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SIMULATING FOREST DYNAMICS OF A TROPICAL MONTANE FOREST IN SOUTH ECUADOR

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With 5 figures and 2 tables
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Summary: The montane forests of Ecuador are part of one of the world's hotspots of biodiversity and they also suffer the highest deforestation rate amongst South American countries. The processes that drive the dynamics of these highly diverse ecosystems are poorly understood. This is particularly true for transient dynamics, which are crucial for the protection and sustainable management of such forests. Dynamic simulation models can be used to analyse the growth of forests, but so far they have been applied mostly to temperate forests and to some few tropical lowland forests. In this study we investigate whether a process-based, individual-oriented simulation model like FORMIND is capable of reproducing the dynamics of tropical montane forests. For this purpose we develop a parameterisation for the model and validate the model against field observations of different (structural) patterns. We then analyse the predicted succession dynamics. The model is capable of reproducing the structure and dynamics of mature ridge forest on different levels of complexity. The main results indicate that, in terms of relative abundances of different species groups and stem size distribution in the tree community, our model predicts the observed patterns in the field. Additional field studies and model modifications are required to simulate the succession processes that follow different types of disturbances. FORMIND is a promising tool for the extrapolation of local measurements and for simulating the dynamics of tropical montane forests. Parameterisations of the model for further forest types within the research area are intended. The model has a number of potential applications, ranging from investigating the impact of (different) natural disturbances on forest structure and tree species diversity to analysing different potential management strategies.

Zusammenfassung: Die tropischen Bergregenwälder Ecuadors sind Teil eines der weltweiten Hotspots der Biodiversität und erfahren gleichzeitig die höchste Entwaldungsrate Südamerikas. Das Verständnis der Prozesse, die diese hochdiversen Ökosysteme strukturieren, ist noch lückenhaft. Dies betrifft insbesondere transiente Dynamiken, die entscheidend für den Schutz und ein nachhaltiges Management dieser Wälder sind. Waldwachstumsmodelle untersuchen die Dynamik von Wäldern. Sie wurden allerdings bisher hauptsächlich in temperierten Wäldern und vereinzelt in tropischen Tieflandregenwäldern angewandt. In dieser Studie untersuchen wir die Dynamik eines tropischen Bergregenwaldes mit dem prozess-basierten, individuen-orientierten Simulationsmodell FORMIND. Wir entwickeln eine Parametrisierung des Models und vergleichen unterschiedlich komplexe Muster des simulierten Waldes mit Felddaten. Des Weiteren analysieren wir die Sukzessionsdynamik des Waldes. FORMIND reproduziert die Struktur und Dynamik des ausgewachsenen Gratwalds auf verschiedenen Komplexitätsebenen. Unsere Resultate zeigen eine gute Übereinstimmung von im Feld beobachteten Mustern und Modellergebnissen, insbesondere von relativen Häufigkeiten funktioneller Baumartengruppen und Stammzahl-Durchmesserverteilungen. Die Modellierung der Sukzession nach verschiedenartigen Störungen erfordert weitere Feldstudien sowie zusätzliche Modellanpassungen. Das Waldwachstumsmodell FORMIND ist ein vielversprechendes Werkzeug zur Untersuchung der Dynamik tropischer Bergregenwälder. Parametrisierungen des Modells für weitere Waldtypen innerhalb des Untersuchungsgebiets sind geplant. Anwendungen des Modells reichen von der Untersuchung des Einflusses verschiedener natürlicher Störungen auf die Waldstruktur und Baumartenreichtum bis hin zur Analyse verschiedener Managementstrategien.

Keywords: forest growth model, FORMIND, simulation, plant functional types, tropical montane forest

1 Introduction

Tropical montane rain forests have received less scientific attention compared to tropical lowland forests, but they are considered to be just as highly endangered, due mainly to conversion of forests into pastures or the exploitation of high timber value species (Mosandl et al. 2008) and climate change (Colwell et al. 2008). Ecuadorian forests suffer the highest deforestation rate in South America (1.7%, FAO 2009). Nonetheless, as part of the Tropical Andes, the Andean forests of Ecuador belong to one of the world's hotspots of biodiversity (Brummitt and Lughadha 2003).

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The processes that drive the dynamics of these highly diverse forest ecosystems are poorly understood. This is particularly true for transient dynamics such as forest regrowth after disturbances. To ensure the protection and sustainable management of timber, water and other ecological services of these forests, we need to broaden our knowledge of these ecosystems and their dynamics.

Forest simulation models can play an important role in incorporating available (local) data and process understanding for extrapolation to larger temporal and spatial scales (Pacala and Kinzig 2002). Process-based spatially explicit forest growth models such as FORMIND (Köhler 2000) simulate ecological processes like recruitment, mortality and growth explicitly and allow for the simulation of spatiotemporal forest dynamics over several hectares and centuries (Pacala et al. 1996). There is a rich literature describing quantitative and qualitative fundamental ecological processes in forests and a long tradition of different forest modelling approaches (Shugart 1998, 2002). The high number of tree species found in the tropics poses a challenge for any study. The concept of plant functional types (PFT), where species are grouped according to selected functional attributes, has proven to be a useful approach for analysing such diverse ecosystems (Jeltsch et al. 2008; Köhler et al. 2000; Smith and Shugart 1997). Commonly used traits for the categorisation of plant functional types (PFT) in tropical forests are shade tolerance and maximum potential height (e.g. Poorter et al. 2006). Most applications of process-based forest models in montane regions have so far concentrated on temperate forests (e.g. Goreaud et al. 2006; Rammig et al. 2006).

In this study, we investigate whether the dynamics of a montane rain forest in South Ecuador can be described using the individual-oriented, process-based forest model FORMIND. We reformulate parts of the model to achieve a unified model structure which allows for more time-efficient simulations (see Appendix). We develop a parameterisation of the model and validate the model against field observations of different structural patterns and then analyse the predicted succession dynamics. The exploration of undisturbed forest dynamics is an indispensable prerequisite for the investigation and comparison of the effect of different natural and human-induced disturbances on the forest. Within our research area, disturbances caused by landslides are a main source of natural disturbance and are therefore of special interest (Bussmann et al. 2008; Restrepo et al. 2009, Richter et al. 2009).

2 Study area

Study site is the evergreen montane forest of the Reserva Biológica San Francisco (3°58'S, 79°04'W), located on the eastern slopes of the Andes in southern Ecuador. The reserve stretches from 1800 up to 3200 metres above sea level (a.s.l.). With an average slope of 40° the terrain is very steep. Shallow landslides are a common disturbance; approximately 3.5% of the area is covered with visible traces of landslides (Stoyan 2000). To date, more than 280 tree species have been identified in the 1000 ha area (Homeier and Werner 2007). The forest can be divided into four forest types which differ strongly in structure and species composition (Homeier et al. 2008.). At the level between 1900 and 2100 m a.s.l. we distinguish between ridge and ravine forest. The ridge forest has a higher stem density, lower basal area and also a lower canopy height (15−20 m) compared to the more species-rich ravine forest. The remaining two forest types are located at higher elevations; canopy height, stem density and species richness decrease on these sites (Homeier et al. 2002). Our study focuses on the analysis of the ridge forest (1900–2100 m a.s.l.). We utilize data from repeated inventories (2004, 2005, and 2007) of 4.88 ha, in which all trees with a breast height diameter (dbh) > 20 cm where surveyed. In addition, we utilize data from 1200 m^2 with all trees above dbh=5 cm measured (and extrapolate this data to 1 ha).

3 Model description

In the following we give a detailed description of the forest model FORMIND. The model description follows the ODD protocol (**O**verview, **D**esign concepts, **D**etails (Grimm et al. 2006)) and updates previous descriptions (see Appendix in Grimm et al. 2006, Köhler 2000). Here we present the first two parts of the protocol (i.e. overview and design concepts), the submodels are described in detail in the Appendix.

3.1 Overview

Purpose – FORMIND is designed to analyse the dynamics of uneven-aged species-rich forest stands with a focus on the impact of natural or anthropogenic disturbances on forest structure and composition.

State variables and scales – The FORMIND model is a spatially explicit, individual-based forest model. Forest stands from one hectare up to several square kilometres can be simulated. Each hectare is divided into patches of 20 × 20 square metres. Within a patch trees do not have a spatial explicit position. To enable an individual-based simulation of species-rich forest communities, tree species are grouped into plant functional types (PFT) according to the physiological attributes maximum attainable diameter at breast height (dbh) and maximum annual diameter growth. Figure 1 shows snapshots of a visualisation of FORMIND.

The smallest entity of the model is a single tree. Trees of the same size and PFT within one patch are assumed to have the same physiological attributes. The shape of a tree is simplified and described by assuming a cylindrical crown and a conic stem. Each tree is described by its aboveground biomass; the tree geometric attributes, e.g. dbh, tree height and crown diameter are derived from biomass using allometric relationships (see Appendix). Each patch is characterized by the list of its trees and its location within the simulation area. We use periodic boundary conditions at the border of the simulation area. FORMIND works with an annual time step and usually several hundreds of years are simulated.

Process overview and scheduling – The model comprises four submodels characterizing establishment, mortality, recalculation of light climate and growth, which are applied in this order. While establishment and light climate are calculated on the patch level, mortality and growth are applied on the level of individual trees. Trees can establish if light climate on the forest floor is adequate and if space in lower height layers is sufficient.

There are different sources of mortality: normal mortality due to ageing, increased mortality for small trees, mortality due to high tree density (self-thinning) and mortality due to gap creation when large trees fall and damage other trees.

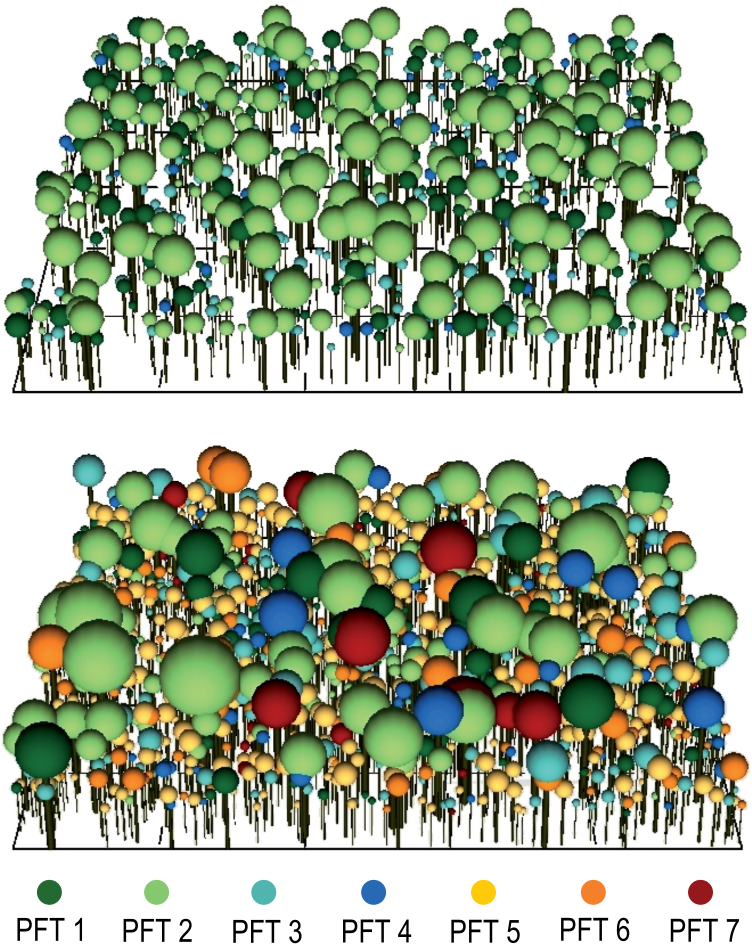

Fig. 1: Visualisation of FORMIND, showing all trees above a threshold dbh of 5 cm on an area of 1 ha. Each colour represents one PFT. (a) Snapshot after 20 years of simulation. The dominant canopy group comprises the fastest growing species (PFT 2) that reach a potential dbh of 70 cm, see table 1. (b) Snapshot after 400 years.

It is assumed that light availability is the main driving force for individual tree growth and forest succession. Within each patch all trees compete for light and space. Light climate is calculated via a light extinction law according to the distribution of leaves in a patch (Monsi and Saeki 1953). Tree growth is calculated on the basis of carbon balance according to light availability and the main physiological processes photosynthesis and respiration. The process of calculating respiration rates has been revised for this study (see Appendix).

3.2 Design concepts

FORMIND is built in the tradition of forest gap models (Shugart 1998; Bugmann 2001). Competition for light and space are assumed to be the dominant driving factor of forest dynamics; competition for nutrients is included indirectly. Light climate strongly influences the process of growth and also establishment; the competition for space is realized by implementing a crowding mortality.

Emergence – All facets of forest structure, for instance PFT abundances and tree size distributions emerge through the characteristics of trees and interactions among trees. Realized annual diameter growth rates and recruitment rates are not directly built into the model but result from the light climate in patches.

Sensing/Interaction – Trees react on the light climate they are exposed to, which is mainly influenced by surrounding trees, i.e. they "sense" other trees indirectly. Large tree crowns can grow into neighbouring patches. Direct interaction between trees of different patches occurs when dying large trees fall over and destroy a proportion of trees in the patch where their crown hits the ground.

Stochasticity – All sources of mortality are modelled as stochastic processes. Mortality due to space competition affects randomly chosen trees. A "tree fall probability" determines, if a dying tree will fall.

Collectives – Tree species are grouped into different plant functional types (PFT). All trees of the same PFT that establish at the same time are grouped into one cohort.

Observation – The individual-based approach allows us to compare model outcomes with field observations on the individual tree level, on the population level as well as on the level of the entire tree community. The main output variables we analyse are: basal area, stem number and tree size distribution on hectare level over all PFTs as well as PFT-specific.

Initialisation – We start from a treeless area which is assumed to be suitable for regeneration of all PFTs. Simulation area is normally 4 hectares.

Input – Site conditions are assumed to be homogeneous and there is no inter-annual variability of environmental conditions. Table 1 gives an overview of the parameters of FORMIND.

Parameterisation – On the basis of field observations and expert knowledge we grouped 71 tree species of the ridge forest into seven PFTs according to the characteristic maximum attainable diameter and maximum annual growth (see Tab. 2). To estimate the growth capacity of species in the Reserva Biológica San Francisco, we referred to expert knowledge on the maximal annual growth rates for each PFT (Tab. 2). Assuming that nutrient limitation is correlated to tree growth, the competition for nutrients is implicitly included by using the diameter growth rates. Parameters for mortality, recruitment and the potential maximum growth curve (see Tab. 1) were then calibrated by iterated simulations so that the model output fits the observed stem size distribution. We developed diameter-height relationships for each PFT according to the maximal height reached by trees of the respective PFT (see *Tree geometry* in the Appendix and Tab. 1).

4 Results

As a first step we calibrated the model (see Parameterisation). The full parameterisation is presented in table 1. After calibration, we found a good agreement of predicted and observed stem size distributions (Fig. 2). The model accurately reproduces abundances for trees in different size classes, but the frequency of larger trees is slightly overestimated. On the level of single PFTs we also find a reasonably good agreement of simulated and observed stem size distributions.

The model accurately predicts basal area on different levels, for trees with dbh above 5 cm, and 20 cm respectively (Fig. 3a, b). Simulated basal area matches very well to the observed basal area for overall as well as PFT-specific basal area on both levels. The rank of PFTs differs significantly between the two levels: while PFT 5 contributes the second highest share to basal area of trees with dbh above 5 cm, it contributes only marginal to the basal area of trees with dbh above 20 cm. The PFT 5 comprises those species that grow in the understorey and reach a maximum dbh of 25 cm (see Tab. 2). The overall stem numbers of trees

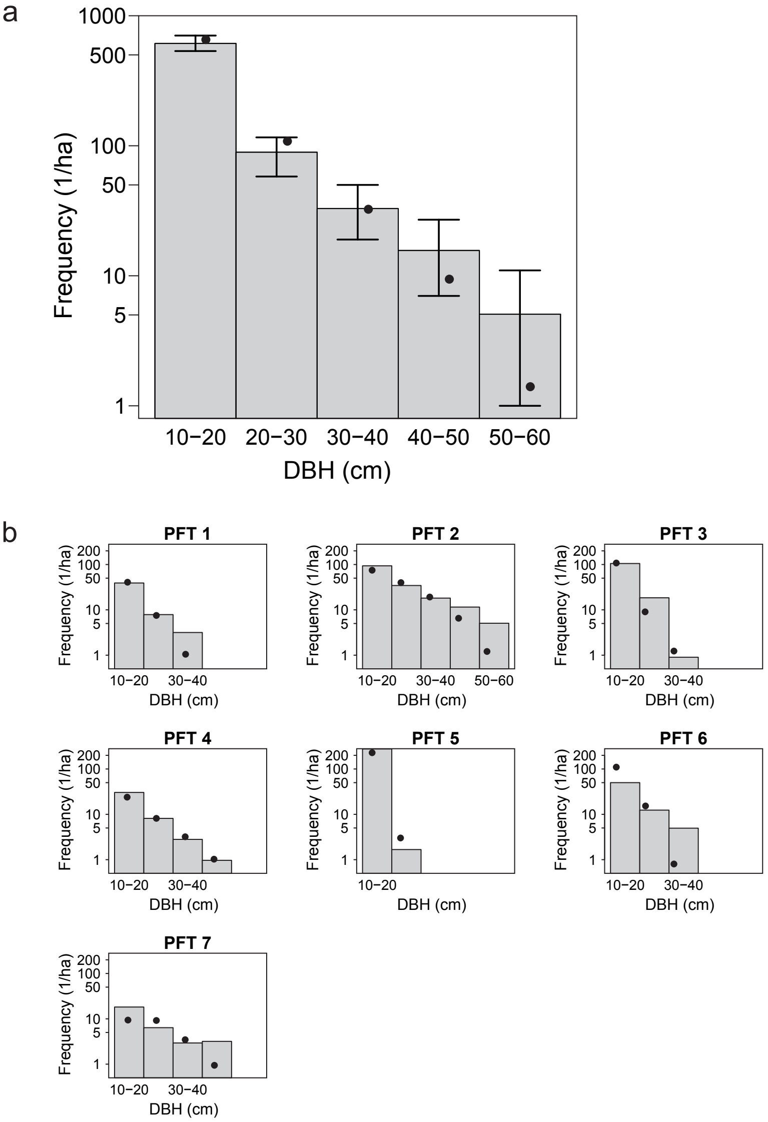

Fig. 2: Stem size distribution of the whole stand and for each individual PFT. Red dots show observed frequencies; bars show the averages of the model taken from different points in time of one run, error bars show minimum and maximum frequencies occurring over time. Note the logarithmic scale, which is used to better display abundances of large trees.

with dbh above 5 cm are slightly underestimated by the model (Fig. 3c); this is mainly due to the underestimation in stems of PFT 5. Stem numbers of the remaining PFTs are predicted fairly well. Also for trees with dbh above 20 cm we observe a good fit between model and data (Fig. 3d).

To examine model variation we reduce the simulated area to one hectare and depict several single model runs (Fig. 4). There is a notable temporal variation of overall basal area within single model runs (and within short time) that generally fits to the variation we find between plots. The mean overall basal area is slightly overestimated by the model compared to the basal area of the whole inventory plot (cf. Fig. 3b again). This is due to a slight overestimation of the fast-growing species (Fig. 4b). The overall temporal variation is mainly caused by the variation of these species.

The succession of overall basal area shows a rapid increase within the first 40 years and a slight overshoot before basal area reaches a stable level, where stems with dbh above 5 cm comprise a ba-

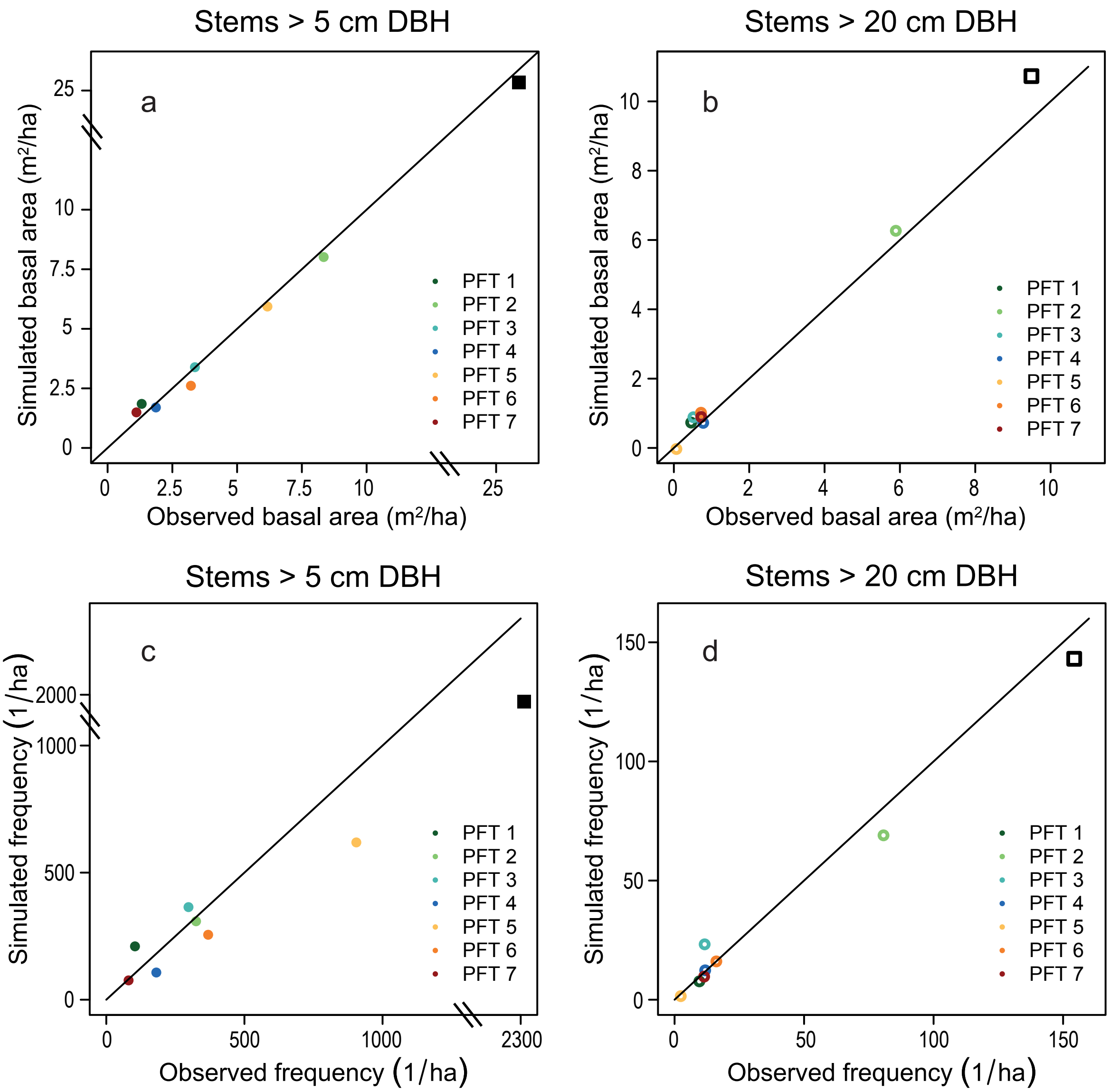

Fig. 3: Simulated versus observed basal area (a, b) and stem number per hectare (c, d). Trees above 5 cm dbh are shown with filled symbols, trees above 20 cm dbh with open symbols.

sal area around 25 m^2 per hectare (Fig. 5a). On the level of single PFTs (Fig. 5b) it takes much more time for basal area to reach a stable level than for the overall basal area. The overshoot in overall basal area in the beginning of simulation is caused by the overshoot in basal area of PFT 2. Only the fast-growing species groups (PFT 1 and 2) display an excess in basal area in the early phase of succession, the other groups approach their stable basal area with different paces. It takes around 500 years for all species groups to reach a stable basal area.

5 Discussion

In this study we applied the forest model FORMIND to simulate the dynamics of the ridge forest of the Reserva Biológica San Francisco in southern Ecuador. The strength of the individual-based model approach is that it allows us to distinguish patterns on different spatial and temporal levels, ranging from individuals to entire landscapes. These different patterns have been intensively investigated and compared with available field data from various tropical sites (cf. e.g. Huth and Ditzer 2000;

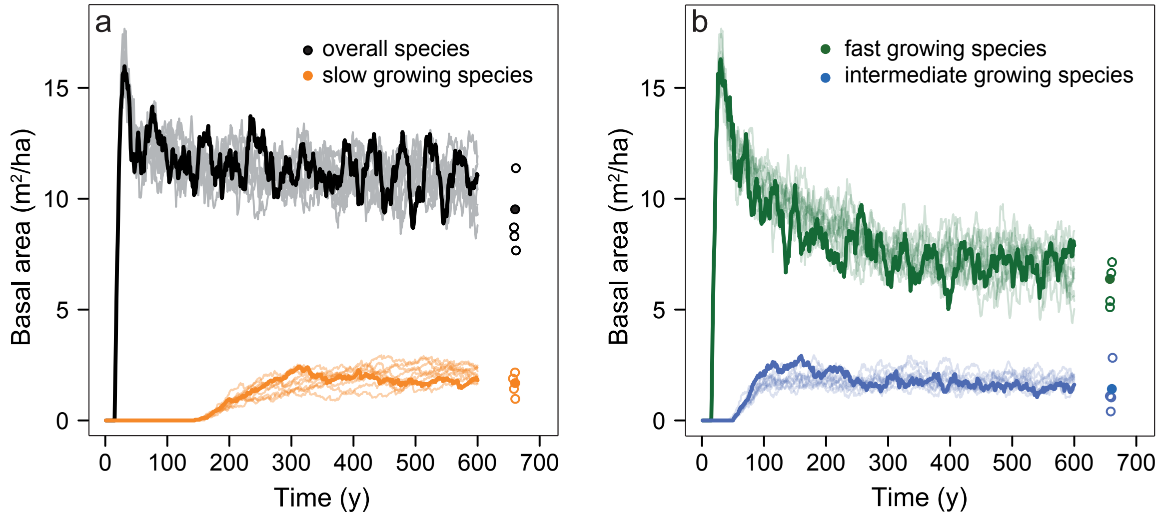

Fig. 4: Succession of basal area of trees with dbh > 20 cm dbh. Ten model runs of a 1 ha area (nine of them in paler shades) show variation between model runs and fluctuation within single runs. The filled points show data of the whole inventory area (4.88 ha), open circles show data from 1 ha subplots of the inventory area. For convenience of illustration we aggregated PFT into fast-growing species (PFT 1 and 2), species with intermediate growth rates (PFT 3 and 4) and slow-growing species (PFT 5, 6 and 7).

Köhler et al. 2003; Rüger et al. 2008). These studies have shown that in those cases FORMIND accurately reproduces patterns on different levels of complexity.

Our main results indicate that the model predicts the main structural patterns of the ridge forest observed in the field i.e. the relative abundance of different PFTs (Fig. 3), variation of model runs (Fig. 4) and stem size distribution in the tree community (Fig. 2). In addition, we used the model to investigate the course of succession (Fig. 5); this comprises the opportunity for further investigation of the different characteristics of succession in relation to the type of disturbance. As stated in the introduction, shallow landslides form one major source of natural disturbance in our research area (Vorpahl et al., submitted). The version of FORMIND presented here did not explicitly include landslides as a disturbance, since the inventory data used were derived from plots in which the disturbance of landslides is expected to be of minor importance.

Two interesting insights gained from the model are (i) that we did not observe a species group that displayed typical "pioneer" behaviour and (ii) that there is a high temporal variability in the overall basal area, which occurs within short time ranges and does not subside with time (cf. Fig. 4). These two patterns are further discussed in detail below.

As evident from figure 5, we observe two main successional responses concerning basal area in time: (1) species exhibiting rapid growth overshoot their stable state of basal area at the beginning of succession and reduce with time (fast-growing PFT 1 and 2), and (2) species reaching their stable basal area at different speeds without overshooting (medium and slow-growing PFT 3–7). The fast-growing groups, however, do not display the behaviour of typical "pioneers", which show high abundances in early stages of succession and are later replaced by other "climax" groups (Shugart 1998). Instead, the fastest growing PFT 2, which dominates the first phase of succession, retains the major share of basal area throughout the succession. Species of Podocarpaceae, (*Podocarpus oleifolius* is the most abundant species in PFT 4) are considered to form the climax stage of many natural stands around the Podocarpus National Park (Lozano 2002). They can reach diameters of up to 100 cm (Günter, Homeier pers. observ.; Marín Velez 1998). However, in our study area the maximum diameter observed is only approximately 50 cm. There are two possible explanations for this: either edaphic conditions prevent the development of *Podocarpus oleifolius* (and hence PFT 4) so that it does not become as dominant as in other primary forests of the region, or that the forest has not yet reached the climax stage. However, the dominance of PFT 2 might also relate to the heterogeneous nature of the ridge forest, where trees stay small in height and disturbances due to natural landslides are frequent. Thus, even in a mature ridge forest, there exist abundant locations with suitable condi-

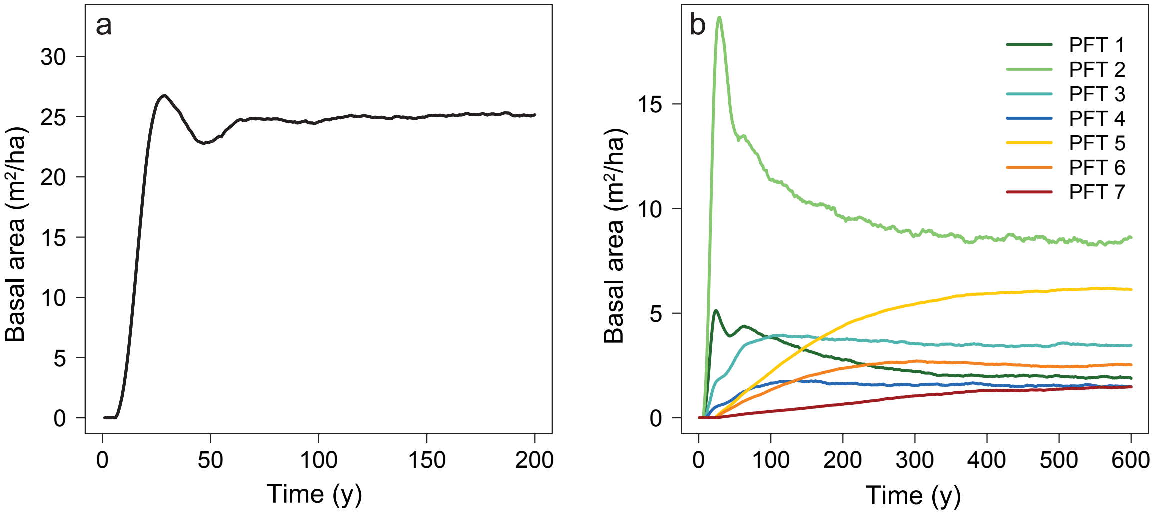

Fig. 5: Succession of basal area. Lines show the average of 10 single model runs with simulated area of 4 ha. (a) Overall basal area for all trees above 5 cm dbh. (b) Basal area above 5 cm dbh for each PFT. Please note the different time scales.

tions for these rather fast-growing species. Apart from this, it might also be the case that in our list of species (Tab. 2) some species with typical pioneer behaviour are missing, since the data we utilize was collected primarily on trees greater then 20 cm in diameter.

As evident from figure 4, the model produces a high variability of basal area in time. Figure 4b shows that in fact most of this variability originates from the fast-growing trees, due to their high abundance and rapid response; the slower growing species groups do not compensate these fluctuations. A comparison of model variation with temporal variability within sites would require long-term field measurements across several decades. At present such measurements are not available for our study site. But the extent of variability between sited fits to the model variation. This means that the variability between sites can in fact represent temporal and not only spatial heterogeneity.

The structural reality of the forest model used corresponds with its relatively high number of parameters. Unfortunately, as is the case for most applications of rather detailed models, not all parameters can be estimated with empirical data from the specific study site. Parameters for mortality, recruitment and growth are particularly difficult to obtain. To gather reliable information on these parameters, one needs to collect data over long periods and over large areas (Whitmore 1998). We used a combination of data from the literature, expert knowledge and calibration processes to determine these parameters (see Tab. 1). The applied parameter values lie within occurring ranges for tropical forests (Phillips and Gentry 1994). One would also expect higher mortality rates for fast-growing species compared to slow growing species since they exhibit more "pioneer characteristics" (e.g. lower wood density). However, we noted that the realized simulated growth is slightly faster than the majority of observed growth. As a consequence, the calibrated mortality and recruitment rates should be considered as preliminary, in particular for the fast-growing species and species with intermediate growth rates (see Tab. 1). In the mature forest, only few individuals come close to reaching their estimated growth potential. This calls for more empirical data from disturbed localities or from experimental data, where competition is removed to assess reliable values for potential diameter growth.

The predicted speed of accumulation of the overall basal area is based on the assumption that the unforested site in the initialisation is equally suitable for regeneration of all PFTs and also recruitment rates are not limited, e.g. due to environmental constraints. As a consequence, the time until the forest reaches its mature state in the model should be considered as a lower limit. Depending on different initial environmental conditions, one can expect succession to proceed differently, most probably more slowly; also seed dispersal limitation might influence recruitment success on larger unforested areas. In the study area, empty sites might occur as a result of landslides, fire, logging or pasture abandonment; each of these events probably result in very different conditions for regeneration concerning e.g. the size of the disturbed area or nutrient and mycorrhiza limitations of the ground. Following a landslide for example, it takes several years before trees start recolonising a site (Bussmann et al. 2008).

Another caveat originates from the fact that all empirical data that was used for this study was taken from "mature" forest sites. Results of a study on a 38-year-old secondary forest (Günter et al. 2007) and observations on a 15-year-old site (Homeier, pers. comm.) confirm that most species in early successional stages belong to the fast-growing group PFT 2 (particularly *Alchornea grandiflora*, *Alzatea verticillata*, *Hieronyma moritziana*). However, on the 38-year-old site, also slow-growing species as *Graffenrieda emarginata* (PFT 6) and *Purdiaea nutans* (PFT 7) where found. Thus slow- and fast-growing species can simultaneously be members of the same successional stage. To investigate transient dynamics of these forests, additional data from disturbed sites would be useful in order to analyse early-stage succession in more detail.

Our study demonstrates that FORMIND is a promising tool for the simulation of tropical montane forests dynamics. This model will help to further our understanding of certain aspects of the complex dynamics of these highly diverse and vulnerable ecosystems.

6 Perspectives

Currently, efforts are being made to link the model to landslide disturbances, which are one main cause of natural disturbance in our research area (Bussmann et al. 2008). In the future, we intend to develop parameterisations for the remaining forest types: the ravine forest, which differs substantially from the ridge forest in terms of structure, growth dynamics and species richness, and the forest types at higher elevations. Covering all main forest types of the Reserva Biológica will allow developing a model that simulates forest dynamics on a regional scale. Such an integration of models for different forest types over large altitudinal gradients is a unique exercise which has not been attempted before. The model has a number of potential applications ranging from investigating the impact of different natural disturbances on forest structure and tree species diversity, to analysing different potential management strategies. The latter aspect is of great importance due to the high pressure on Andean montane forests and the need to develop ecologically sustainable, economically attractive strategies as an alternative to livestock farming.

Acknowledgments

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Table 1: Parameters of FORMIND for the ridge forest of the tropical montane rain forest of the Reserva Biológica San Francisco, South Ecuador.

Parameter	Description	Unit	PFT 1
	Environmental Parameters		
k	Light extinction coefficient	m^{2}ground m^{-2}leaf	
I_0	Average irradiance above canopy	µmol(photons) m^{-2}s^{-1}	
s_d	Length of daily photosynthetic active period	h	
	Recruitment Parameters		
d_s	Diameter of ingrowing trees	m	
I_m	Minimum light intensity for establishment	% of I_0	10
N	Maximum recruitment rates of small trees	ha^{-1}y^{-1}	160
	Mortality Parameters		
m_b	Basic mortality	y^{-1}	0.05
m_u	Maximum mortality of small trees	y^{-1}	
d_s	Diameter up to which mortality is increased	m	
d_f	Minimum diameter of falling trees	m	
p_f	Falling probability of dying trees	%	
	Tree Geometry Parameters		
H_1	Diameter-height relationship		
H_2			0.56
F_1	Form factor		
F_2			
C_0	Crown diameter as function of diameter-curves		
C_1			
C_2			
g_m	Maximum diameter growth	mm y^{-1}	10
d_m	Maximum diameter	cm	40
h_m	Maximum height	m	20
c_1	Crown length factor as function of height-curves		
L_1	Leaf area index per tree		
L_2			
σ	Fraction of stem wood biomass to total biomass		
	Biomass Production Parameters		
p_m	Maximum photoproducitvity for different lgrp	µmol(CO$_2$)m^{-2}s^{-1}	7
α	Slope of light response curve for different lgrp	µmol(CO$_2$) µmol(photons)$^{-1}$	0.2
ϱ	Wood density for different lgrp	t m^{-3}	0.40
r_g	Parameter of growth respiration		
G_3	Parameter of maximum diameter growth curve		-0.02344
G_2			-0.12500
G_1			0.03458
G_0			0.00767
m	Transmission coefficient of leaves		
φ	Parameter of conversion in organic dry matter	t µmol(CO$_2$)$^{-1}$	
	Technical Parameters		
a	Patch size	m^2	
Δh	Step width of vertical discretization	m	

PFT 2	PFT 3	PFT 4	PFT 5	PFT 6	PFT 7	Reference
		0.6				estimated
		700				Bendix et al. 2008
		12				Rüger 2007
		0.01				technical parameter
10	5	5	1	1	1	Rüger 2006
300	150	50	200	280	50	calibrated
0.09	0.05	0.05	0.006	0.016	0.008	calibrated
		0.1				Rüger 2007
		0.1				Rüger 2007
		0.1				estimated
		20				estimated
		2.5				derived from inventory data
0.54	0.56	0.59	0.55	0.56	0.53	
		0.77				calibrated
		-0.18				
		0.2				estimated
		0.1				
		0.5				
20	6	6	2	2	2	S. Günter and J. Homeier pers. Comm.
70	40	50	25	40	50	derived from inventory data
25	20	25	15	20	20	derived from inventory data
		0.25				Rüger 2007
		2.2				estimated
		0.1				
		0.6				estimated (Nenninger 2006)
7	5	5	3	3	3	estimated
0.2	0.25	0.25	0.4	0.4	0.4	Rüger 2006
0.40	0.57	0.57	0.60	0.60	0.60	estimated (Nenninger 2006)
		0.2				Ryan 1991
0.36581	0.27328	-0.03537	0.42989	-0.07212	-0.03673	calibrated
-0.48239	-0.21630	-0.02452	-0.18816	0.01995	0.01261	
0.14906	0.03076	0.01112	0.01260	-0.00147	-0.00114	
0.00656	0.00481	0.00499	0.00189	0.00201	0.00201	
		0.1				Larcher 2001
		0.63 *44e(-12)				Larcher 2001
		400				technical parameter
		0.5				technical parameter

Table 2: Grouping of tree species into plant functional types. Common species are printed in bold type.

Group	Maximum diameter at breast height (cm)	Maximum annual diameter growth (mm/year)	Species
PFT 1	40	10	*Hieronyma asperifolia* Pax & K. Hoffm.
			Hieronyma duquei Cuatrec.
			***Myrcia* sp. nov.**
			***Ocotea aciphylla* (Nees) Mez**
			Vismia cf. *tomentosa* Ruiz & Pav.
PFT 2	70	20	***Alchornea grandiflora* Müll. Arg.**
			***Alzatea verticillata* Ruiz & Pav.**
			Clethra revoluta (Ruiz & Pav.) Spreng.
			***Clusia* cf. *ducuoides* Engl.**
			***Hieronyma moritziana* (Müll. Arg.) Pax & K. Hoffm.**
			Nectandra lineatifolia (Ruiz & Pav.) Mez
			Persea ferruginea Kunth
			Persea sp.4
			Persea sp.5
			Tapirira guianensis Aubl.
PFT 3	40	6	*Abarema killipii* (Britton & Rose ex Britton & Killip) Barneby & J.W. Grimes
			***Aniba muca* (Ruiz & Pav.) Mez**
			Calyptranthes cf. *pulchella* DC.
			Elaeagia pastoense L.E. Mora
			Elaeagia utilis (Goudot) Wedd.
			Endlicheria griseo-sericea Chanderbali
			Eugenia sp.
			Hedyosmum goudotianum Solms
			Ilex hippocrateoides Kunth
			Inga striata Benth.
			Ladenbergia stenocarpa (Lamb.) Klotzsch
			Lauraceae sp.
			***Matayba inelegans* Spruce ex Radlk.**
			Nectandra membranaceae (Sw.) Griseb.
			Ruagea glabra Triana & Planch
PFT 4	50	6	*Ficus cuatrecasana* Dugand
			Meliosma sp.
			Micropholis guyanensis (A. DC.) Pierre
			***Myrsine coriaceae* (Sw.) R. Br. ex Roem. & Schult.**
			***Naucleopsis francisci* Berg & Homeier (ined.)**
			***Podocarpus oleifolius* D. Don ex Lamb.**
PFT 5	25	2	*Alchornea triplinervia* (Spreng.) Müll. Arg.
			Aniba sp.
			Clusia sp. 1
			Eschweilera sessilis A.C. Sm.
			Faramea coerulescens K. Schum. & K. Krause
			Guatteria sp. 1
			***Hedyosmum anisodorum* Todzia**
			***Miconia* cf. *calophylla* Triana**

			Miconia tinifolia Naudin
			Miconia theaezans (Bonpl.) Cogn.
			Ocotea sp.1
			Persea areolatocostae (Allen) van der Werff
			Persea subcordata (Ruiz & Pav.) Nees
			Persea weberbaueri Mez
			Schefflera sp.
			Siphoneugena sp. 1
			Sloanea sp. 1
			Weinmannia cf. sp.1
			Weinmannia elliptica Kunth
			Weinmannia haenkeana Engl.
			Weinmannia sorbifolia Kunth
PFT 6	40	2	*Chrysophyllum lanatum* T.D. Penn.
			Graffenrieda emarginata **(Ruiz & Pav.) Triana**
			Ilex cf. *amboroica* Loes.
			Licaria subsessilis van der Werff
			Meriania franciscana Ulloa & Homeier
			Miconia punctata **(Desr.) D. Don ex DC.**
			Ocotea benthamiana Mez
			Ocotea sp.2
			Ocotea sp.4
			Roupala montana Aubl.
PFT 7	50	2	*Endlicheria oreocola* Chanderbali
			Nectandra subbullata Rohwer
			Purdiaea nutans **Planch.**
			Stilpnophyllum oellgaardii L. Andersson

Appendix

We reformulated parts of the model structure compared to previous applications of FORMIND (e.g. Appendix in Grimm et al. 2006; Köhler 2000). We use power laws for the diameter-height relations as well as for the form factor; as a result of these modifications, the biomass is also a power law of the diameter. Hence we can directly recalculate the maintenance respiration from the maximal growth curve and the biomass (see below). Previously, these calculations where performed using look-up tables, which is more time-consuming than a direct calculation.

Tree geometry

Tree height h is calculated as a power law from the diameter at breast height d

$$h(d) = H_1 \cdot d^{H_2}.$$

Crown length c_l is a constant fraction of tree height

$$c_l(h) = C \cdot h.$$

Crown diameter c_d is calculated as

$$c_d(d) = C_0 \cdot d + C_1 \cdot exp(-C_2 \cdot d).$$

Crown area c_a is calculated as

$$c_a(c_d) = \frac{\pi}{4} \cdot c_d^2.$$

The form factor f is the correction factor for the deviation of stem form from a cylindrical shape. It is calculated as a power law

$$f(d) = F_1 \cdot d^{F_2}.$$

(For this study, we calibrated F_1 and F_2, such that the resulting tree biomass suits observed diameter-biomass relationships (Nenninger 2006; Chave et al. 2005))

Aboveground tree biomass b is a central variable of the model; it is connected to d, the diameter at breast height, via the equation

$$b(d) = \underbrace{\frac{\pi}{4} \cdot d^2 \cdot h(d) \cdot f}_{\text{stem volume}} \cdot \frac{\varrho}{\sigma},$$

where f is the form factor, ϱ is the wood density and σ the fraction of stem wood biomass to total aboveground tree biomass. Using the above stated relations we arrive at

$$b(d) = \left(\frac{\pi}{4} \cdot H_1 \cdot F_1 \cdot \frac{\varrho}{\sigma}\right) \cdot d^{2+H_2+F_2}. \quad (1)$$

Submodels of FORMIND

Within one year the four submodels – establishment, mortality, recalculation of light climate and tree growth – are applied in the following order.

Establishment

If the irradiance on the forest floor in a patch exceeds the minimum light I_m for establishment of a PFT, a new cohort of small trees with dbh=1 cm establishes. The number of recruits per hectare is calculated as the maximum number of recruits per hectare N_m divided by the number of patches per hectare (25). Additionally, it is checked that the layer of seedling crowns is not completely crowded prior to establishment.

Mortality

There are different sources of mortality:

1. Normal mortality: each species group (PFT) has a specific basic mortality rate m_b

2. Mortality of small trees: trees with diameter $d<d_s$ are affected by an additional size dependent mortality m_s

   $$m_s = \begin{cases} m_u \cdot \left(1 - \dfrac{d}{d_s}\right), & \text{if } d < d_s \\ 0 & \text{, else} \end{cases}$$

   where m_u is the maximum size-dependent mortality of small trees. (For cohorts with less than 100 individuals or diameter $d \geq 10$ cm, mortality is stochastically determined for each tree of the cohort. Otherwise, the number of dying trees is calculated deterministically.)

3. Self-thinning: if height layers in a patch are overcrowded with tree crowns, i.e. crown area exceeds patch area, mortality of trees with crowns in these layers is increased due to competition for space. Trees are randomly removed until tree crowns fit into the patch (crown area ≤ patch area).
4. Gap building: Large falling trees kill a proportion of the trees in the patch where their crown hits the ground. When a tree with diameter $d > d_f$ dies, it falls with probability p_f. The falling direction is determined randomly and the probability that a tree in the target patch is killed is proportional to the ratio between the crown projection

area c_a of the falling tree and the patch size a. (Again, for tree cohorts with <100 individuals and diameter $d \geq 10$ cm, the number of killed trees is determined stochastically for each tree, otherwise it is calculated deterministically.) Only trees, which do not overtop the falling tree by more than 1 metre, can be killed.

Light climate

The vertical distribution of leaf area determines the light climate in a patch. Each tree has a leaf area index L_T that is calculated as

$$L_T(d) = L_1 \cdot d^{L_2}.$$

The forest canopy is divided into height layers of size Δh in each patch. A tree contributes leaf area to the height layers that contain a part of the tree crown. The leaf area index L_i of height layer i is calculated as

$$L_i = \frac{1}{a} \cdot \sum_{\text{trees in layer } i} c_a \cdot L_T \cdot \frac{\Delta h}{c_l},$$

where c_a is the crown area, c_l the crown length, L_T the leaf area index of the tree and a the area of a patch. The cumulative leaf area index $\widetilde{L}_i$ of a layer i is the summed up leaf area index of all height layers above layer i

$$\widetilde{L}_i = \sum_{j>i} L_j.$$

For a tree, the amount of light that reaches the top of its crown I_{T_i} in layer i is then calculated via an extinction law

$$I_{T_i} = I_0 \cdot e^{-k \cdot \widetilde{L}_i},$$

where I_0 is the average irradiance above the canopy, and k the light extinction coefficient of the forest.

Tree growth and light competition

We calculate light extinction within the forest canopy and leaf-level rates of photosynthesis following the classical approach of Thornley and Johnson (1990). For calculation of tree growth, incident irradiance and photosynthesis rate are considered on the level of a single leaf (per unit leaf area) and on tree-crown level (per unit crown projection area). Accounting for self shading of leaves, a single leaf at height i within the canopy receives the irradiance of

$$I_L = \frac{k}{1-m} \cdot I_{T_i},$$

where k is the light extinction coefficient and m the transmission coefficient of leaves. The rate of photosynthesis for a single leaf P_L (per unit leaf area) is then calculated as a saturation function

$$P_L(I_L) = \frac{\alpha \cdot I_L \cdot p_m}{\alpha \cdot I_L + p_m},$$

where α is the initial slope of the light response curve and p_m the maximum rate of photosynthesis. For the calculation of the instantaneous rate of photosynthesis of a tree P_T (per unit crown projection area), P_L is integrated over the leaf area index of the tree

$$P_T = \int_0^{L_T} P_L(\widetilde{L})\, d\widetilde{L},$$

where $\widetilde{L}$ is the cumulative leaf area index of the tree. Solving this integral leads to

$$P_T(I_T) = \frac{p_m}{k} \ln \frac{\alpha \cdot k \cdot I_T + p_m \cdot (1-m)}{\alpha \cdot k \cdot I_T \cdot e^{-k \cdot L_T} + p_m \cdot (1-m)}$$

(Thornley and Johnson 1990).

For the calculation of annual gross biomass production of the tree P_B, the photosynthesis rate has to be multiplied by the duration of the photosynthetic active period over the year s, the crown area of the tree c_a and the conversion coefficient (φ) from absorbed CO_2 to organic dry mass:

$$P_B = P_T(I_T) \cdot s \cdot c_a \cdot \varphi.$$

One way to calculate s in seconds is $s = 365 \cdot s_d \cdot 60 \cdot 60$ where s_d is the average daily photosynthetic active period in hours. The model utilizes a maximal diameter growth curve $g(d)$ reflecting the maximal diameter increments under full light condition

$$g(d) = G_3 \cdot d^3 + G_2 \cdot d^2 + G_1 \cdot d + G_0 \cdot \qquad (2)$$

Respiration processes consist of growth and maintenance respiration. Growth respiration is assumed to be a constant fraction of net biomass production; maintenance respiration depends on the biomass of the tree. The increment in biomass b_i is calculated as

$$b_i = (1 - r_g) \cdot \underbrace{(P_B - r_m \cdot b)}_{\text{net biomass production}}, \qquad (3)$$

where r_g is the parameter for growth respiration, b the biomass and r_m the fraction of biomass that is lost due to maintenance respiration. Maintenance respiration is calculated such that under full light the maximal diameter growth is realized. That means, under full light conditions we assume (for clarity, the diameter is now denoted with *D*)

$$
\begin{aligned}
b_i &= \frac{db}{dt} = \frac{db}{dD} \cdot \frac{dD}{dt} \\
&= \frac{d\left(\left(\frac{\pi}{4} \cdot H_1 \cdot F_1 \cdot \frac{\varrho}{\sigma}\right) \cdot D^{2+H_2+F_2}\right)}{dD} \cdot g\,(D) \quad \text{(Eq. (1) and (2))} \\
&= \left(\frac{\pi}{4} \cdot H_1 \cdot F_1 \cdot \frac{\varrho}{\sigma}\right) \cdot \left(2 + H_2 + F_2\right) \cdot D^{1+H_2+F_2} \cdot g\,(D).
\end{aligned}
$$

Inserting this expression in equation (3) and using the diameter-biomass relation (1), we arrive at

$$
\begin{aligned}
r_m\,(D) &= \frac{P_B}{b\,(D)} - \frac{2 + H_2 + F_2}{(1 - r_g) \cdot D} \cdot g(D) \\
&= \frac{P_B}{\left(\frac{\pi}{4} \cdot H_1 \cdot F_1 \cdot \frac{\varrho}{\sigma}\right) \cdot D^{2+H_2+F_2}} - \frac{2 + H_2 + F_2}{(1 - r_g) \cdot D} \cdot (G_3 \cdot D^3 + G_2 \cdot D^2 + G_1 \cdot D + G_0).
\end{aligned}
$$

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