

Modeling the Effects of Type and Intensity of Selective Logging on Forests of the Amazon

Theodore N.S. Karfakis, Anna Andrade, Carolina Volkmer-Castilho, Dennis R. Valle, Eric Arets, and Paul van Gardingen

Abstract—The aim of the work presented here was to either use existing forest dynamic simulation models or calibrate a new one both within the SYMFOR framework with the purpose of examining changes in stand level basal area and functional composition in response to selective logging considering trees ≥ 10 cm d.b.h for two areas of undisturbed Amazonian non flooded tropical forest in Brazil and one in Peru. Model biological realism was evaluated for forest in the undisturbed and selectively logged state and it was concluded that forest dynamics were realistically represented. Results of the logging simulation experiments showed that in relation to undisturbed forest simulation subject to no form of harvesting intervention there was a significant amount of change over a 90 year simulation period that was positively proportional to the intensity of logging. Areas which had in the dynamic equilibrium of undisturbed forest a greater proportion of a specific ecological guild of trees known as the light hardwoods (LHW's) seemed to respond more favorably in terms of less deviation but only within a specific range of baseline forest composition beyond which compositional diversity became more important. These finds are in line partially with practical management experience and partially basic systematics theory respectively.

Keywords—Amazonbasin, ecological species guild, selective logging, simulation modeling.

I. INTRODUCTION

BRAZILIAN Amazonia contains the largest area of remaining tropical forest in the world and is regarded as a cradle of biological diversity at the global level [20], [28], [34]. Therefore the quantification and study of any form of perturbation on this system is of great scientific importance. The most common form of direct anthropogenic disturbance upon these forests in general other than fragmentation is selective logging for purposes of timber harvesting [20]. This has been proven to be directly measurable on the trees which

are the physiognomic dominant of the community by periodic mensuration of permanent sample plots [1], [7], [8], [32], and [33]. Several studies have dealt with the impact of logging disturbance on the tree community [1], [9], [5], [23], [28], [32], [33], and [35]. The consensus is that this practice leads to drastic opening of the forest canopy in relation to baseline conditions. This in series promotes changes in the functional composition of the affected site that are proportional to the intensity and duration of the relevant disturbance regime. Specific ecological effects include the increased growth and recruitment of more disturbance adapted tree species due to the shift to environmental conditions favoring them and a general increase in stand level biomass productivity. In studies dealing with functional composition response to disturbance it is common to aggregate tree species into a small number of ecological guilds for purposes of statistical analysis [1], [10], [19], and [35]. This is because of the relatively small numbers of individuals per species in the sample plots used to study these [1], [19], [32], and [35]. Stand level structural variables like volume or basal area are also commonly used [8], [9], [28], and [32]. A common methodology in such studies is to use forest dynamic simulation models as long term datasets from many areas are often fragmentary [16], [25], and [30]. An example of this is the SYMFOR modeling framework [21]. This is a collection of interrelated models designed to simulate forest dynamics in a spatially explicit manner by modeling each individual tree occupying a forest stand within the scale of one to few hectares. The aim of this study was to evaluate the impact of selective logging on the long term structural and compositional dynamics of three areas of Brazilian non flooded Amazonian forest over a gradient of harvest intensity disturbance. To achieve this permanent sample plot data from Brazil and Peru are used to calibrate suitable forest dynamic models within SYMFOR and initialize relevant simulations.

II. DESCRIPTION OF MODELS

A. Overview

Three separate forest dynamics models were used in this project that were developed based on permanent sample plot data from a number of areas. All were within the SYMFOR modeling framework [21]. The first was originally developed using permanent sample plot data from the Tapajos national forest and Jari lands in the state of Para, Brazil for considering trees ≥ 5 cm d.b.h [25] and later modified for considering datasets with trees ≥ 10 cm d.b.h which was the version used in

T. N. S. Karfakis is with Division of Biology, Imperial College of Science, Technology and Medicine, Ascot, SL5 7PY, United Kingdom (e-mail: theokarfak@gmail.com).

A. Andrade is with the Biological Dynamics of Forest Fragments Project, Institute for research in the Amazon (INPA), Manaus, Amazonas, Brazil (e-mail: titian@inpa.gov.br).

C. V. de Castilho is with EMBRAPA, Boa Vista, Roraima, Brazil (e-mail: Carolina@inpa.gov.br).

D. R. Vale is with the Faculty of Ecology, Duke University, and Durham, NC, USA (e-mail: drvalle1@gmail.com).

E. Arets is with the subdivision of Forest and Landscape Ecology, Wageningen Agricultural University, Wageningen, Netherlands (e-mail: Eric.Arets@wur.nl).

P. R. van Gardingen is with the School of Geosciences, Edinburgh University, Edinburgh, Scotland, United Kingdom (e-mail: p.vangardingen@ed.ac.uk).

this project [31]. The other two were developed based on data from the Manaus region in Brazil and the Puerto Maldonado region in Peru for the purposes of this study. Each model includes representations of the three main demographic processes in populations of forest trees, namely, growth, mortality and recruitment. The rates of these processes for individual trees depend on their own size and competition with other trees mainly for light, and were parameterized from data. The minimum diameter for all models is 10 cm. The models are individual-based and spatially explicit, meaning that all trees are individually represented and occupy a unique spatial position in the simulated forest stand. For the Manaus and Puerto Maldonado model the minimum spatial unit is the 20 m × 20 m grids square while for the Tapajos/Jari version a 10 m × 10 m one. All models used were stochastic and probabilities ranged from 0 to 1 unless otherwise stated specifically.

B. Competition Modeling

Competition among individuals is represented as a distance and size dependent competition index that is explicitly derived from the data. For the Tapajos/Jari model this index C_t is based on 3 competition intensity zones. Zone 1 is a 10 m × 10 m grid-square containing tree t , and zones 2 and 3 are defined relative to zone 1 as shown in Fig. 1. Here, $z_1 \dots z_3$ are coefficients for the relative competition importance of zones 1, 2 and 3, respectively, i, j, k are the over-topping trees in the three zones, $n_1 \dots n_3$ are the total number of over-topping trees in the three zones and $D_i \dots D_v$ is the diameter at breast height of tree $i, j, \dots v$. Equation (1) describes this.

$$C_t = z_1 \sum_{i=1}^{n_1} D_i/D_t + z_2 \sum_{j=1}^{n_2} D_j/D_t + z_3 \sum_{k=1}^{n_3} D_k/D_t \quad (1)$$

Competition was then modeled as a function of diameter as described by (2), and the modeled value was then subtracted from the absolute value. This is described by (3). This leads to a competition index (C) symmetric about zero, and, on average, independent of tree diameter.

$$C_{ti} = \frac{b_0}{b_1 + D} + b_2 \quad (2)$$

$$C = C_t - C_{ti} \quad (3)$$

For the model version used for the Manaus and Puerto Maldonado regions the competition index was the sum of all trees ≥ 10 cm d.b.h in a 20 m × 20 m subplot.

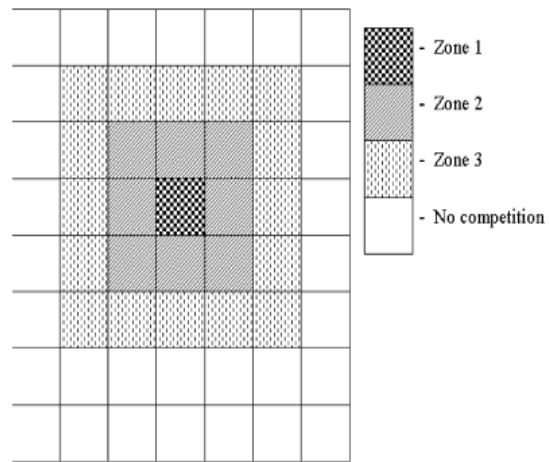


Fig. 1 The different zones of competition for the competition index of the Tapajos/Jari model, for a tree in zone 1, using a 10 m × 10 m grid square resolution

C. Growth Modeling

In the models trees have a diameter at breast height (d.b.h) that is updated each time-step using the diameter-growth function. This is the same for both models and is calculated as diameter growth rate in cm per year (I) which is a function of diameter at breast height (diameter of tree at 1.3 m from the ground) of the tree and the relevant competition index. Here, $a_0 \dots a_4$ are model parameters, D is the diameter at breast height, C is the diameter independent competition index and e is the mathematical constant represented by this symbol. Equation (4) describes this.

$$I = D(a_0 + a_1 e^{-a_2 D}) + a_3 C + a_4 \quad (4)$$

D. Recruitment Modeling

The recruitment function describes the appearance of new trees at the minimum d.b.h threshold, which was 10 cm for all three areas. The probability of recruitment (F) of a new trees in a grid-square of 100 m² for the Para model and 400 m² for the Manaus and Puerto Maldonado models, depends on the light availability in that grid-square. All three models run with annual time-steps. Here, $r_1 \dots r_2$ are model parameters, I_{10} is the diameter growth rate in cm per year of the hypothetical tree of the minimum d.b.h of 10 cm in the center of a 20 m × 20 m gridsquare for the Manaus/Puerto Maldonado model and 10 m × 10 m for the Tapajos/Jari model and e is the mathematical constant represented by this symbol. The growth rate is predicted using the growth model described for a tree with the same diameter at the minimum d.b.h threshold of 10 cm. The function used for Puerto Maldonado and Manaus is a simple linear regression and is described by (5a). The equation for the model used for Caxiuana or the Tapajos/Jari model is (5b).

$$F = r_1 + r_2 I_{10} \quad (5a)$$

$$F = r_1 e^{-r_2 I} + r_2 \quad (5b)$$

For both models a model parameter, T_i represents the time required (in years) for ingrowth as the number of years required for a tree to grow from seed to a d.b.h of 10 cm. It is used in the simulation when an area of ground is cleared of seedlings, for example when the soil surface is mechanically scarified and compacted during log extraction. This is different for all three areas and ecological guild within each area.

E. Mortality Modeling

Mortality (m_i) is modeled in the same ways across the three sites. This is modeled on an annual basis based on size (d.b.h). The annual mortality probability (as a percentage) is given by (6) where N_o is the total numbers of stems of the particular functional group at the beginning of the time interval t , and N_m is the number of recorded dead trees during the interval. The dynamics of the mortality model are described by system of (7). Here, $b_1 \dots b_3$ are model parameters, b_m is the bin width or 5th percentile of the diameter distribution and D_i is diameter at breast height of the tree i .

$$m_i = 1 - \left[1 - \frac{N_o - N_m}{N_o} \right]^{1/t} \quad (6)$$

$$m_i = \begin{cases} b_1, & D_i < b_m + 10 \\ b_2 + b_3 D_i, & D_i \geq b_m + 10 \end{cases} \quad (7)$$

F. Allometric Functions

Other allometric properties, like height and crown width of the trees are determined using functions with d.b.h. References [25] and [31] describe these extensively and provide relevant coefficient values.

G. Drought Mortality Pulse

Differences in forest dynamic behavior between wet and dry season across time are considered by incorporating a deterministic drought mortality pulse. This artificially increases tree mortality in the forest at regular intervals as determined by forest permanent sample plot and relevant environmental data from the Manaus and Puerto Maldonado regions. Values were set to 45% increase in relation to the baseline tree mortality of the forest on a 12 year interval for the forest of the Manaus region and 70% on a 9 year interval for the forest of Puerto Maldonado. Data from rainfall and temperature measurement stations run by the Brazilian national institute of meteorology (INMET) along with direct forest permanent sample plot demographic data were used. References [39],[40] provide practical justification for the use of these figures. The Tapajos/Jari model used for modeling the Caxiua forest did not include a drought mortality pulse.

III. DATA AND MODEL CALIBRATION

A. Data

Permanent sample plot (PSP) data have been recorded from forests in the Manaus region in Amazonas state the Caxiua region in the state of Para in Brazil and the Puerto Maldonado region in the Madre de Dios area in Peru.

The series of plots in Manaus are clustered in four locations. The first is the Adolpho Duke Forest reserve located 26 km outside the city of Manaus (02°, 55'S, 59°, 59'W). These are in undisturbed forest and composed of 72 plots each of 0.96 ha within which trees and shrubs of all species ≥ 1 cm d.b.h are identified, tagged and their diameter at breast height measured on a censored basis. Plot shape is curvilinear following the topographic contour in each location. For the purposes of these investigation only measurements of trees down to 10 cm d.b.h were used. The plots have been measured in 2004 and 2008. Data from both of these periods were made available for the trees. Reference [6] provides details of the data and the environment of the plots.

The second is the Biological Dynamics of Forest Fragments Project (BDFFP) undisturbed forest plots located 90 km outside the city of Manaus (2°51'31.24"S; 59°53'17.36"W). This is composed of 18 plots each of 1 ha in size and of square shape. They are further artificially subdivided in 20 m \times 20m subplots for purposes of mensuration. They have been censused at various intervals since 1981 with the last campaign made available in 2004. In them all trees of all species ≥ 10 cm d.b.h are monitored. Reference [27] provides details of the environment of these plots.

The third series of plots was the TEAM network early warning system for nature permanent sample plots. Plots are located 100 km outside the city of Manaus (2°56'41.22"S, 59°56'37.73"W). This is composed of 6 plots in undisturbed forest each of 1 ha in size and square shape. They are further artificially subdivided in 20 m \times 20m subplots for purposes of mensuration. In them all trees of all species ≥ 10 cm d.b.h are monitored. They have been censused three times: in 2003, 2005 and 2007. Reference [27] provides details of the environment of these plots.

The fourth series of plots was the Precious Woods Amazonas ltd permanent sample plots which is located 250 km outside the city of Manaus (2° 57' N, 58° 42' W). These are composed of 18 plots each of 0.5 ha which are artificially subdivided in 10 m \times 10m subplots. They are located in selectively logged forest. In them all trees of all species ≥ 50 cm d.b.h are monitored. From 50 to 30 cm d.b.h of all commercial or potentially commercial species are monitored. A semi random subsample of 50% of the subplots is made in which commercial and potentially commercial trees with a minimum d.b.h of 15 cm are monitored in this. Two measurement campaigns have been made available one in 2003 and another in 2006. Reference [36] provides details of the environment of these plots.

The series of plots in Puerto Maldonado, Peru are clustered in two locations 120 km outside the city of Puerto Maldonado in the Madre de Dios province of Peru

(12°40'59.20"S, 69°13'1.50"W). They are known as Tambopata and Cuzco Amazonico. The Tambopata is composed of 6 plots of 1 ha and the Cuzco Amazonico is composed of 4 plots of 1 ha. They are located in undisturbed forest. They are square in shape and artificially subdivided in 20 m × 20m subplots. In them all trees of all species ≥ 10 cm d.b.h are monitored. Data from two measurement campaigns were available for each of these areas on average 13 years apart. The first of these was in 1994 for all plots except for 1 in Cuzco Amazonico for which it was 1998. The next census made available for all plots was in 2009. Reference [27] provides details on the environment of these plots.

The series of plots in Caxiua are clustered in one location, the Caxiua national forest 350 km outside the capital city of Belem in the state of Para, Brazil (1°51'17.26"S, 51°40'5.03"W). They are composed of 6 plots of 1 ha and are located in undisturbed forest. Within them all trees ≥ 10 cm d.b.h of all species are monitored and precise x, y coordinates are noted for each individual tree. Two measurement campaigns have been made in 2002 and 2006. Reference [27] provides details of the environment of these plots.

B. Tree Species Ecological Grouping

For the purposes of this research the FAO convention of the definition of a tree species was used which was that of a woody perennial of a maximum potential height of at least 5 m. For the Manaus and Puerto Maldonado sites we classified all tree species a priori using all possible combinations of three bole wood specific gravity (g cm^{-3}) and three adult stature classes (maximum potential height classes). These are traits which are known to correlate well with the individual processes of growth, recruitment and mortality as well as with the process of ecological succession [4], [17], [18], [19], [26]. The result of this was nine groups or guilds. The nine groups represent all possible combinations of the two traits divided each in three classes. The approach was originally developed and tested for rainforest in Malaysia [19] and has been validated and used for Neotropical rainforest for purposes of forest dynamics modeling [1], [7], and [15]. For the Caxiua site we used a pre-existing classification with 10 analogous guilds to the aforementioned 9 guild system to assign tree species in the permanent sample plots using mean diameter growth (cm yr^{-1}) and the 95th percentile of diameter adult stature (D95) based statistics derived from permanent sample plot data. The assumption was that diameter growth is generally inversely related to wood density and diameter is positively related to tree height and hence both are analogous measures of adult stature. The procedure involved two stages. The first was to use discriminant analysis to assign tree species in the plots with at least 20 individuals to the original guilds using values for diameter growth and D95. The centroids of those groups were developed by clustering analysis of a large network of permanent sample plots elsewhere for use with the Tapajos/Jari model that is also used in this study [25]. The second stage was subjective and it involved assigning tree species with less than 10 individuals to the guilds using taxonomical and other relevant morphological

criteria.

With the above information on individual species it was possible to classify tree species in the plots in the C-S-R plant functional type system [11] and accept analogies with both aforementioned grouping (guild) systems with respect to this on the basis of previous work with datasets from European tree species [2], [3]. It was also possible to accept analogies with the general ecological grouping of tropical tree species [1], [19], [25] and the tropical tree three ecological group systems of climax, light hardwoods (LHW) and true pioneers [37]. Wood density and adult stature in meters varied according to the general ecological group based on data from the 9 guild system used for Manaus and Puerto Maldonado tree species for this study (Table I).

TABLE I
ECOLOGICAL GROUPING SYSTEMS USED IN THIS STUDY WITH TRAIT
STATISTICS FROM THE MANAUS AND PUERTO MALDONADO (PM) PLOT DATA

General Ecological Group	Manaus PM	Tapajos/Jari	C-S-R System	Whitmore Group	WD	AS
Slow growing emergent	1	8	SC	Climax	≥ 0.70	$H_{\max} \geq 35$
Slow growing canopy	2	1	SC	Climax	≥ 0.70	$15 \geq H_{\max} \geq 30$
Slow growing subcanopy	3	2	C/SC	Climax	≥ 0.70	$H_{\max} < 15$
Medium growing emergent	4	5	S/SC	Climax	$0.49 \geq WD \geq 0.69$	$H_{\max} \geq 35$
Medium growing canopy	5	3	SC/SCR	Climax	$0.49 \geq WD \geq 0.69$	$15 \geq H_{\max} \geq 30$
Medium growing subcanopy	6	4	S/CSR	Climax	$0.49 \geq WD \geq 0.69$	$H_{\max} < 15$
Fast growing emergent	7	10	S/CSR	Light hardwoods	< 0.48	$H_{\max} \geq 35$
Fast growing canopy	8	6	S/CSR	Light hardwoods	< 0.48	$15 \geq H_{\max} \geq 30$
Fast growing subcanopy (true pioneers)	9	7+9	CSR	Pioneers	< 0.48	$H_{\max} < 15$

Table I: PM = Puerto Maldonado

C. Model Calibrations

A new model for the Manaus and Puerto Maldonado areas was necessary for two reasons. The first was that the spatial position of trees in the datasets that did not include precise x, y coordinates in space or a 10 m × 10m grid square resolution as with other modeling efforts for similar non flooded forests of Brazilian Amazonia for the Paragominas [28] and Tapajos regions [25] respectively. The second was that both these areas had significant differences both in relation to the aforementioned regions but also between them. More

specifically there were significant differences in both mean annual rainfall (2285 mm yr⁻¹ in Manaus, 2110 mm yr⁻¹ in Tapajos and Caxiuana, 1750 mm yr⁻¹ in Paragominas and, 1568 mm yr⁻¹ in the Puerto Maldonado area of Peru) and intensity of the dry season (2 months with rainfall < 100 mm in Manaus, 4 months in Tapajos and Caxiuana and 5 months in Paragominas and Puerto Maldonado in Peru) [27]. Edaphic (Oxisols/yellow latosols) and topographic conditions (gently rolling) were similar across [27]. The procedure of calibration involved firstly the calculation of values of the parameters used in the model using relevant permanent sample plot information by the use of regressions of the data from these areas for completion or the dynamics equations and estimation for allometric functions. The second stage was the evaluation of model performance in terms of biological realism in terms of conformation to the dynamic equilibrium assumption [38] of the undisturbed forest and realistic response to a single relatively heavy selective logging event (all trees of commercial species ≥ 45 cm d.b.h) over a 90-year simulation period. This is in line with other modeling efforts both in the SYMFOR framework [1], [22], and [23] but also elsewhere [15]. For this purpose 4 square permanent sample plots of 1 ha were used to initialize simulations for the Manaus and Puerto Maldonado areas respectively. 10 simulations for each 1 ha plot were run for each plot of the two areas and the number of live stems and total basal area in m² of live stems ≥ 10 cm d.b.h for each ecological guild within each 1 ha plot at 5 year intervals were outputted. Graphical exploration of these datasets was done for these two variables in their behavior as a function of time for biological realism of the forest both in its undisturbed and selectively logged state, in line with other studies within SYMFOR [1], [22], and [23]. For each of the three areas a diagram of mean basal area over 100 years of simulations for each of the three ecological guilds in the Whitmore (1989) classification of was produced. Then using the number of live trees by ecological guild in the C-S-R system a diagram of the average weighed ordinate value of the tree community in C-S-R space for each of the three areas over a 100-year simulation period of undisturbed forest.

IV. SIMULATION EXPERIMENTS

A. Experimental Protocol

The experiments were conducted using a nested design. Four square 1 ha plots were used to initialize simulations for each of the three areas. For each plot there were five disturbance treatments. These were unharvested forest which was the control (C), light high grading (LHG), reduced impact logging on a 30 year rotation (RL30), conventional logging on a 30 year rotation (CL30) and heavy high grading (HRG). The aforementioned treatments represent a gradient of increasing disturbance in terms of biomass loss (owing to a gradual increase in the number of trees harvested, dead trees owing to logging, and liana cutting in certain scenarios), biomass damage (owing to damaged trees during logging operations) and opening up of the forest canopy (due to tree harvesting and skid trails). All scenarios were run for a 100 year period

with the first logging event occurring at year 10 of the simulations. 10 simulation runs were performed for each of the four individual PSP and for each logging scenario in each of the three areas. Details on the experimental design are provided in Appendix I. The initial conditions of the plots in terms of stand density, commercial volume in m³ and proportion of Light hardwood (LHW) and true pioneers in the three group system are given along with their respective standard error in Table II.

TABLE II
DESCRIPTION OF PERMANENT SAMPLE PLOTS USED TO INITIALIZE
SIMULATIONS BASED ON DATA FROM TREES ≥ 10 CM (MEAN \pm STANDARD
ERROR)

Stand Characteristics	Manaus	Caxiuana	Puerto Maldonado
Total volume (m ³ ha ⁻¹)	311 \pm 14	293 \pm 11	243 \pm 19
Commercial volume (m ³ ha ⁻¹)	97 \pm 12	129 \pm 16	136 \pm 20
Percent volume of Light hardwood species	3 \pm 1	6 \pm 2	8 \pm 2
Percent volume of pioneer species	2 \pm 0.6	4 \pm 1	7 \pm 1

B. Experimental Data and Treatment

For the purposes of the questions to be addressed two variables were chosen. The first was basal area in m² and the second numbers of live trees ≥ 10 cm d.b.h for each of the ecological guilds for each 1 ha plots. These were outputted at three intervals within the 100 simulation window at 15, 50 and 90 years respectively after the beginning of the simulations.

We then used the absolute difference of treated with untreated (control) stand basal area (1 ha plot) for each individual time point for each permanent sample plot to derive a figure for each time point for each logging scenario with the undisturbed forest for that specific plot, time point and logging scenario of biomass deviation from primary forest conditions.

Using the abundances of each individual ecological group of trees it was possible to derive a functional signature for each individual PSP in the competition-stress rudrance (C-S-R) system of vegetation functional classification using the C-S-R CALCULATOR software package [14] for each 1 ha PSP for each individual time point outputted. It was then possible to estimate the degree of deviation for each logging scenario relative to undisturbed forest conditions by using the net position of the vegetation in each of the three PSP sites for each of the two aforementioned variables. This procedure gave a total of 12 observations for each logging scenario within triangular C-S-R space measured as the net Euclidian distance of that time point for that plot with respect to undisturbed forest (control) position in three dimensional Cartesian space. For each of the two variables the statistical mean of the 10 simulation runs was used for each of the three successive time points for each of the four 1 ha plots used to initialize simulations. Final values for this latter variable were multiplied by 100 to allow for statistical testing as decimal figures were too many for analyses.

C. Statistical Analyses

The effects of different selective logging intensities on the function composition and the stand basal area both within and between each of the three permanent sample plot sites were investigated separately by means of a general linear model (GLM) to perform an analysis of variance in the GENSTAT v12.1 program. For purposes of analyses all successive time points were pooled together for each of the three areas thereby eliminating the temporal component and examining the net effect of selective logging measured as deviation from primary forest conditions over an 80 year period following the initial (and for some scenarios unique) logging event.

V. RESULTS AND DISCUSSION

A. Evaluation and Calibration of Models

When the calibrated model had been implemented in the SYMFOR framework for both Manaus and Puerto Maldonado, initial simulations of undisturbed forest showed significant compositional changes occurring with an increasing dominance of more early successional groups. More specifically using the 9 guild system, for Manaus significant positive changes occurred for groups 6, 8, 2 and 9 relative to the other ecological groups. The same was also true for Puerto Maldonado for groups 2, 7 and 8. This was probably a result of slight imbalances between the growth, mortality and recruitment sub-models resulting as an almost inevitable consequence of the uncertainty in parameter values calibrated from a limited dataset a common problem with efforts in SYMFOR so far [22], [23], [24], [25], [28], [38]. This was considered to be in direct violation of the dynamic equilibrium assumption that dictates compositional and structural stability of undisturbed forest within the time scales addressed in this study based on other modeling efforts [15], [16], [22], [23], [24], [25], [28], [29], [30], [38].

To address this issue selected model parameters were modified (tuned) incrementally within their respective 95% confidence intervals to improve performance in order to demonstrate a dynamic equilibrium in primary forest in line with other modeling efforts in the SYMFOR framework [1], [22], [23], [24], [28]. For the Manaus version this resulted in a model steady state (equilibrium) in which although some compositional changes occurred these remained well within the limits of the forest plot data used to initialize simulations (Fig. 2 (a) and (b)). This was also the case for the Puerto Maldonado version (Fig. 2 (c), (d)). Results following tuning were also consistent with other studies [1], [22], [23], [25], and [28]. The resulting model parameters for both regions from this procedure for the growth model can be seen in Table III while for the mortality and recruitment models in Table IV. In response to a heavy single logging event the forests of both Manaus and Puerto Maldonado exhibited significant compositional and biomass changes in response to logging. More specifically more early successional species groups benefited at the expense of more late successional ones. Following the event succession towards a steady state dominated to a greater extent by more shade loving early

successional species with a higher wood density followed (Figs. 2 (e), (f) and (g), (h), respectively). Results were in agreement with other studies within SYMFOR [1], [22], [23] but also elsewhere [5], [12], [13], [15], and [16].

TABLE III
PARAMETERS FOR THE GROWTH MODEL FROM THE MANAUS AND PUERTO MALDONADO DATA

	Group	a ₀	a ₁	a ₂	a ₃	a ₄
Manaus	1	0.0004	0.0001	3.178	-0.0177	0.202
	2	0.0001	0.0004	2.388	-0.055	0.217
	3	0.0054	-0.0005	2.101	0.0417	0.1114
	4	0.0023	0.00001	4.28	-0.0522	0.212
	5	0.007	-0.002	3.188	-0.0533	0.165
	6	0.0055	-0.0004	2.0633	-0.0037	0.161
	7	0.0038	-0.0002	5.776	-0.106	0.258
	8	0.0073	-0.0009	2.54	-0.137	0.270
	9	0.282	-0.0005	0.0211	-0.058	0.0018
Puerto Maldonado	1	-0.0034	0.1	0.1	-0.093	0.059
	2	-0.0054	0.1	0.1	-0.213	0.0185
	3	-0.15	0.1	0.1	-0.156	0.088
	4	-0.0043	0.1	0.1	-0.117	0.25
	5	-0.0095	0.1	0.1	-0.078	0.16
	6	-0.027	0.1	0.1	-0.2	0.19
	7	-0.0034	0.1	0.1	-0.11	-0.0038
	8	-0.0039	0.1	0.1	-0.158	0.153
	9	-0.0063	0.1	0.1	-0.0148	0.133

TABLE IV
PARAMETERS FOR THE MORTALITY AND RECRUITMENT MODELS FROM THE MANAUS AND PUERTO MALDONADO DATA

	Group	r ₁	r ₂	Ti	b ₁	b ₂	b ₃	Bin (cm)
Manaus	1	-1.41	0.0074	49.4	1.76	0.0037	0.0396	2.6
	2	0.0749	0.0021	52	2.2	-0.0039	0.944	4.4
	3	-2.351	0.004	65	1.44	-0.0137	1.0	3.5
	4	-2.862	0.024	40	1.36	-0.0069	0.011	1.5
	5	-0.021	0.0329	45	5.166	0.0053	0.933	7.5
	6	0.823	-0.0088	50	8.13	-0.0209	4.32	5.3
	7	-0.104	0.0246	35	7.128	-0.0091	1.7	3.5
	8	0.2658	-0.0246	32.1	8.3216	-0.0156	1.807	3.3
	9	0.479	-0.0002	22	8.379	0.2694	2.27	2.4
Puerto Maldonado	1	0.014	0.0012	50	0.8372	-0.0132	1.421	1.9
	2	0.0574	0.0011	30	1.4396	-0.0076	1.3225	3.3
	3	0.2394	-0.0176	43	1.09	0.0243	0.0406	4.1
	4	-0.0434	-0.3869	55	0.875	-0.0093	0.5175	2.2
	5	-0.1723	-0.1496	33	1.6133	-0.0175	0.74	1.9
	6	-0.5416	0.03	43	1.19	0.0284	0.132	5.2
	7	0.0	0.011	16	2.4	-0.0151	2.5574	2.7
	8	0.0	0.00159	11	1.525	-0.0181	2.7868	2.1
	9	-0.1782	0.0904	12	1.898	-0.0491	5.57	3.9

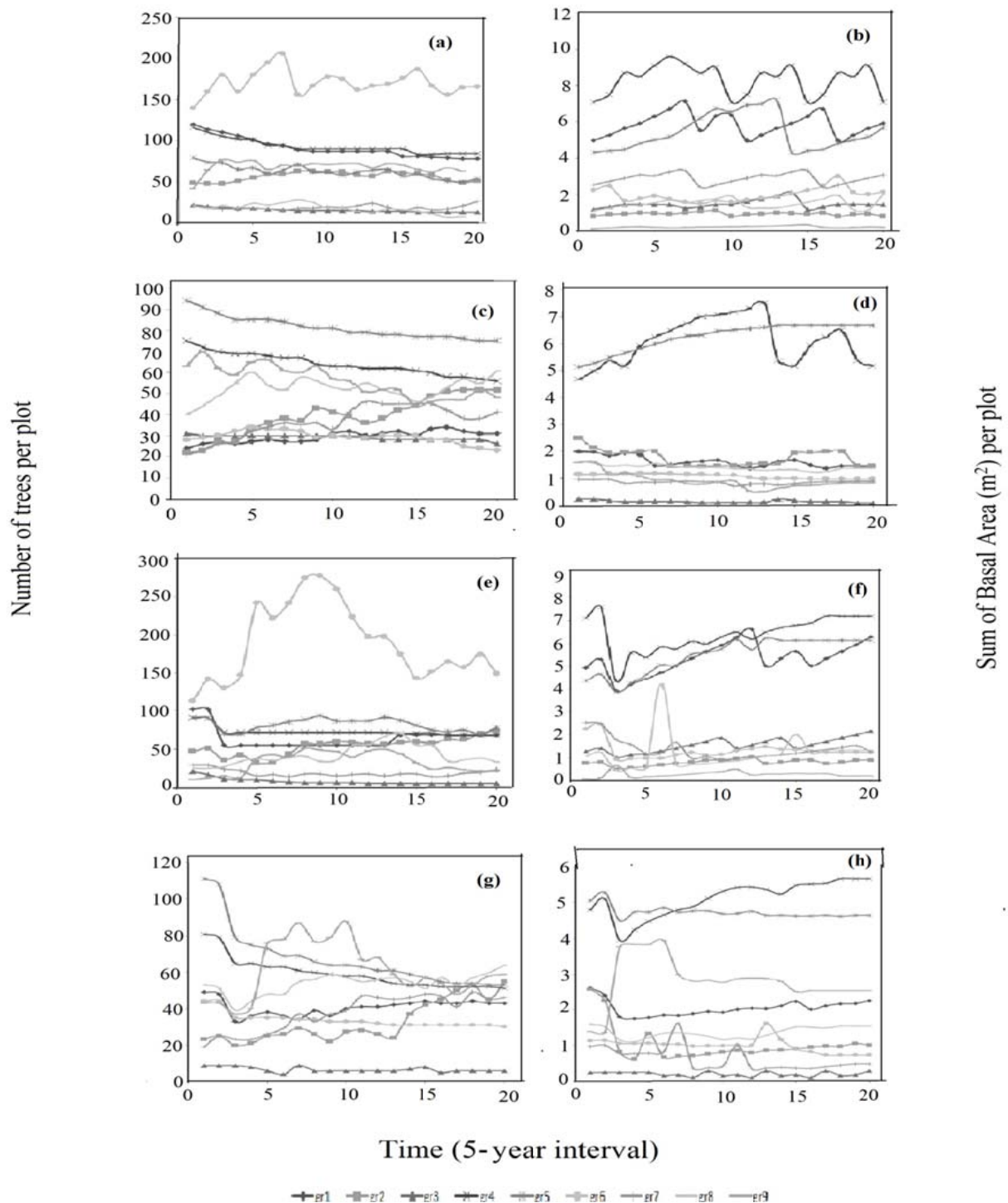


Fig. 2 Variation in the behavior of the 9 ecological guilds in the 9 guild system (gr1-gr9) over a 100-year simulation period following model calibration in mean number of live trees and the mean sum of basal area per plot for undisturbed forest of the Manaus (a, b) and Puerto Maldonado areas (c, d) and for selectively logged forest of Manaus (e, f) and Puerto Maldonado (g, h) for a relatively heavy harvest using four 1 ha plots from each area to initialize simulations. First harvest was done at year 10 of the simulations

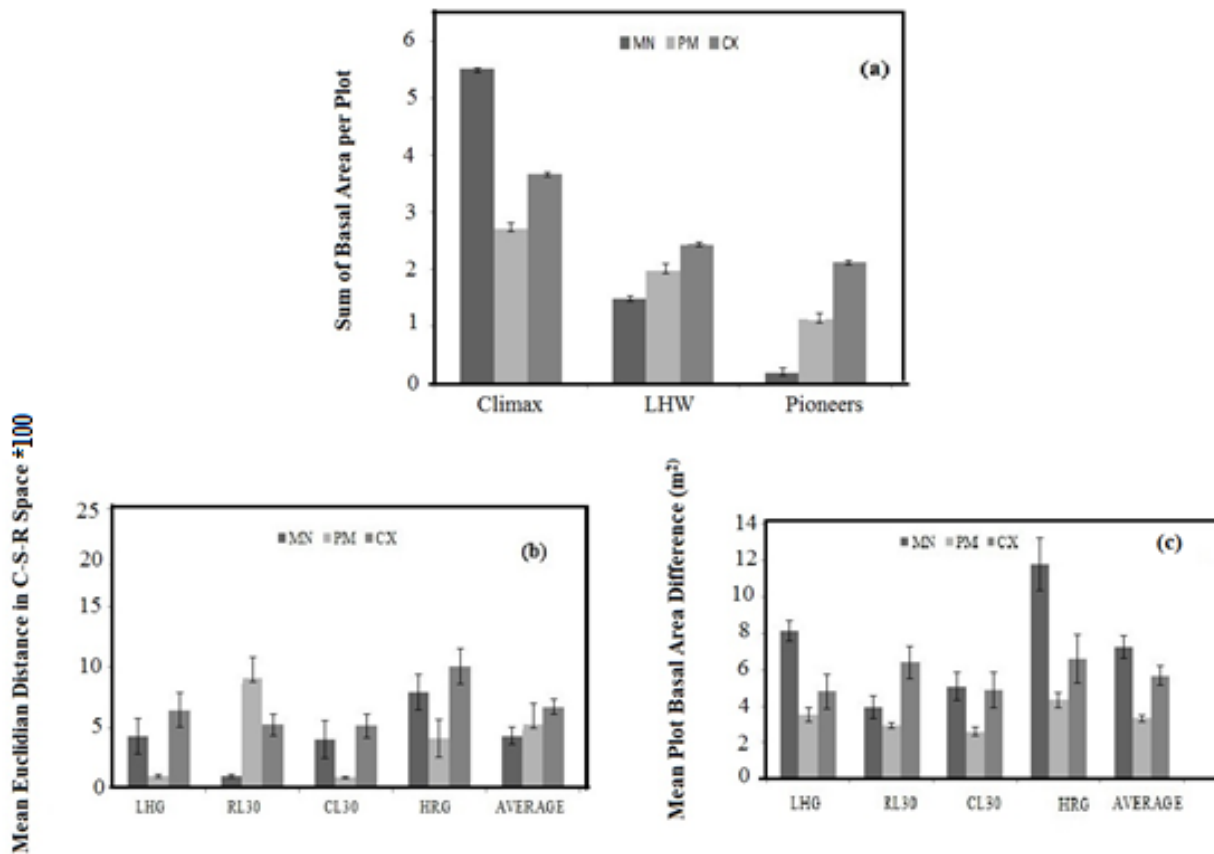


Fig. 3 Simulated 100 year statistical mean for the three permanent sample plot sites used to initialize simulations in this study of the three undisturbed forest communities of (a) stand basal area in m^2 of the three basic ecological groups of tree species of Amazonian terra firme forests (Climax, light hardwoods-LHW- and true pioneers), (b) absolute difference in stand basal area in m^2 and (b) Euclidian distance in C-S-R space multiplied by 100 for each scenario between that scenario and undisturbed forest of the four 1 ha plots used to initialize simulations based on averages C, S, and R ordinate values for that plot for a specific of three time points over the 90 year period. Error bars represent standard error of the mean. Site codes; MN=Manaus, PM=Puerto Maldonado, CX=Caxiuna. Logging treatment codes; LHG=Light high grading, RL30=Reduced impact logging on a 30 year rotation, CL30=conventional logging on a 30 year rotation, HRG=Clearfelling, AVERAGE=average across treatments

B. Simulations of Undisturbed Forest after Calibration

Following model calibration simulations of undisturbed forest showed that the forest in all three areas maintained its compositional integrity over a 100 year period in relation to the initial conditions of the specific permanent plots based on data used to initialize simulations (Table II) in terms of proportions of ecological guilds in the three guild system (Fig. 3 (a)). This provides further support for validity of the calibrations in the models for the Manaus and Puerto Maldonado especially with respect to the dynamic equilibrium assumption() assuming that the unlogged forest data used to initialize simulations represented the dynamic equilibrium [25]. Overall it is apparent that there are significant differences in the dynamic equilibrium of the undisturbed forest between the three areas that were directly proportional to the initial conditions of the forest based on the specific permanent sample plots used (Table II). This is in agreement with the prevailing axiom of the significant effect of the initial conditions on the system on simulation model results [16],

[30], [38]. Overall the forest of Manaus appeared to be at a later stage of ecological succession followed by the forest of Caxiuna and finally the forest of Puerto Maldonado. These results are in agreement with other studies based on permanent sample plot data from these areas [34].

C. Effects on Stand Functional Composition and Density

As far as mean Euclidian distance in C-S-R space (was concerned there was a statistically significant difference between the different selective logging disturbance treatments and across the different areas from which plots were used to initialize simulations ($F=7.12$, $p<0.001$). The pattern was that of essentially increasing Euclidian distance in C-S-R space with increasing logging intensity over the 100 year period overall and apparently greater deviation of the Caxiuna area followed by Manaus and finally Puerto Maldonado (Fig.3 (b)). The overall pattern was apparently closely related to the initial conditions of the system but also especially the behavior of the undisturbed forest. More specifically forests composed

but especially whose dynamic equilibrium of undisturbed forest is dominated to a greater extent from true pioneers or light hardwood tree species (LHW's) show less deviation from primary forest conditions in response to logging disturbance but only to a certain threshold. This in partial agreement with earlier studies [29], [33], [35] and knowledge of response to disturbance [5], [7], [9], [12], [13], [32], [33]. A possible explanation for this is that the forest of Caxiuana that had a dynamic equilibrium composed to a greater extent of true pioneers showed an overall greater degree of deviation from both Manaus and Puerto Maldonado in relation to the undisturbed forest simulations. Forests stands composed to a greater extent from early successional species and more specifically light hardwoods and true pioneers are indeed more resilient to selective logging but only to a certain point in baseline functional composition. The greater adaptation of true pioneers and light hardwoods to the conditions of disturbance caused by selective logging which are more limiting to growth and survival offers a competitive advantage to such a forest stand [1], [7], [8], [9]. However these traits also mean that they will also tend to dominate at the expense of more late successional species and thereby stands composed to a greater extent from a certain proportion and above will outcompete them to the extent that there will be changes in functional composition. This would be in agreement with practical knowledge of stand functional response to selective logging [37].

Moving on to mean stand absolute basal area difference in m^2 there was a statistically significant difference between the different selective logging disturbance treatments and across the different areas from which plots were used to initialize simulations ($F=1.95$ $p=0.029$). The forest of Puerto Maldonado showed consistently the smaller deviation both across the selective logging treatments and on average followed by the forest of Caxiuana and finally the forest of Manaus which showed the largest deviation (Fig. 3 (c)). It would seem that there is a correlation with the dynamic equilibrium of the undisturbed forest (Fig.3 (c)) and more specifically that stands with greater proportions of light hardwood tree species are able to maintain their density more easily than ones with less comparatively but also to ones composed to a greater extent from pioneers relatively. This was not an expected pattern because both light hardwoods and pioneer tree species are expected to grow faster and respond more readily to gap formation and decrease in stand density caused by disturbance and mortality of stems leading to decreased competition for remaining ones as well as the general increased light conditions [1], [9], and [35]. A possible explanation for this pattern is that none of the selective logging treatment resulted in adequate disturbance and release from competition that would allow the stems already present to grow faster and propagate with time changing the composition to a forest with greater proportion of these species which would contribute to faster stand growth rates in addition to this. It did however do this for the light hardwoods which are later in the process of ecological succession.

APPENDIX I

Site	Treatment	Skid Trail Planning	Lianas Cut on Harvestable Tree prior to Logging	Directional Felling	Number of Harvest events (90 year period)	Minimum Felling Diameter (cm)	Trees Harvested per event	Minimum Bole Quality Score	% of Total Stand Volume Harvested for all Events (ha^{-1})	% of Total Stand Commercial Volume Harvested for all Harvest Events (ha^{-1})	% Area in Skid Trails	% Trees Damaged (average)
Manaus	Control	no	no	no	0	0	0	-	0	0	0	0
Manaus	LHG	no	no	no	1	50	1	0.4	3.5	8	5.3	8
Manaus	RL30	yes	yes	yes	2	50	3	0.5	20	25	3	5
Manaus	CL30	no	yes	no	2	50	4	0.5	23	27	9	10
Manaus	HRG	no	no	no	1	35	10	0.2	33	40	13	14
Caxiuana	Control	no	no	no	0	0	0	-	0	0	0	0
Caxiuana	LHG	no	no	no	1	50	2	0.4	4.1	12	7	6
Caxiuana	RL30	yes	yes	yes	2	50	4	0.4	23	28	4	5
Caxiuana	CL30	no	yes	no	2	50	5	0.4	26	29	7	9
Caxiuana	HRG	no	no	no	1	35	12	0.2	35	52	10	11
PM	Control	no	no	no	0	0	0	-	0	0	0	0
PM	LHG	no	no	no	1	50	2	0.3	5	11	6	10
PM	RL30	yes	yes	yes	2	50	4	0.6	22	34	3.4	6
PM	CL30	no	yes	no	2	50	6	0.5	26	37	7	11
PM	HRG	no	no	no	1	35	11	0.2	30	48	11	16

Appendix I: PM=Puerto Maldonado

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