} \text{ha}^{-1}$  [Click here to access/download;F](#)



*successional  
type:*

climax

mid

pioneer

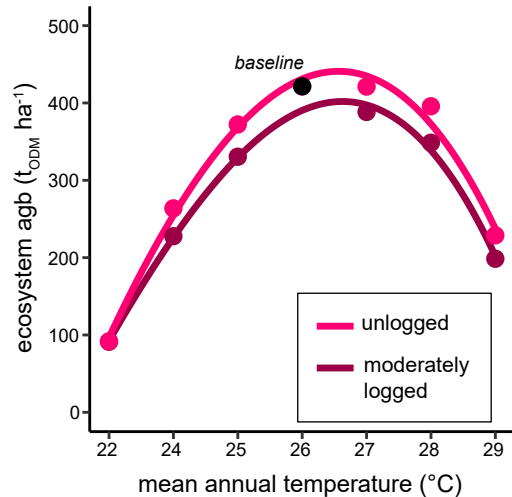
total

*data:*

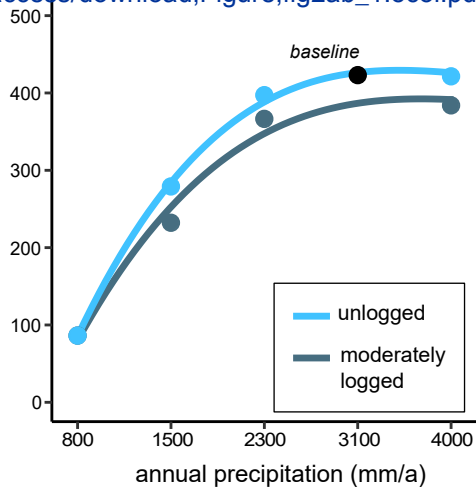
simulated

○ observed

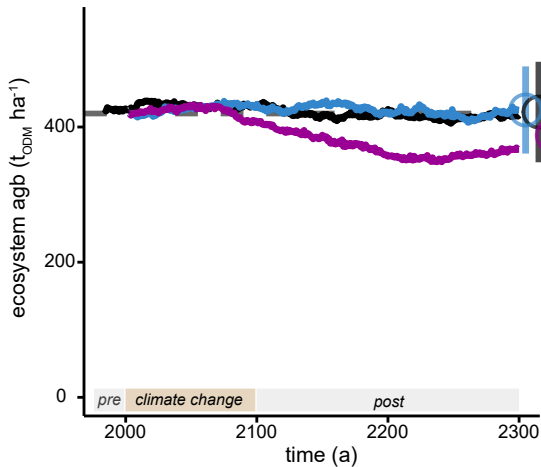
a) Figure 2, 1.5 column width



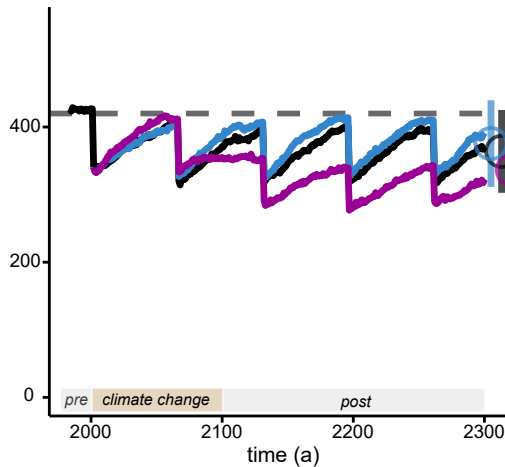
b) [Click here to access/download;Figure;fig2ab\\_1.5col.pdf](#)



a) Figure 3, 1.5 column width  
no logging



b) Click here to  
access/download; Figure; fig3ab\_1.5col.pdf  
moderate logging  
Rotation cycle: 65 yrs.



IPCC AR5-  
based scenario:

— RCP 0.0

— RCP 2.6

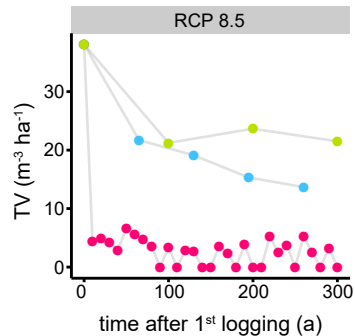
— RCP 8.5

statistics:

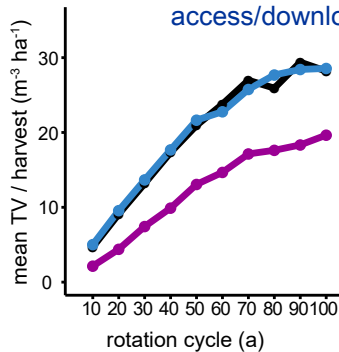
○ arithmetic mean

▮ standard deviation

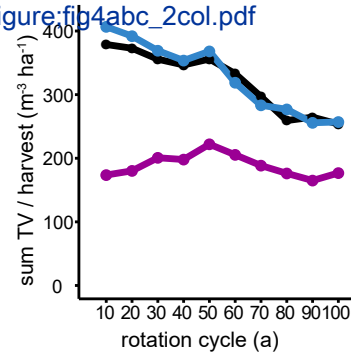
a) Figure 4, 2 column width



b)



c)



rotation cycle (a):

● 10 ● 65 ● 100

IPCC AR5-based scenario:

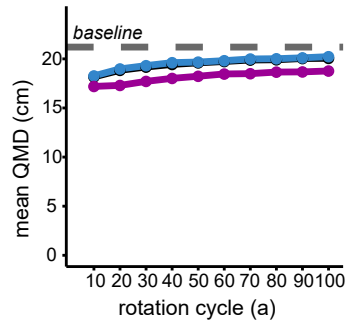
— RCP 0.0

— RCP 2.6

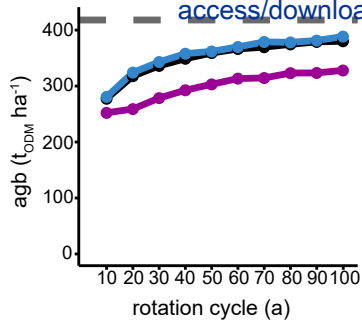
— RCP 8.5

[Click here to access/download;Figure:fig4abc\\_2col.pdf](#)

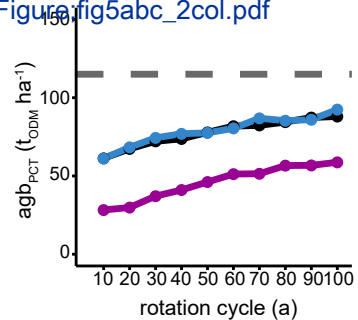
a) Figure 5, 2 columns width



b)



c)



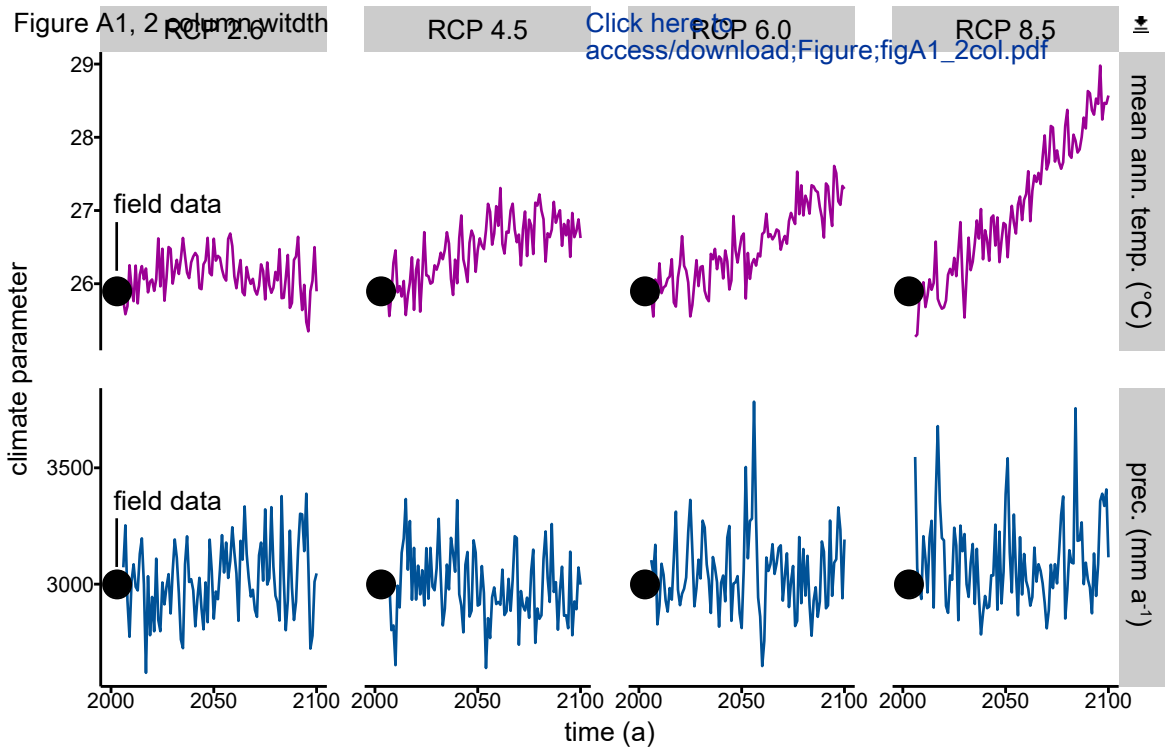
IPCC AR5-

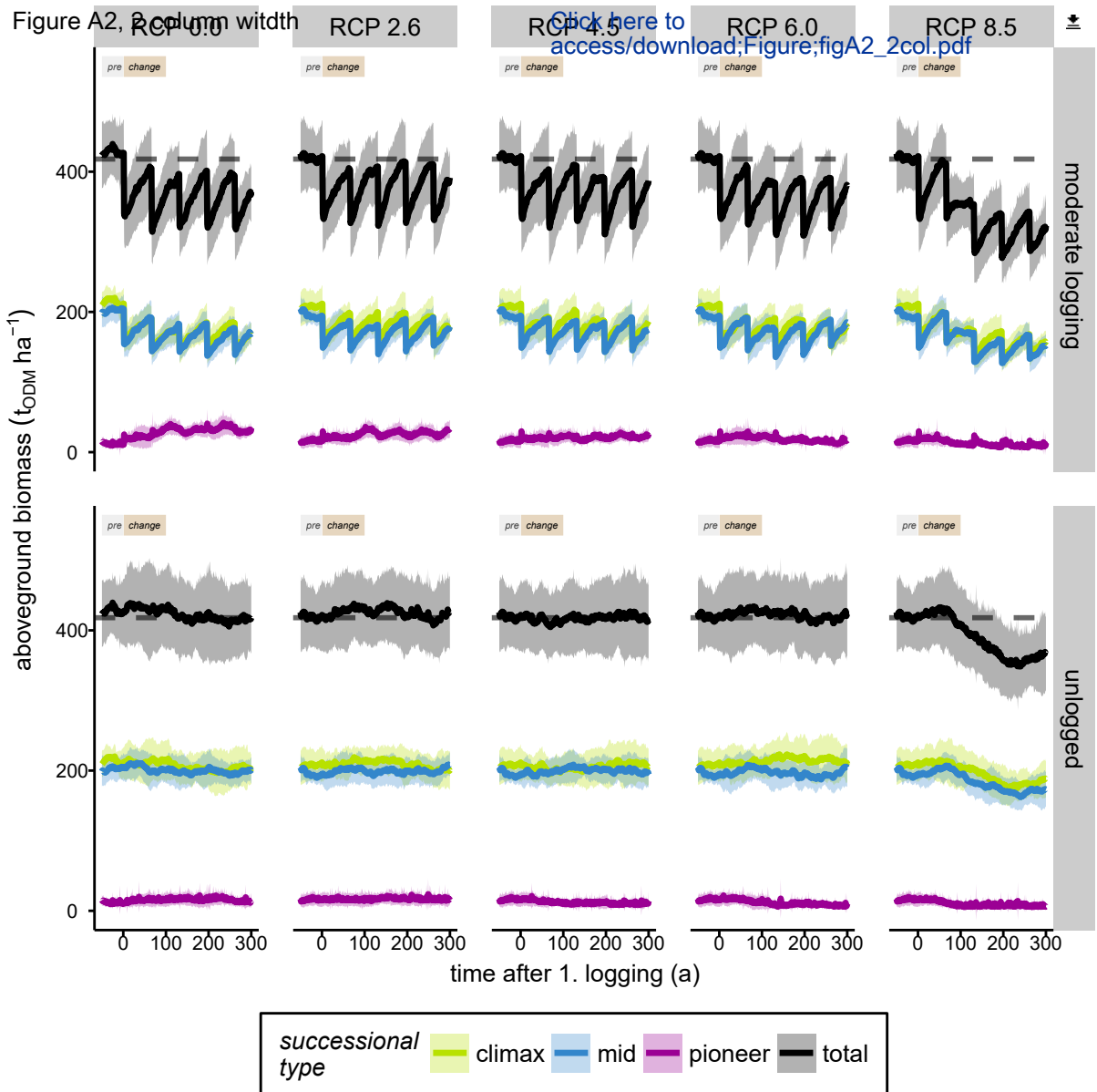
based scenario:

— RCP 0.0

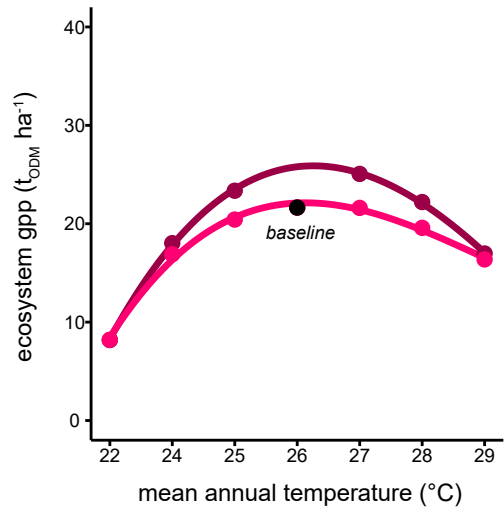
— RCP 2.6

— RCP 8.5



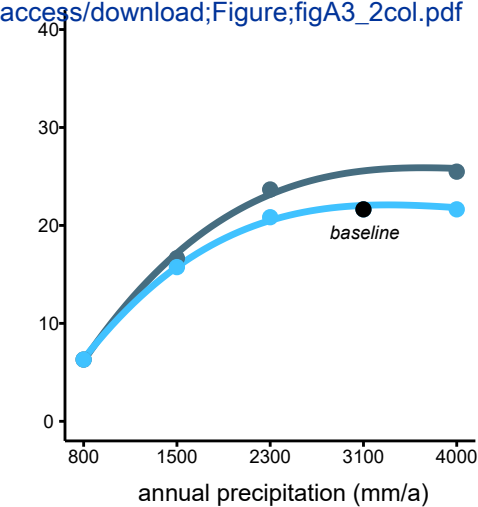


a) Figure A3, 2 column width

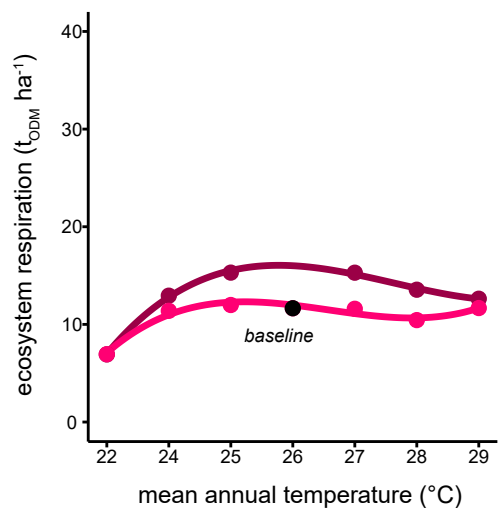


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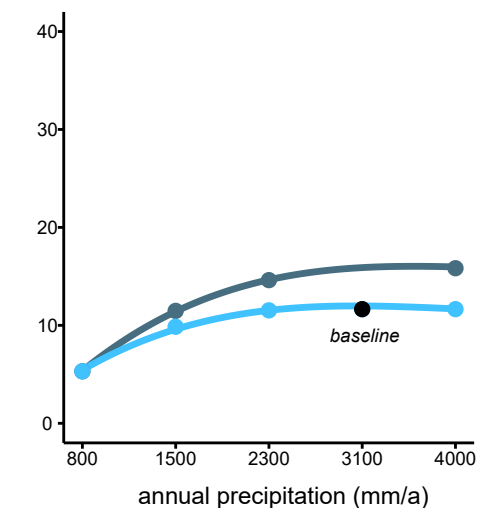
[Click here to access/download;Figure;figA3\\_2col.pdf](#)



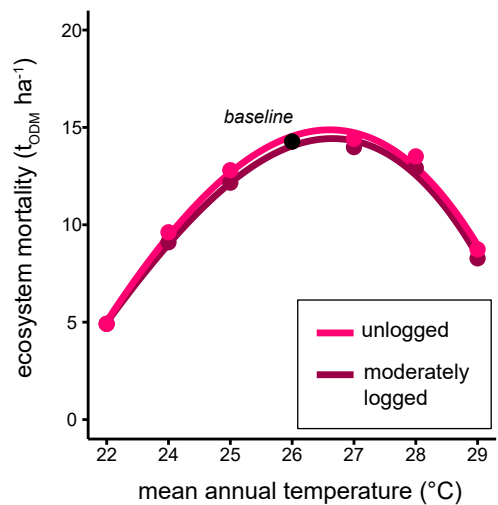
c)



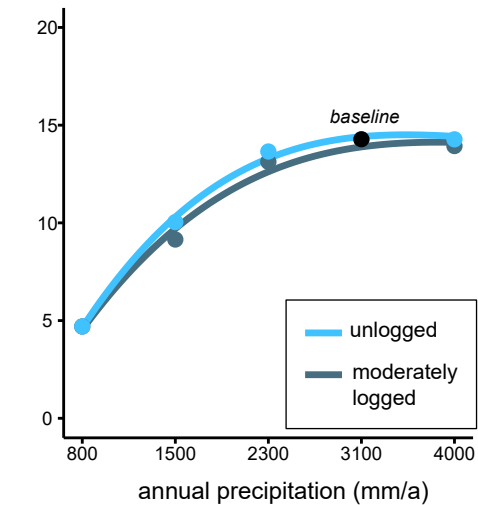
d)

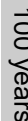


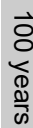
e)

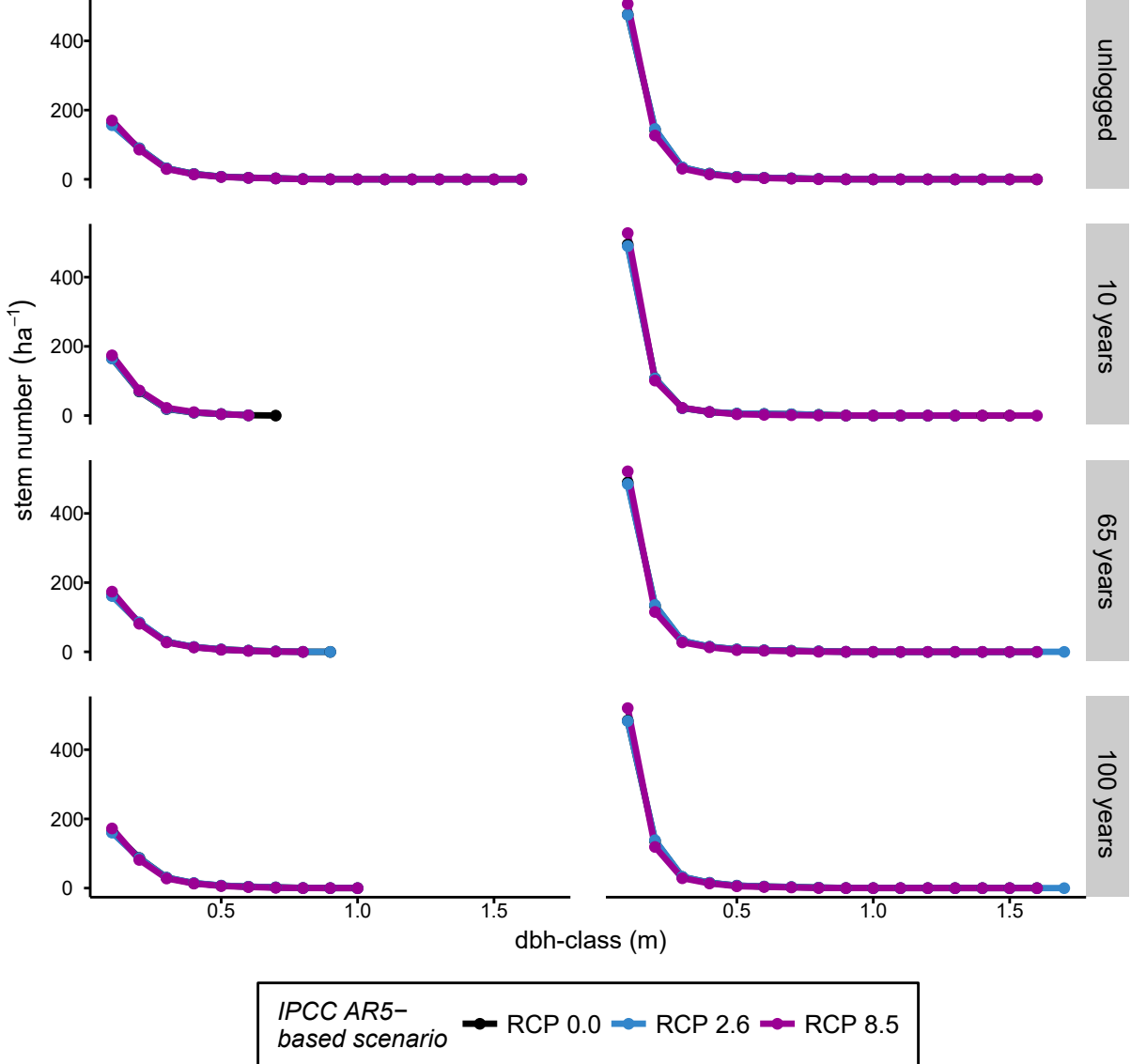


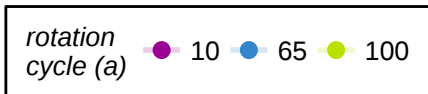
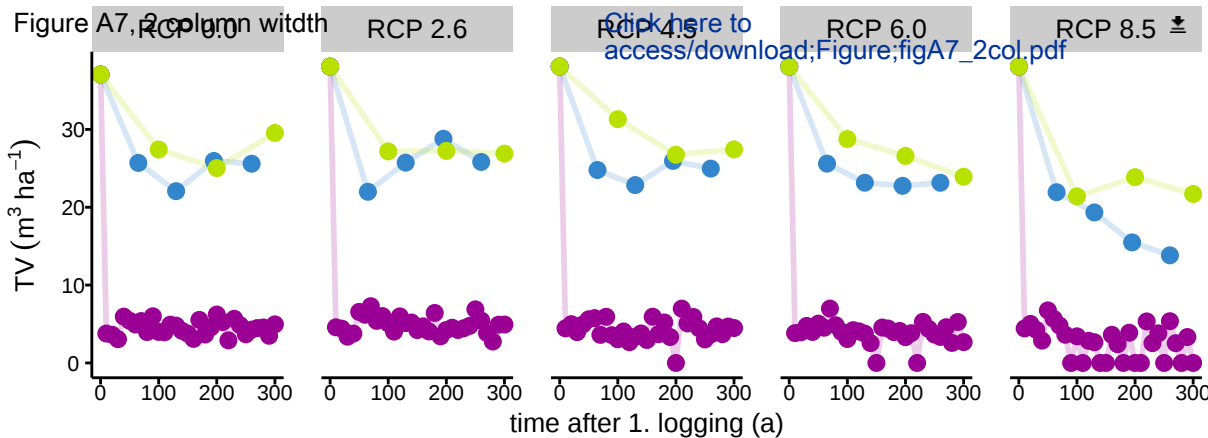
f)











## Tables

Table 1: Overview about the simulation settings of the model parameters varied to develop the selective logging scenarios. Each single logging scenario was paired with all five climate scenarios developed.  $\text{dbh}_{\text{min}}$ : minimum stem diameter at breast height of the lower cutting threshold of commercial trees.

| Variable                                                  | Unit | Value                  |
|-----------------------------------------------------------|------|------------------------|
| <b>Moderate logging:</b>                                  |      |                        |
| Rotation cycle                                            | a    | 65                     |
| $\text{dbh}_{\text{min}}$                                 | cm   | 55                     |
| Damages to the forest by falling trees                    | -    | controlled             |
| <b>Other logging scenarios based on moderate logging:</b> |      |                        |
| Rotation cycle                                            | a    | {10, 20, 30, ..., 100} |
| Damages to the forest by falling trees                    | -    | un-controlled          |

Table 2: Overview about the simulation settings for the sensitivity analysis of temperature (T) and precipitation (P) altering climate factors individually. The amount of variation in T and P was added or subtracted from the daily values of the RCP 0.0 climate scenario.

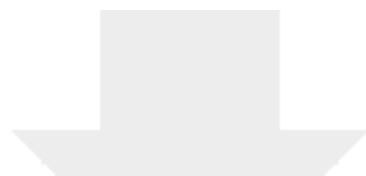
| Variable          | Unit               | Amount of variation               |
|-------------------|--------------------|-----------------------------------|
| <b>Set T</b>      |                    |                                   |
| $\Delta T$        | °C                 | {-1.0, -2.0, -4.0, 1.0, 2.0, 4.0} |
| Forest management | -                  | {moderate logging, unlogged}      |
| <b>Set P</b>      |                    |                                   |
| $\Delta P$        | mm a <sup>-1</sup> | {-25%, -50%, -75%, 25%, 50%, 75%} |
| Forest management | -                  | {moderate logging, unlogged}      |

## **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.

### **Author's statement**

A.H., R.F., and U.H. conceived and designed the experiments. B.H. and U.H. acquired and managed the data. A.Ho. contributed in eddy covariance data processing. U.H. performed the simulations. A.B., A.H., B.H., R.F. and U.H. contributed in analysis and discussion. U.H. wrote the manuscript. A.B, A.H., A.Ho., B.H., R.F., and U.H. reviewed the manuscript.



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**Supplementary Material**

**Appendices\_FORECO\_2019\_1263\_R3\_final.DOCX**

