

# Spatial modeling of primary and secondary forest growth in Amazonia

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## Abstract

A stand level growth model for primary and secondary forest in the Amazon region is presented. The approach is empirical and relies on an extended amount of forest inventory data for model calibration. We used a total of 368 sample plots with 469 ha from primary forest and 330 sample plots with 30.8 ha from secondary forest. The data come from eight countries and are distributed over tropical forests in all of Amazonia. We interpolated primary forest descriptors spatially in virtue of their dependence on biophysical conditions. Secondary forest parameters were described by a set of differential equations, in which the primary forest functioned as asymptotes of the growth processes. A state-space approach to growth modeling allowed for derivation of other forest parameters from models for state variables by auxiliary relationships. The fitted models offer a spatially explicit description of growth and increment over all the tropical forests in Amazonia on a large scale. As a function of biophysiology and of forest age, the models specify individual secondary forest growth curves at the level of grid cells. We calculated grids for forest parameters and their increments in primary and secondary forests of various ages. In primary forest, total basal area ranged between 22 and 33 m<sup>2</sup> ha<sup>-1</sup>, top height was 10–35 m, there were 400–850 individuals per hectare, and standing alive above-ground biomass ranged between 110 and 370 t ha<sup>-1</sup>. The biomass model was validated by comparing predictions at various successional stages from different locations in Amazonia against independent reference data. Despite a small negative bias, the RMSE for standing alive above-ground biomass amounted to only 38 t ha<sup>-1</sup>.

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## 1. Introduction

The growth of the Amazon forest and its dynamics receive scientific attention both in the context of forest

management (Silva et al., 1996), and of ecology and global change (Moorcroft et al., 2001; Zarin et al., 2001). For some regions growth models have been proposed (Neeff and dos Santos, 2005; da Silva et al., 2002; Silva et al., 1996) and efforts are being undertaken to unify data sources (Malhi et al., 2002). However, science is still far from achieving accurate

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and comprehensive description of forest conditions and dynamics over the vast and diverse Amazon region.

Biomass and its spatial distribution are key variables for carbon budget estimation. The scientific community recognizes the need for accurate methods to determine biomass in the Amazon (Schimel et al., 2001; Houghton et al., 2000). Vegetation models are considered indispensable, because common remote sensing data sources are incapable to directly measure biomass (Houghton et al., 2001). While remote sensing could provide information on distribution and extension of vegetation types, models of vegetation characteristics are required that would describe potential biomass stocks and dynamics for a forest of a given type and a certain age at a specific location (Neeff et al., 2005). Forest growth models provide means to accurately estimate forest biomass and carbon sequestration rates when linked to data on primary and secondary forest cover (Moorcroft et al., 2001).

In this paper, we venture to describe the growth and increment of tropical forests in the Amazon region. This research largely represents a generalization of methods developed by Neeff and dos Santos (2005), who applied a standard approach for stand level forest growth modeling. Empirical models that base on biophysical parameters were adjusted to a large dataset of forest inventories. The presented growth model encompasses the major descriptors of tropical forests across Amazonia at arbitrary successional stages. In a larger research effort, we intend to link the growth model to large-scale remote sensing results and a land-use change model (Neeff et al., *in press*). Our ultimate goal is to extend methods for carbon budgeting applied by Neeff et al. (2005) to all of Amazonia in order to describe the carbon balance arising from forest dynamics during the last decades in a spatially explicit way.

## 2. Material

### 2.1. Collection of forest inventory data

The classical experimental design to collect data for forest growth modeling consists of permanent forest plots, that are inventoried periodically over an extended period of time (Vanclay, 1994). Such data are not easily available for the case of tropical primary and

secondary forest (Vanclay, 1994). Therefore, we used a collection of plots from several sites, various years, and of different sizes. All of them were measured, adopting similar methods in field work, and all of them represent tropical forests in Amazonia. We compiled a dataset of primary and secondary forest inventories from a variety of different sources, both published forest inventory results and original forest inventory data were collected (see Appendix A).

A major problem in using published forest inventory results is the incompatibility of the methodologies for field work and data processing applied by the researchers. Differing minimum measured diameters, varying treatments of dead trees or nontree species, and differing allometric equations can be an additional source of variance and potentially introduce bias into the analysis. Therefore, an effort was undertaken to collect original tree-by-tree data from forest inventories conducted by many researchers in Amazonia. Additionally, a number of sample plots were compiled from literature. Here, we had less control over forest measurement methodology, but we felt it was necessary to complement the original tree-by-tree data with data from other sources (see Appendix A).

A number of datapoints were excluded from the analysis for one of the following reasons: minimum diameters from field measurements were too high, the plots were too small to compute the standard forest parameters (particularly top height), the plot did not correspond to a forest ecosystem, or supposedly primary forest underwent logging before. In total, the database on forest growth, that we deemed appropriate for calibration purposes, contained 60.7 ha (172 plots) of primary forest inventories on a tree-by-tree basis and 385.9 ha (186 plots) from other sources. Secondary forest inventories amounted to a total of 16 ha (230 plots) on a tree-by-tree basis and 5.3 ha (64 plots) from other sources. Validation data, where only biomass measurements were conducted, were available for 22.4 ha (10 plots) of primary forests and for 9.5 ha (36 plots) of secondary forests. The data were collected from the 1950s till present. The data come from almost all countries that share the Amazon forest: Bolivia, Brazil, Colombia, Ecuador, French Guiana, Peru, Suriname, and Venezuela; the plots were widespread over Amazonia (see Fig. 1).

Different minimum diameters are commonly applied when dealing with forests at different ages.

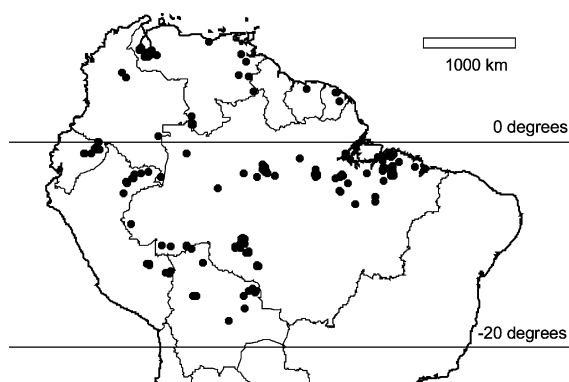


Fig. 1. Dataset of tropical forest inventories in the Amazon. Plots come from a variety of different sources as listed in Appendix A.

We attempted to use a minimum diameter of 3 cm for initial regrowing vegetation at 4 years or less of age, of 5 cm for secondary forest above age five, and of 10 cm for advanced secondary forest above age 50 and for primary forest. All data sources where the minimum measured tree diameter was above 10 cm were excluded. This is why forest inventories mainly aiming for economic forest assessment (e.g. Radam-brasil) could not be incorporated.

## 2.2. Processing of forest inventory data

We calculated standard forest parameters as defined by Loetsch et al. (1973): total basal area  $B$ , top height  $H$ , number of individuals  $N$ , mean basal area  $\bar{b}$ , mean diameter at breast height  $\bar{d}_{1.3}$ , and mean height  $\bar{h}$ . The concept of top height builds on taking the arithmetic mean of only a subset of the tallest individuals of a stand, such that  $H \geq \bar{h}$  (Loetsch et al., 1973). Here, the subset corresponded to the tallest 20% of all individuals.

Above-ground biomass  $AGB$  was derived tree-wise from an allometric equation published by Brown et al. (1989) for tropical moist forest ( $n = 168$ ,  $r^2 = 0.97$ ), that draws on diameter at breast height  $d_{1.3}$  (cm) and total tree height  $h$  (m) to arrive at the total above-ground biomass (kg per tree):

$$AGB = \exp\{-3.1141 + 0.9719 \log(d_{1.3}^2 h)\}. \quad (1)$$

We used only one allometric equation for all types of forest and all diameter ranges, and we made no

allowance for differences in tree shape or wood density. Standwise biomass was computed by summing up all trees. We did not deal with any other biomass fractions than standing alive above-ground biomass of tree species.

## 2.3. Biophysical dataset

A climatological and geophysical dataset for Amazonia was collected for compilation of a database on possible biophysical determinants of forest growth (see Appendix B). All input grids were resampled by a nearest-neighbor algorithm to a cell size of 0.1 decimal degrees (ca. 11 km at the equator). In principle, other resolutions are possible. All data processing took place in a geographical projection system. In some cases data had to be reprojected before incorporation into the database.

We recovered the area extension of the tropical Amazon forest by a map of global ecological zones that is based on the results of FAO's Forest Resource Assessment (see Appendix B).

The distance to the equator  $D_E$  and the distance to the coastline  $D_C$  were derived from a South America map.

Elevation over sea level  $E$  was derived from the digital elevation model of the GTOPO30 project (Appendix B). GTOPO30 is a global digital elevation model at a spatial resolution of 30 arc seconds that has been compiled from a number of different sources. The vertical accuracy is specified by the providers by an RMSE ranging mostly between 18 and 97 m.

An appropriate climate dataset was provided by the LBA Hydronet collection, which contains long-term monthly averages (1961–1990) of various climatic variables gridded at  $0.1^\circ$  resolution (Appendix B). These data have been interpolated from station data. From the climatological dataset we generated the following variables:  $T$  is the long-term mean annual temperature,  $T_\Delta$  the difference between mean temperature of hottest and coldest month,  $P$  the long-term mean annual precipitation,  $P_\Delta$  the difference between mean precipitation of wettest and driest month,  $C$  the long-term mean cloud cover, and  $V$  the long-term mean vapor pressure.

Our data on soil properties based on the FAO soil map of the world (Appendix B). The classification holds soil texture  $Tx$  in seven levels at coarse, medium, fine and organic. Soil profile depth  $PD$  is an estimate

of the depth from the soil surface to bedrock or other impermeable layers.

### 3. Methods

#### 3.1. Overview

We endeavour to model growth and increment of tropical forests in Amazonia. Our model addresses natural forests as it grows spontaneously at terrestrial sites after disturbance. While plantations are not included, the model describes vegetation at all successional stages from early regrowth to primary forests.

Stand level forest growth was modeled by a classical ecological approach based on state variables (Vanclay, 1994). The state space approach to modeling forest growth images the stand by a few stand parameters (here, total basal area, top height, and number of individuals). Other forest parameters of interest (diameter, biomass, etc.) are incorporated by auxiliary relationships. It is assumed that the state variables sufficiently summarize the stand, and that growth can be predicted just by updating the state variables (Vanclay, 1994).

Primary forest parameters at stand level as given by forest inventories (Appendix A) were related to biophysical parameters as given by regional maps (Appendix B). In a first step, we derived equations that described the statistical relationship of forest parameters to the biophysical site properties. In a second step, we applied these equations to derive grids of potential primary forest conditions for all tropical forests of Amazonia. Later, the grids were used as asymptotic conditions for secondary forest growth.

Secondary forest parameters were modeled as a function of time by a set of differential equations. We introduced a spatial component into a common model for forest growth by an extension: we considered growth asymptotes as locally differing according to site properties, while maintaining the other growth parameters as global variables. The local growth asymptotes corresponded to the primary forest conditions and were dealt with in the primary forest model, separately from the secondary forest model. The global parameters of secondary forest growth were fitted using the forest inventory dataset. The

fitted model describes secondary forest growth on a pixel grid.

All calculations, particularly the fitting of both linear and nonlinear least-squares models, accounted for different plot sizes. According to the approach from Neeff and dos Santos (2005) all reported statistics were area-weighted. Given the spatial heterogeneity of forest descriptors even between close-by locations, the use of plots at different sizes with differing numbers of tree individuals would otherwise lead to a nonconstant variance. Thus, the variance function of any forest parameter  $Y$  must include the forest area  $A$ , the parameter refers to:

$$\text{Var}(Y) = \frac{\sigma_Y^2}{A}. \quad (2)$$

#### 3.2. Primary forest modeling

We consider a primary forest parameter  $Y_a$  (i.e. primary forest total basal area, primary forest top height or primary forest stem density) as a function of biophysics:

$$Y_a = f(\vec{X}), \quad (3)$$

where  $\vec{X}$  represents a vector of biophysical site parameters:  $\vec{X} = \{\text{distances, elevation, precipitation, temperature, etc.}\} = \{D_E, D_C, E, T, T_\Delta, P, P_\Delta, C, V, T_x, PD\}$ . On the other hand, these site parameters are given by the biophysical dataset (see Appendix B), and thus are a function of the location in Amazonia  $\vec{s} = \{\text{latitude, longitude}\}$  only, such that  $\vec{X} = f(\vec{s})$ , and therefore

$$Y_a = f(\vec{X}) = f(\vec{s}). \quad (4)$$

Multivariate weighted linear regression models were established for total basal area, top height and number of individuals in primary forest

$$Y_a = \vec{X}\vec{\beta}_Y + \epsilon, \quad (5)$$

where  $Y_a$  is again the primary forest parameter in question,  $\vec{X}$  is a vector of biophysical site properties, and  $\vec{\beta}_Y$  is a vector of regression coefficients. We assume the error  $\epsilon$  to be normally distributed with the variance given by Eq. (2). In order to assure that the model could be reproduced, weighted stepwise regression was run. Stepwise regression automatizes model selection by a penalized likelihood criterion. The final

model was defined, starting with an initial full model, and iteratively dropping and adding terms.

### 3.3. Secondary forest growth modeling

Secondary forest growth was modeled as a function of age adopting a set of differential equations with three parameters, two of them relate to the shape of the growth curve and were treated here as global parameters, i.e. parameters that are equal for every secondary forest in Amazonia. The third parameter is the asymptote of the growth process and was considered local, i.e. it differs according to site properties. In a first step, the primary forest model described the growth asymptotes. In a second step, we plugged the asymptotes into the secondary forest growth equation, and the equation was fitted to the datapoints. The fitted model described secondary forest growth pixel by pixel with an individual growth curve.

The employed approach to secondary forest description builds on the following assumptions:

- (1) Leaving site properties apart, tropical secondary forest grows somewhat similarly within all of Amazonia, independent of slight differences in weather conditions between years, and independent of site history, i.e. of former use and circumstances of forest cutting. We did not account for the differences in growth dynamics caused by these factors (Brown and Lugo, 1990).
- (2) Secondary forest growth can be described by global parameters. Differences in biophysical site conditions result only in various asymptotes of the growth process (Garcia, 1983). Growth in all stands with the same local asymptote follows the same pathway.
- (3) Secondary forest again develops towards a mature forest with properties equal to those of the primary forest before cutting (Brown and Lugo, 1990). Mature forest is equal in properties to primary forest. Hence, primary forest conditions can be considered an asymptote for second growth.

The Bertalanffy–Chapman–Richards growth model is a common model for ecological growth processes, that has been used extensively for description of forest growth (Vanclay, 1994). Neeff and dos Santos (2005) used the following equation for the growth of a forest

parameter  $Y$  based on a convenient reformulation of the original equations by Garcia (1983):

$$\frac{d}{dt} Y^{c_Y} = m_Y (Y_a^{c_Y} - Y^{c_Y}). \quad (6)$$

The forest parameter  $Y$  is a function of age  $t$  and of its three growth parameters, where  $Y_a$  is the asymptote of  $Y(t \rightarrow \infty)$ ;  $m_Y$  and  $c_Y$  are shape parameters,  $m_Y$  relating to the growth rate, i.e. to when the curve approaches  $Y_a$ , and  $c_Y$  to the sigmoid shape of the curve.

The asymptote  $Y_a$  was recovered from primary forest characteristics, i.e. as a function of the location  $\vec{s} = \{\text{latitude, longitude}\}$ . Hence,  $Y_a$  is a *local* parameter. Conversely, the shape parameters  $m_Y$  and  $c_Y$  are *global* parameters, that do not depend on the location. The parameter  $Y$  is thus considered as a function of forest age  $t$ , the shape parameters  $m_Y$ ,  $c_Y$  and the asymptotic  $Y$ , i.e.  $Y_a$  that itself depends on the forest location  $\vec{s}$ :  $Y = f(t, Y_a(\vec{s}), m_Y, c_Y)$

$$\frac{d}{dt} Y^{c_Y}(t, Y_a(\vec{s}), m_Y, c_Y) = m_Y (Y_a^{c_Y}(\vec{s}) - Y^{c_Y}). \quad (7)$$

Eq. (7) can be integrated incorporating an initial condition  $(t_0, Y_0)$ . The starting point of the process is age  $t_0 = 0$  and  $Y_0$  is the level of the forest parameter at age  $t_0$  (which is not always 0)

$$\begin{aligned} \hat{Y}(t, \vec{s}) \\ = Y_a(\vec{s}) \left( 1 - \left[ 1 - \left( \frac{Y_0(\vec{s})}{Y_a(\vec{s})} \right)^{c_Y} \right] e^{-m_Y(t-t_0)} \right)^{1/c_Y}. \end{aligned} \quad (8)$$

Eq. (8) with fitted coefficients allows to compute the level of a given forest parameter  $Y$  in a secondary forest of a certain age  $t$  at a specific location. The first derivative yields the increment of the respective forest parameter  $I_Y$ :

$$I_Y = \frac{d}{dt} Y, \quad (9)$$

$$\frac{d}{dt} Y = \frac{m_Y}{c_Y} Y_a e^{-m_Y t} (1 - e^{-m_Y t})^{(1/c_Y)-1}. \quad (10)$$

Eq. (8) was fitted to the data by weighted nonlinear least squares. The weights were given by the areas of the sample plots (Eq. (2)). The deviations between the model and the observations are a function of the two parameters to be fitted ( $m_Y$  and  $c_Y$ ) and the results of

the primary forest model ( $Y_a$ ). Hence, the function that was minimized during model fitting is the sum of squares over all secondary forest plots  $i$ :

$$SS = \sum_i A_i \cdot [Y_i(t, \vec{s}) - \hat{Y}_i(t, \vec{s}, \hat{m}_Y, \hat{c}_Y, \hat{Y}_a(\vec{s}))]^2, \quad (11)$$

where  $Y(t, \vec{s})$  is the observed secondary forest parameter  $Y$  in field work for a forest of a certain age  $t$  at a certain location  $\vec{s}$ , and  $\hat{Y}_i(t, \vec{s})$  comes from Eq. (8) with fitted global parameters  $\hat{c}_Y$  and  $\hat{m}_Y$ , and fitted local parameter  $\hat{Y}_a(\vec{s})$ . Model fitting in virtue of minimizing Eq. (11) does not rely on distributional assumptions. We understand the variance function to be given by Eq. (2).

### 3.4. Auxiliary relationships for other forest parameters: biomass

We derived other forest parameters (mean diameter at breast height, mean height, etc.) from the state variables by auxiliary relationships. In all cases, the functional forms developed by Neeff and dos Santos (2005) were employed as auxiliary relationships. Other forest parameters  $Z$  depend on the state variables  $\vec{Y}$  by:

$$Z = f(\vec{Y}) = \vec{Y} \vec{\beta}_Z + \epsilon, \quad (12)$$

where  $\vec{\beta}_Z$  is a vector of fitted regression coefficients, and  $\epsilon$ , is assumed to be normally distributed with nonconstant variance according to Eq. (2). The state variables were given from previous model fitting as functions of time, and their increment corresponds to the first derivative in respect of time. Hence, the auxiliary relationships describe other forest variables as functions of time as well  $Z = f(t)$ . The growth of other forest parameters with increasing forest age can be expressed by updating the state variables only. Increment in other forest parameters is therefore given by:

$$I_Z = \frac{d}{dt} Z = \vec{\beta}_Z \frac{d}{dt} \vec{Y}. \quad (13)$$

There is particular interest in forest biomass in the context of the discussion about carbon balances. Therefore, we treat biomass in more detail as an example of the derivation of other forest parameters. The description of standing alive above-ground biomass  $AGB$  as a function of forest volume is common practice. Forest volume is given standwise from basal

area and height by a form factor  $F$  (Loetsch et al., 1973):  $AGB \propto FBH$ .

The form factor was derived in a weighted linear regression model with fixed intercept  $\beta_0 = 0$ ,  $\beta_1 = F$ . Hence, for the special case of biomass, the vector of regression coefficients in Eq. (12) was  $\vec{\beta}_Z = \vec{\beta}_{AGB} = \{0, F\}$ . The regression model corresponded to:

$$AGB = F(BH) + \epsilon. \quad (14)$$

Increment in biomass per unit of time  $I_{AGB}$  was retrieved by derivation of Eq. (14):

$$I_{AGB} = \frac{d}{dt} AGB = F \left( B \frac{d}{dt} H + H \frac{d}{dt} B \right). \quad (15)$$

### 3.5. Model assessment and validation

The fit of the model for mean secondary forest growth was assessed by a Monte-Carlo approach with 1000 runs at level  $\alpha = 0.05$ . The nonlinear regression procedure does not provide a closed expression for confidence intervals. However, by a normality assumption on the distribution of the parameter estimates, the intervals could be arrived at by repeated simulation from a multivariate normal distribution.

In validating the presented growth models, we validated the biomass model exemplarily. We presume that models for other parameters entail less error, because the biomass model accumulates errors from all the relevant sources: the errors committed in field work, the errors in modeling primary forest top height and primary forest basal area, the estimation errors of secondary forest parameters, and the error of the auxiliary relationship between forest volume and biomass. Therefore, by looking at the errors of the biomass model we considered a “worst case” scenario. If the errors were small to tolerable for forest biomass, we expected much less error for other forest parameters. We validated biomass predictions on behalf of our growth model in general.

## 4. Results: primary forest

### 4.1. Data range

For all primary forest inventory plots, we extracted the geophysical and climatological determinants of



forest growth from the biophysical dataset. Fig. 2 illustrates the spread of the datapoints for total basal area across the biophysical space of Amazonia. When pairing and plotting the available biophysical variables, a predominant range of the respective parameters can readily be recognized. The datapoints from field inventories encompass the predominant range, and exceed at lower densities. We used the extreme points to create domain boundaries that would provide an indication of the validity of the forest growth models in order to avoid extrapolation errors. These limits are also provided in Fig. 2. The data range encompasses most of the Amazon region.

#### 4.2. Biophysical model fitting and assessment

Primary forest variables were regressed against biophysical parameters. A step-wise approach to model selection drew on a penalized likelihood criterium. Therefore, model selection is automated and the independent variables differ between the primary forest descriptors. Table 1 displays the coefficients of the final biophysical models. In order to mirror the whole diversity of biophysical variables, it was sensible to include a higher number of explanatory variables in the models at the cost of accepting lower limits of significance of the respective parameters. Since the total number of points was also large, we did not observe problems of over-fitting, and all fitted coefficients are significant. We did not aim

for ecological interpretation of relative magnitude and effect of the factors. Even though such interpretation may be possible for identification of growth trends, our research is merely descriptive, and the equations served as a black box device for spatial interpolation. The models feature coefficients of determination  $r^2$  of 0.26 for basal area, 0.49 for top height, 0.31 for number of individuals.

The expected variance structure was compared to the observations in order to assess the validity of our presumptions. The expectations introduced the area of sample plots as determinant in Eq. (2). Fig. 3 plots the variance function of the model for primary forest total basal area as an exemplary case.

The residuals from model fitting were used for area-classwise empirical estimation of variance. The coherence between estimated and modeled variance for parameters that refer to a given forest area underlines the sensibility of the adopted approach for parameter estimation. For instance, for forest areas of 1 ha, standard deviation of total basal area amounts to approximately  $5.0 \text{ m}^2 \text{ ha}^{-1}$ . The standard deviation comes down to less than  $0.5 \text{ m}^2 \text{ ha}^{-1}$  for larger areas at the size of the grid cells used in data processing (about  $100 \text{ km}^2$ ).

#### 4.3. Potential forest state

The models in Table 1 were applied to generate grids of primary forest conditions in Amazonia.

Table 1  
Results of stepwise weighted linear regression

Variable	B				H				N			
	$\hat{\beta}$	$\hat{\sigma}_{\beta}$	Min	Max	$\hat{\beta}$	$\hat{\sigma}_{\beta}$	Min	Max	$\hat{\beta}$	$\hat{\sigma}_{\beta}$	Min	Max
$\beta_0$	66.42	8.67	NA	NA	-208.01	32.59	NA	NA	1020.25	174.05	NA	NA
$D_E$	0	0	0	16.2	-0.82	0.25	0	16.2	-14.84	3.9	0	16.2
$D_C$	0.32	0.12	0	11.03	0.94	0.15	0	12.08	14.77	3.85	0	12.08
$E$	0.01	0	0	3091.13	0	0	0	358.46	0.11	0.04	1	3091.13
$T$	-1.04	0.35	17.31	28	12.14	1.61	24.75	27.06	0	0	17.31	28
$T_{\Delta}$	-3.22	0.42	0	5.26	0	0	0	5.26	-32.25	14.67	0	5.26
$P$	0	0	777.78	2988.97	-0.01	0	1155.41	2737.09	0	0	777.78	2988.97
$P_{\Delta}$	0	0	0	409.56	0	0	0	385.13	-0.37	0.11	0	409.56
$V$	-0.23	0.06	43.47	66.58	-0.68	0.21	48.5	66.58	-7.58	2.42	43.47	66.58
$C$	0	0	1.47	3.02	-12.05	4.67	2.25	3.06	0	0	1.47	3.06
$T_x$	1.16	0.36	1	5	0	0	3	5	-15.51	10.08	1	5
$PD$	0	0	10	600	0.01	0.01	120	270	0.9	0.13	10	600

Models of primary forest parameters in Amazonia from biophysical determinants:  $B \text{ (m}^2 \text{ ha}^{-1})$  is the total basal area,  $H \text{ (m)}$  the forest top height,  $N \text{ (ha}^{-1})$  the number of individuals. Fitted coefficients  $\hat{\beta}$  are provided along with standard errors  $\hat{\sigma}$ , and the respective data range. Coefficients of determination and number of datapoints amount to –  $B$ : 0.26, 348;  $H$ : 0.49, 158;  $N$ : 0.31, 350.

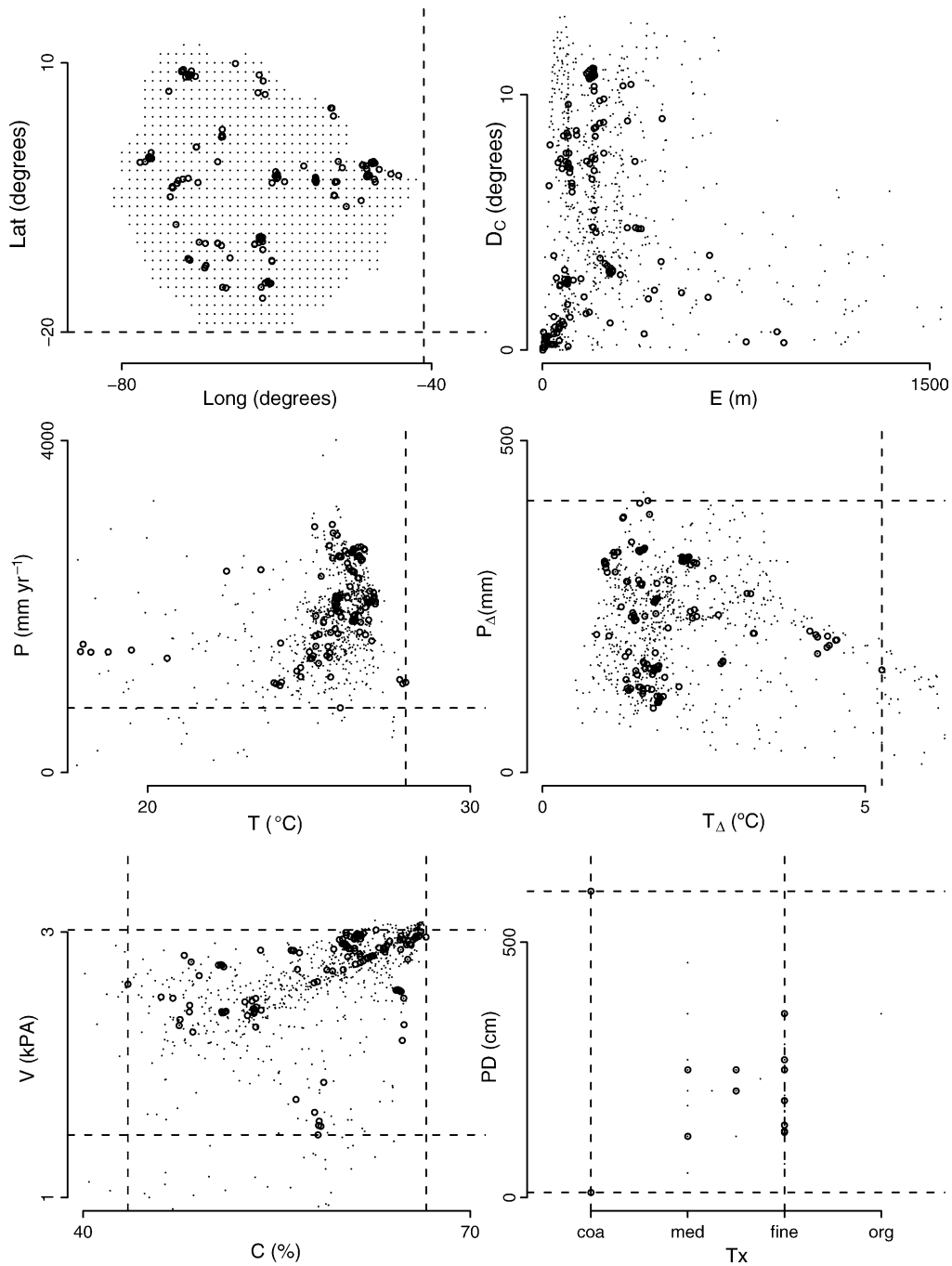


Fig. 2. Distribution of forest inventory dataset over the biophysical space of the Amazon region. Lat: latitude, Long: longitude,  $E$ : elevation,  $D_C$ : distance to coast line,  $T$ : mean annual temperature,  $P$ : mean precipitation,  $T_\Delta$ : difference between mean monthly temperature of hottest and coldest month,  $P_\Delta$ : difference between mean monthly precipitation of wettest and driest month,  $C$ : mean annual cloud cover,  $V$ : mean annual vapor pressure,  $T_x$ : soil texture class,  $PD$ : soil profile depth. The points correspond to all grid cells of the study area, sampled at an interval of  $1^\circ$ . Available forest inventory plots for total basal area are symbolized by circles. The dotted lines represent the data range.



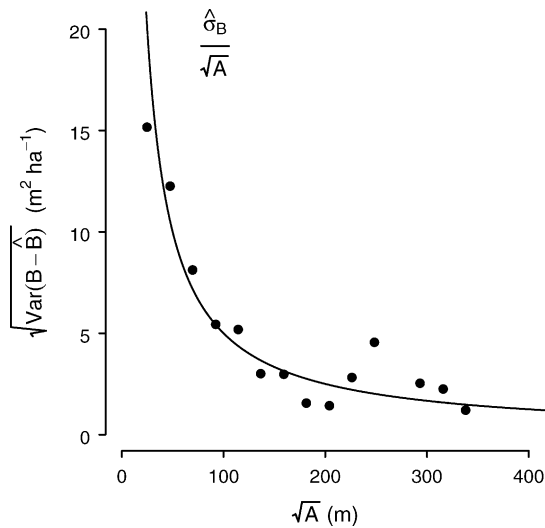


Fig. 3. Variance in the modeling of primary forest parameters. The standard deviation of residuals ( $B - \hat{B}$ ) from area-weighted linear model fitting for primary forest total basal area was estimated classwise (class width is  $500 \text{ m}^2$ ), and plotted against the square root of the respective forest area  $A$ . The fitted line draws on the variance function  $\text{Var}(B) = \sigma_B^2/A$  (Eq. (2)).

The maps in Fig. 4 display the potential state of the Amazon forests, i.e. they refer to the hypothetical conditions of undisturbed primary vegetation. The modeled basal area mainly varied between  $22$  and  $33 \text{ m}^2 \text{ ha}^{-1}$ ; top height ranged between  $10$  and  $35 \text{ m}$ ; and there were  $400$ – $850$  individuals per hectare. Total above-ground biomass ranged between  $110$  and  $370 \text{ t ha}^{-1}$ . The maps in Fig. 4 suggest great differences in potential forest conditions, thus reconfirming the need for spatial explicitness in dealing with forest conditions in Amazonia.

## 5. Results: secondary forest

### 5.1. Model fitting and assessment

The previously established primary forest models provided the asymptotes  $Y_a$  of the secondary forest growth processes. The initial parameters at  $t_0 = 0$  for total basal area and top height were zero,  $B_0 = 0$ ,  $H_0 = 0$ . The initial number of stems  $N_0$  was obviously different from zero. Neeff and dos Santos (2005) described the

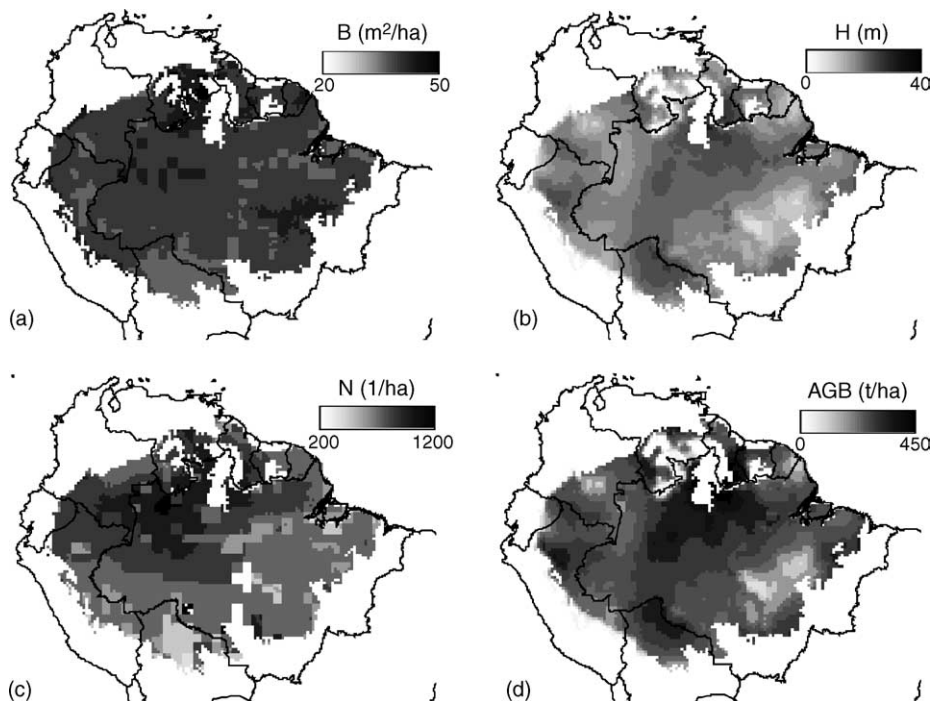


Fig. 4. Primary forest parameters in Amazonia as derived from the biophysical model. (a) Total basal area  $B$ ; (b) forest top height  $H$ ; (c) number of individuals  $N$ ; (d) total above-ground biomass  $AGB$ .

initial stem density as a multiple of the asymptotic stem density  $N_0 = \text{rat}_N N_a$ , where the factor  $\text{rat}_N$  was derived by a weighted local regression approach on initial succession forest inventory plots. Here, we approximated the number of individuals at initial forest growth by the stem density of secondary forest plots at ages  $2 \leq t \leq 5$  year ( $n = 74$ ). The ratio  $N_0/N_a$  came out as  $\text{rat}_N = 5.1$ , with a standard error  $\sigma_{\text{rat}_N} = 1.1$ .

The shape parameters  $m_Y$  and  $c_Y$  were estimated by minimizing Eq. (11) and fitting Eq. (8). Neeff and dos Santos (2005) made positive experience in dropping the power term from the model for stem density ( $c_n = 1$ ), we followed this procedure. In Table 2 the fitted model coefficients are displayed along with the respective standard errors. All coefficients are highly significant.

Fig. 5 plots the fitted secondary forest growth models. We display the scatterplot of all available forest inventory data along with fitted curves for various asymptotes. Fig. 5 also displays a close-up of three example regions (Rondônia state, Brazil; Pará state, Brazil; Bolivia). The scatterplots of all data in Fig. 5 feature a large variance. Only the identification of growth trajectories (as we did in virtue of asymptotes) provided means for statistical description. When examining the case studies in Fig. 5, it must be born in mind, that the models have not been fitted to these observations only, but to the entire dataset. Due to the large number of datapoints, variance in estimation was far lower than the scatterplots suggest, and the confidence intervals are quite narrow, indicating a good model fit. The scattering width does not provide any indication of the stringency of

the relation, but the coincidence between modeled growth trend and the mean of the observations does. The concept of description of growth by only one local parameter and the procedures utilized for parameter estimation were successful.

## 5.2. Secondary forest growth

The models in Table 2 were applied to derive grids of secondary forest properties at a sequence of successional stages: 5, 10, 15, 25 years. In Fig. 6 the results for the case of total basal area in secondary forest are displayed. Corresponding grids could be derived for other parameters or other ages as well. Applying Eq. (8) with fitted coefficients allows for computation of secondary forest parameters at different locations and at any age.

## 6. Results: auxiliary relationships

### 6.1. Auxiliary models

Other forest parameters were described by auxiliary relationships from the state variables. We employed the functional forms from Neeff and dos Santos (2005), that were fitted to our new dataset from large areas across Amazonia. Table 3 provides the models for total above-ground biomass, mean basal area, mean diameter, and mean height. All fitted regression coefficients are highly significant. The coefficients of determination were high, even though in all cases we dropped the intercepts from the models. Standard model assessment procedures provided confidence in model fit.

### 6.2. Potential biomass

Biomass receives special attention due to its importance for the estimation of carbon balances. The auxiliary relationship displayed in Table 3 was stringent ( $r^2 = 0.97$ , if the model had an intercept, which is not significant). The form factor amounted to  $F = 0.3873$  with an estimated standard error  $\hat{\sigma}_F = 0.0036$ .

Fig. 4 displays biomass of primary forest. We also used Eqs. (14) and (15) to calculate forest biomass and its increment for two successional stages of 5 and 15 years (Fig. 7).

Table 2

Growth models for secondary forest parameters in Amazonia

<i>Y</i>	<i>B</i>	<i>H</i>	<i>N</i>
<i>n</i>	348	158	350
<i>Y<sub>a</sub></i>	Table 1	Table 1	Table 1
$\sigma_{Y_a}$	Table 1	Table 1	Table 1
$\text{rat}_{Y_0}$	0	0	5.1
$\sigma_{\text{rat}_Y}$	0	0	1.1
<i>n</i>	273	219	270
<i>m<sub>Y</sub></i>	0.062	0.048	0.026
$\sigma_m$	0.012	0.008	0.006
<i>c<sub>Y</sub></i>	1.325	1.703	1
$\sigma_c$	0.24	0.208	0

The fitted parameters of Eqs. (8) and (10) are given: *B* is the total basal area, *H* the forest top height, *N* the number of individuals.  $\sigma$  the standard errors, *n* the number of datapoints.

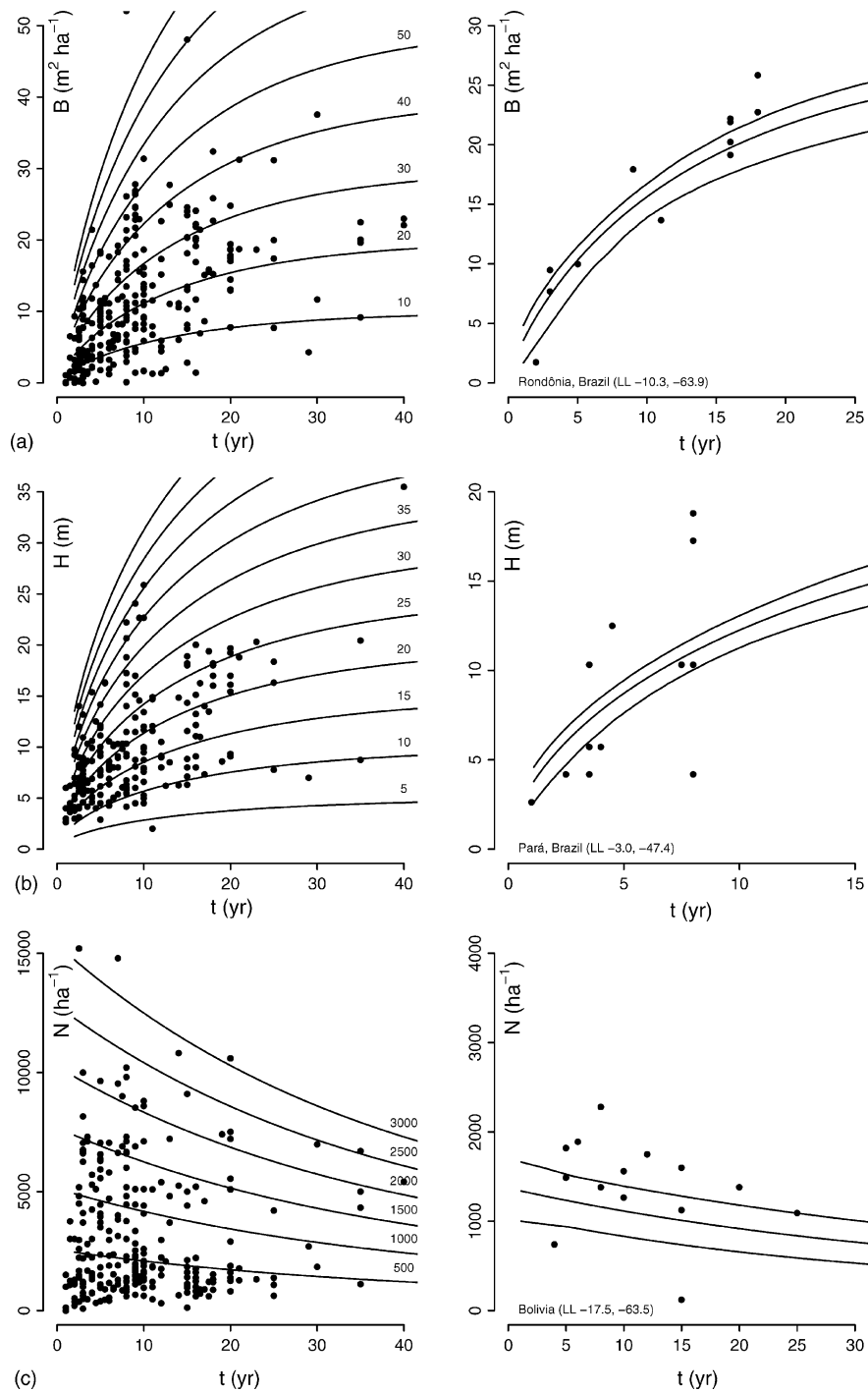


Fig. 5. Growth models for three example regions: (a) basal area  $B$  against age  $t$  for all data and in Rondônia, (b) top height  $H$  against age  $t$  for all data and in Pará, (c) number of individuals  $N$  against age  $t$  for all data and in Bolivia. The points represent observations in field inventories. The straight lines are estimates from fitting Eq. (8), on the left hand side corresponding to example growth trajectories, and on the right hand side corresponding to the respective site. The dotted lines represent Monte-Carlo confidence intervals for the mean ( $n = 1000$ ,  $\alpha = 0.05$ ).

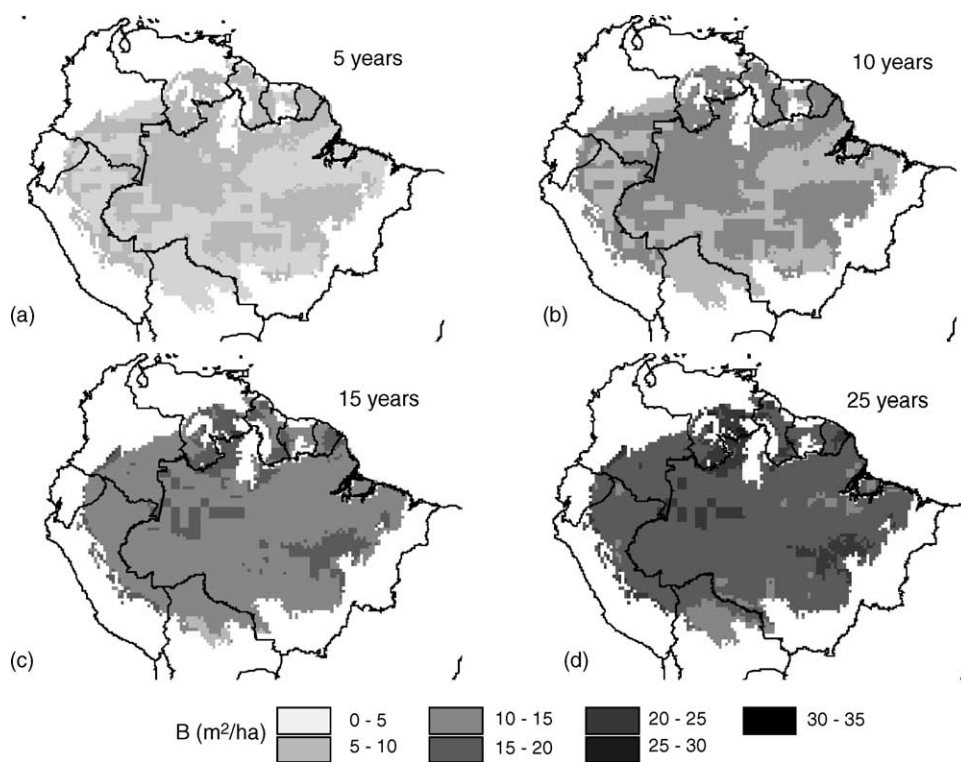


Fig. 6. Output of the model for secondary forest total basal area in Amazonia at different ages: (a) 5 years; (b) 10 years; (c) 15 years; (d) 25 years.

In 5 year old secondary forest, biomass largely ranged between 25 and 50 t ha<sup>-1</sup>. At more advanced successional stages the spatial pattern became more heterogeneous. In some locations, biomass of 15 year old regrowth exceeded 100 t ha<sup>-1</sup>. In other regions, e.g. in the Brazilian Mato Grosso state, secondary forest accumulated only half as much biomass at the same age. Regrowth is fastest and most persistent in the northern Brazilian Amazon where the biomass stocks of 15 year old succession could exceed 150 t ha<sup>-1</sup>.

### 6.3. Validation

The biomass model in primary and secondary forests was validated by testing against published biomass inventory data from 46 locations (Appendix A). In Fig. 8 the deviations between predictions and field observations are plotted. In one case the model underestimated forest biomass by as much as 100 t ha<sup>-1</sup>. The biomass model was negatively biased with an area-weighted mean error of

Table 3

Auxiliary relationships of other forest parameters to state variables (Neeff and dos Santos, 2005)

Parameter	Unit	$Y(t)$	$I_Y(t) = \frac{d}{dt} Y(t)$
AGB	t ha <sup>-1</sup>	$0.3873(BH)$	$0.3873\left(B \frac{d}{dt} H + H \frac{d}{dt} B\right)$
$\bar{b}$	m <sup>2</sup>	$\frac{B}{N}$	$\frac{N \frac{d}{dt} B - B \frac{d}{dt} N}{N^2}$
$\bar{d}_{1.3}$	cm	$\sqrt{10191.6\bar{b} - 28204.8\bar{b}^2}$	$\frac{10191.6 \frac{d}{dt} \bar{b} + 2(-28204.8) \bar{b} \frac{d}{dt} \bar{b}}{2\sqrt{10191.6\bar{b} - 28204.8\bar{b}^2}}$
$\bar{h}$	m	$0.9919H - 0.0229H^2 + 0.0004H^3$	$0.9919 \frac{d}{dt} H + 2(-0.0229)H \frac{d}{dt} H + 3(0.0004)H^2 \frac{d}{dt} H$

Given are models for growth of forest parameters  $Y$  in time and respective increment  $I_Y$  with fitted coefficients. State variables:  $B$  (m<sup>2</sup> ha<sup>-1</sup>) is the total basal area,  $H$  (m) the forest top height,  $N$  (ha<sup>-1</sup>) the stem density. Other variables: AGB is the above-ground biomass,  $\bar{b}$  the mean basal area,  $\bar{d}_{1.3}$  the mean diameter,  $\bar{h}$  the mean height.

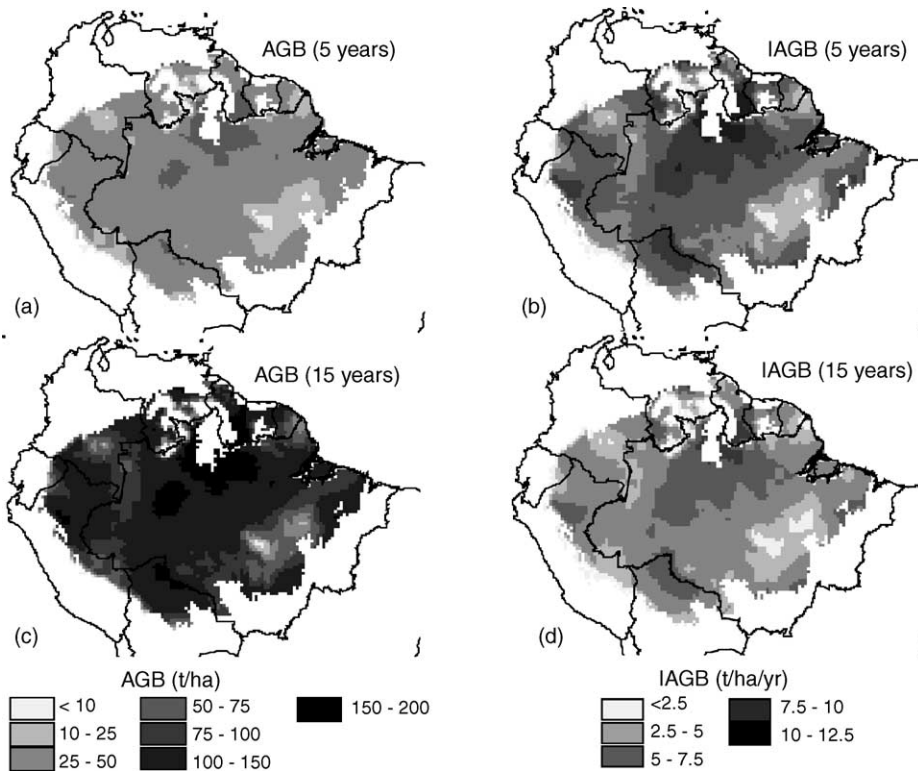


Fig. 7. Spatial distribution of Amazon forest biomass in secondary forest. Four maps are displayed showing standing alive above-ground biomass  $AGB$  and its yearly increment  $I_{ADB}$  in secondary tropical forest.

$ME = -10.5 \text{ t ha}^{-1}$ . The area-weighted root mean squared error came out as  $RMSE = 38.4 \text{ t ha}^{-1}$ . When regressing the fitted on the observed biomass values, the coefficient of determination was  $r^2 = 0.92$ , and the slope was  $\beta_1 = 0.92$ . The bias is slight, and the error ( $38.4 \text{ t ha}^{-1}$ ) is small when compared to primary forest biomass levels ( $110\text{--}370 \text{ t ha}^{-1}$ ). The deviations are tolerable for secondary forests ( $20\text{--}70 \text{ t ha}^{-1}$  at age 5,  $75\text{--}150 \text{ t ha}^{-1}$  at age 15).

When looking closely at Fig. 8, we recognized a tendency of the deviations to increase at higher biomass levels. Applying a local-regression smoother to the data clearly depicted, that errors were smaller for forests with lower biomass than for forests with higher biomass. Error of biomass estimation in secondary forests was far below the previously reported RMSE of  $38.4 \text{ t ha}^{-1}$ , that represented an average of all forest types. We did not have sufficient datapoints at high biomass levels to model the error, but even so, calibration of final biomass modeling results reinforced

confidence in the sensibility of the adopted methodology and of the obtained results. Despite a tendency to underestimate, the model generally describes total above-ground biomass in different tropical forest types with good precision in Amazonia.

## 7. Discussion

Tropical forests in Amazonia were described in their growth parameters and their increment. The presented methodology allows for computation of any standard forest parameter at any location in the Amazon forest. We generated corresponding grids for the special cases of total basal area, top height, stem density, total above-ground biomass, and their yearly increments in primary and secondary forests at various successional stages. Biomass predictions were validated against independent reference data in an exemplary manner.

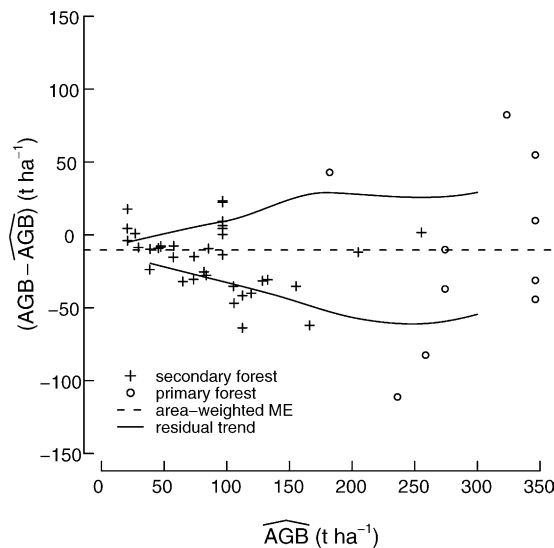


Fig. 8. Validation of biomass modeling results in primary and secondary forest by independent biomass inventory data. Deviations of observed AGB from predicted above-ground biomass  $\widehat{AGB}$  are plotted against predictions. Two separate smoothing lines for positive and negative deviations are also provided.

The proposed model builds on clearly stated assumptions that itself are topics of extended discussion in the literature. These assumptions arose from the quality of the available data and from the effort to employ simple mathematical relationships. Assumption #1 assured methodological feasibility. It also confined diversity and variability of the ecosystems to the least possible amount. A great deal of generalization was necessary to describe secondary forest growth in all of Amazonia by only one mathematical equation. Nevertheless, the adopted approach for validation of model output by independent reference data was convincing in the final results. Assumption #2 related to the use of global parameters in the mathematical description of secondary forest growth. The issue of dependence of growth on site history receives much attention in the literature (e.g. Zarin et al., 2001). A given forest in the field may grow somewhat unlike the broad averages reported here, e.g. if the site has been subjected to heavy prior use, if the soil has suffered from erosion, or if maybe none of those has happened. Also, we assumed (Assumption #3) that mature forest would develop properties equal to that of the primary forest before cutting. This idea underlies many pieces of

research when constructing chronosequences (e.g. Moorcroft et al., 2001). However, the time frame in which mature forest turns primary forest again is vague (Saldarriaga et al., 1988). The assumptions were indispensable for confining the diversity of ecological patterns to the rigidity of a mathematical modeling framework.

The adopted approach is statistically simple and entirely empirical, as opposed to more sophisticated models (e.g. Moorcroft et al., 2001). The structural simplicity ensures reproducibility and easy comprehensiveness. The model allows for easy reparametrization to different or extended datasets. Computation is fast and cheap. On the other hand, due to its empirical foundation, the model performance depends on the availability and quality of calibration data, and hence we had to dedicate great effort to the collection of forest inventory data from literature and from other researchers' field work.

The establishment of centralized databases on tropical forests and the proliferation of standard forest inventory methodology still has a long way to go. In particular, there is a need to develop databases from permanent plot inventories in both primary and secondary forests. We collected a large dataset with 698 sample plots. Similar endeavours to data collection have been undertaken (e.g. ter Steege et al., 2003; Houghton et al., 2001), and efforts are being made to build databases on tropical forests (Malhi et al., 2002). When using data from different sources, compatibility of the methodologies for field work and data processing poses a major problem. We found most reliability in measures of total basal area, top height, and stem density. Stem density and total basal area are quite persistently reported in literature. We experienced biomass measures in literature to be the most difficult to deal with: biomass measures are derived (if not from destructive methods) by one out of a number of commonly used allometric equations; the biomass fractions differ, and different treatments of dead individuals or nontree species introduce additional variance into comparison of biomass estimates. Despite difficulties in gathering and processing data from many different sources, we managed to establish a representative database for primary and secondary tropical forests in Amazonia.

When analyzing forest biomass, we neglected a number of factors that bear on composition of forest



biomass. Vegetation changes rapidly and intensively during succession in Amazonia (Uhl and Jordan, 1984), herbaceous, shrubs, pioneer and forest tree species play different roles in a sequence of successional phases. There are considerable differences in wood density between successional stages and even between primary forests at different locations due to species composition (Baker et al., 2004). We used only one allometric equation, in order to avoid the variance that would have arisen from the use of more than one allometric equation. In some regions bamboo, palms or lianas exert an important influence on the ecosystem (Houghton et al., 2001). We disregarded these nontree species. Nor were other biomass fractions accounted for (below-ground biomass, woody debris, etc.). We addressed standing alive above-ground biomass exclusively. Even though other biomass fractions contribute significantly to forest biomass, standing alive above-ground biomass must be underscored to be the single most important component for assessment of forest biomass in Amazonia (Brown et al., 1989).

The regression models for primary forest serve as a purely empirical algorithm for interpolation of forest growth data. We do not aim for a physiological analysis of ecological factors and the plants' responses. In the literature, there are numerous attempts to assess the effects of given biophysical factors on structure and growth of primary and secondary forests (ter Steege et al., 2003; Zarin et al., 2001; Brown and Lugo, 1990). The available dataset may allow for such an analysis as well, and future research might embody a more profound treatment of ecological aspects.

Previous estimates of forest growth and increment across Amazonia are extremely variable and sometimes even contradictory (Houghton et al., 2001). Houghton et al. (2001) compared biomass maps of the Legal Amazon and concluded that mapping results based on ground inventories depict an accumulation of forests with high biomass along the equator in Central Amazonia. In this study biomass peaks in the north-western Legal Amazon. Zarin et al. (2001) regressed secondary forest biomass on a set of biophysical parameters, including soil and climate variables. Their estimates of accumulated biomass stocks (mainly 26–50 t ha<sup>-1</sup> at 5 years and more heterogeneous at 50–200 t ha<sup>-1</sup> in more advanced 10–20 year old succession) agree with the results we obtained here. ter Steege

et al. (2003) applied regression techniques to a large set of primary forest inventory data in order to estimate forest diversity and density.

The consonance between their estimate of 400 and 750 individuals per hectare and the results we obtained is remarkable. There also is agreement regarding the spatial distribution of stem density, which according to ter Steege et al. (2003) peaks in southern Colombia and the western Brazilian Amazonia state.

The signal-to-noise ratio was fairly low in regressing primary forest characteristics on biophysical parameters ( $r^2$  is 0.26, 0.49, and 0.31 for total basal area, top height and stem density respectively). The biophysical dataset only explained a small part of the observed variation in forest characteristics at the small scale of measurements. Obviously, large-scale information on climate, soil conditions, etc. at grid sizes of 0.1 degrees cannot explain in detail the variation in forest parameters at a scale of square meters. Conversely, variance of forest parameters drops considerably with increasing respective forest area. The established models do not allow for inference on small-scale variability in the Amazon forest. However, at a larger scale the models explain the bulk of the variation and allow one to predict primary forest characteristics with good precision. Therefore, the model does not aim for being employed in a management context unless only the prediction of general trends is required. We built this model for application in the context of large-scale ecological processes, particularly for the estimation of carbon balances.

The established model describes the potential and not the actual forest conditions. Our model is useful for predicting forest characteristics only if combined with information on the distributional patterns of the forest types and age distributions. Results on the actual forest state as opposed to the potential described by forest growth models, can be expected from the large remote sensing campaigns. Eventually, we aim for combining the forest growth description presented here with land-use modeling results (Neeff et al., *in press*). An integration of remote sensing, with land-use models and a forest growth description, will eventually enable the spatial estimation of carbon balances across the Amazon forest (Houghton et al., 2001); a scientific result that has been demanded for a long time (Schimel et al., 2001).

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## Appendix A. Forest inventory data sources

See Table A1.

Table A1  
Dataset of forest inventories in Amazonia

No.	Year	Area (ha)	Type	No. of plots	Country	Avail.	Source
Treewise data available							
1	1972	0.2	PF	1	Br	DH	Prance et al. (1976)
2	1983–1986	0.68	PF	5	Br	DH	Higuchi (2003)
3	1992–1999	12.58	b	209	Br	DH	Brondizio (2003)
4	1993	4.7	SF	16	Br	D	Lucas et al. (2002)
5	1995	1.5	b	15	Br	DH	Alves et al. (1997)
6	1995	0.2	PF	1	Br	DH	Araujo et al. (1999)
7	1995	0.2	SF	2	Br	DH	Gavina Pereira (1996)
8	1996	1.9	b	20	Br	DH	Schmidt (1997)
9	1996	2.5	SF	14	Bo	DH	Steininger (2000)
10	1996	1	PF	1	Br	DH	Graça (1997)
11	1996–2000	5.47	PF	5	Br	DH	da Silva et al. (2002)
12	1998	2	PF	1	Br	DH	Klink et al. (1999)
13	1998–2000	6	PF	3	Br	DH	Moutinho and Nepstad (1999)

Table A1 (Continued)

No.	Year	Area (ha)	Type	No. of plots	Country	Avail.	Source
14	1999–2001	0.48	SF	3	Br	DH	de Carvalho et al. (2001)
15	1999–2001	8	PF	2	Br	DH	Camargo et al. (2003)
16	1999–2002	8.4	b	83	Br	DH	Neeff and dos Santos (2005)
17	2000	14	PF	14	E	D	Pitman et al. (2001)
18	2000–2001	2	PF	2	Br	DH	Brown and Esteves (2003)
19	2002	1.6	PF	11	P	DH	Jarvis (2003)
20	2003	3	PF	3	P	D	Pitman et al. (2003)
21	2003	0.52	SF	2	Br	DH	Coelho et al. (2003)
$\Sigma$		76.9		413			
Plotwise data available							
22	1956–1997	168.37	PF	96	Bo, Br, E, FG, P, V	L	Phillips et al. (2004)
23	1972–1985	9.99	PF	38	V	L	Veillon (1985)
24	1975	0.54	b	5	C	F	Fölster et al. (1976)
25	1975–1979	0.45	SF	6	V	F	Uhl and Jordan (1984)
26	1980	8.88	PF	6	p	L	Pitman et al. (1999)
27	1980	9	PF	1	Br	F	Rankin-de Mérona et al. (1992)
28	1984	1	PF	1	Bo	L	Boom (1986)
29	1985	0.28	PF	4	P	F	Paitán (1985)
30	1985–1986	2	PF	2	Br	L	Balée and Campbell (1990)
31	1986	2.07	b	23	V	L	Saldarriaga et al. (1988)
32	1986–1998	148.2	PF	15	Bo, Br, C, E	L	Malhi et al. (2002)
33	1988	1.77	b	15	Br	F	Uhl et al. (1988)
34	1988	3	PF	1	Br	F	de Lima Filho et al. (2001)
35	1989	1.5	b	2	Br	F	Lisboa (1989)
36	1993	0.5	PF	1	Br	F	Muniz et al. (1994)
37	1994	5	PF	1	Bo	F	Killeen et al. (1998)
38	1995	0.75	PF	1	Br	F	Klinge et al. (1995)
39	1998	3.75	b	6	Br	F	Salomão et al. (1998)
40	2000	0.75	PF	3	Br	L	Miranda (2000)
41	2000	0.7	b	7	Br	F	Vieira et al. (2003)
42	2002	7	PF	1	Br	L	Asner et al. (2002)
43	2002	0.4	SF	10	Br	L	Feldpausch et al. (2004)
44	2002	0.3	PF	2	Br	L	Gerwing (2002)
45	2002	17	PF	3	Br	L	Vieira (2003)
$\Sigma$		393.2		250			
Plotwise biomass reference data available							
46	1975–1998	25.19	b	14	Br, C, FG, V	V	Clark et al. (2001)
47	1980	3.25	PF	1	V	V	Grimm and Fassbender (1981)
48	1993		SF	6	Br	V	Fearnside and Guimarães (1996)
49	1993	1.4	SF	14	Br	V	Lucas et al. (1998)
50	1994	4.5	b	4	Br	V	Johnson et al. (2001)
51	1994	0.2	b	2	Br	V	Fujisaka et al. (1998)
52	1999	1.4	b	14	Br	V	Sorrensen (2000)
$\Sigma$		35.94		55			
$\Sigma$		506.1		718			

Plots are differentiated by forest type – PF: primary forest, SF: secondary forest, b: both; by data availability for tree-by-tree data, D: diameters, H: heights, and for plotwise published data, F: full, L: limited, no height information, V: only biomass measurements; and by country – Bo: Bolivia, Br: Brazil, C: Colombia, E: Ecuador, FG: French Guiana, P: Peru, S: Suriname, V: Venezuela.

## Appendix B. Biophysical data sources

See Table B1.

Table B1

Dataset on climatological and geophysical determinants of forest growth in Amazonia

	Variable	Units	Derived from	Source
	Global ecological zones		Nineteen classes	FAO (2001)
$D_E$	Distance to equator	DD	Latitude	
$D_C$	Distance to coastline	DD	South America map	
$E$	Elevation over sea level	m	DEM	USGS (2003)
$T$	Long-term mean annual temperature	°C	Gridded interpolation monthly station data	WSAG (2003)
$T_\Delta$	Difference between mean temperature of hottest and coldest month	°C	Gridded interpolation of monthly station data	WSAG (2003)
$P$	Long-term mean precipitation	mm yr <sup>-1</sup>	Gridded interpolation of monthly station data	WSAG (2003)
$P_\Delta$	Difference between mean precipitation of wettest and driest month	mm	Gridded interpolation of monthly station data	WSAG (2003)
$C$	Long-term mean cloud cover	%	Gridded interpolation of monthly station data	WSAG (2003)
$V$	Long-term mean vapor pressure	kPa	Gridded interpolation of monthly station data	WSAG (2003)
$T_x$	Soil texture	class	FAO soil map	GSFC (2003)
$PD$	Soil profile depth	cm	FAO soil map	GSFC (2003)

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