Lessons learned from applying a forest gap model to understand ecosystem and carbon dynamics of complex tropical forests

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ARTICLE INFO

ABSTRACT

Forests worldwide are threatened by various environmental and anthropogenic hazards, especially tropical forests. Knowledge on the impacts of these hazards on forest structure and dynamics has been compiled in empirical studies. However, the results of these studies are often not sufficient for long-term projections and extrapolations to large spatial scales especially for unprecedented environmental conditions, which require both the identification and understanding of key underlying processes. Forest models bridge this gap by incorporating multiple ecological processes in a dynamic framework (i.e. including a realistic model structure) and addressing the complexity of forest ecosystems. Here, we describe the evolution of the individual-based and process-based forest gap model FORMIND and its application to tropical forests. At its core, the model includes physiological processes on tree level (photosynthesis, respiration, tree growth, mortality, regeneration, competition). During the past two decades, FORMIND has been used to address various scientific questions arising from different forest types by continuously extending the model structure. The model applications thus provided understanding in three main aspects: (1) the grouping of single tree species into plant functional types is a successful approach to reduce complexity in vegetation models, (2) structural realism was necessary to analyze impacts of natural and anthropogenic disturbances such as logging, fragmentation, or drought, and (3) complex ecological processes such as carbon fluxes in tropical forests – starting from the individual tree level up to the entire forest ecosystem – can be explored as a function of forest structure, species composition and disturbance regime. Overall, this review shows how the evolution of long-term modelling projects not only provides scientific understanding of forest ecosystems, but also provides benefits for ecological theory and empirical study design.

1. Introduction

Approximately 25% of Earth's land surface is covered by forests that harbor more than 70% of all terrestrial species (Gibson et al., 2011; Myers et al., 2000; Pimm et al., 2014). Forests contain a huge amount of terrestrial biomass and are therefore an important part of the terrestrial carbon cycle (Grace et al., 2014; Bonan, 2008).

One important factor affecting forest ecosystems is land use. In particular, deforestation poses a major threat to forest ecosystems. Between 2000 and 2012, a loss of 12 million hectares of forest per year was observed, the majority (32%) in tropical forests (Hansen et al., 2013). Degradation of forests caused by tree harvesting

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(Ticktin, 2004), fragmentation (Laurance et al., 2011) as well as climate change (IPCC, 2013) pose additional risks to forests worldwide. Forest loss and degradation result in additional carbon emissions being responsible for about 10% of all anthropogenic carbon emissions (Le Quéré et al., 2015; IPCC, 2013). These processes are also the main drivers of species extinctions (Ceballos et al., 2015). Impacts of disturbances and climate change have been investigated in various field studies (e.g., Debinski and Holt, 2000; Lawton et al., 1998; Anderson-Teixeira et al., 2015). However, to project forest development in the future and to better understand the impacts of multiple anthropogenic threats, ecological models are important tools (Shugart, 2003).

Forest models have a long tradition in ecology and forestry. Starting from simple forest-yield tables in 1787 (Moser, 1980), the incorporation of mathematical equations (representing multiple interacting ecological processes) led in the 1970s to novel types of simulation models, including forest gap models (Botkin et al., 1972) and finally to the development of individual tree-based models (Huston et al., 1988). This development was possible due to the increasing availability of computers.

Gap models have been used to understand forest succession and to investigate the mechanisms underlying the long-term dynamics of forest ecosystems (Bugmann, 2001; Shugart, 1998, 2003; Botkin et al., 1972; Pretzsch, 2009). Initially, forest gap models were applied to temperate forests (Botkin et al., 1972; Bugmann, 2001; Shugart, 1984). For more complex forests found in the tropics, gap models need to account for higher species-richness than in temperate regions. Additionally, unmanaged forests normally consist of patches in different successional stages. Their dynamics are mainly governed by the disturbance events of falling trees creating gaps. Moreover, human-induced disturbances (e.g., logging or fragmentation) affect the overall dynamics of forests in many regions of the world. To include these processes, gap models needed to comprise complexity and structural realism with efficient computing.

Here, we summarize the main achievements of applying the forest gap model FORMIND to complex tropical forests with high species richness, heterogenic structure and dense vegetation. This review addresses the following questions:

(1) How can several hundred different tree species be included in simulations for model applications in species-rich forests?
(2) How can the effect of natural and anthropogenic disturbances on forest structure and forest dynamics be simulated?
(3) How can forest gap models help to project and assess the carbon balance of forests?

2. Developing a forest gap model for complex tropical forests

The first forest gap model JABOWA (Botkin et al., 1972) was designed for a temperate forest. It provided a baseline for the now well-established forest gap modeling paradigm. Gap models share the following principles (Bugmann, 2001):

(i) Forests are represented as a collection of small patches. The forest successional stage and age vary across patches.
(ii) Patches are independent of their neighborhoods and do not interact with other patches. Thus, dynamic processes such as tree recruitment, growth and mortality are calculated separately for each patch.
(iii) All patches are homogeneous in size and resource level (i.e., light reaching the upper canopy). The size of one patch is usually chosen according to the extent of the largest possible tree crown (e.g., 20 m × 20 m). Intra- or interspecific interactions

are simulated for all trees in a patch rather than tree-by-tree, as tree positions are not included.
(iv) Leaves are modeled as thin disks on top of each tree. Trees standing within one patch compete for light due to asymmetric shading effects of larger tree canopies on smaller ones.

Many forest gap models were developed following the same principles (Bugmann, 2001; Bossel and Krieger, 1994; Yan and Shugart, 2005; Köhler and Huth, 1998). For example, in the FORET model, the concepts of JABOWA were adapted to simulate the diverse forests of the southern United States (Shugart and West, 1977). The FORSKA (Prentice and Leemans, 1990) and FORCLIM models (Bugmann, 1996b) adopted the gap model approach to simulate forest dynamics of temperate forests in Europe. Building on the FORET model, the FORICO model was one of the first tropical forest gap models, which was applied in a lower montane rainforest in Puerto Rico (Doyle, 1981). Later, following the gap model approach, FORMIX was applied to tropical forests in South-East Asia (Bossel and Krieger, 1991, 1994; Ditzer et al., 2000). FORMIX accounts for biomass and tree numbers in five distinct canopy layers (each layer has some representative trees similar to size class models).

FORMIND is the process- and individual-based successor of the FORMIX model, in which the concept of distinct layers was discarded. FORMIND was developed in the late 1990's to simulate tropical forest dynamics more realistically than before (Köhler and Huth, 1998, 2004; Köhler et al., 2000; full publication list see Appendix A). Within FORMIND, physiological processes such as photosynthesis and respiration are simulated at the tree level (process-based model). Forests of several hundred hectares can be simulated over a time period of a few centuries. The simulation area is a composite of 20-m × 20-m patches typical for forest gap models. In FORMIND, these patches may interact via seed dispersal and the falling of large trees. The basic model consists of four main processes: tree growth, tree mortality, recruitment of tree seedlings, and competition between trees (Fig. 1, full model description see Appendixes B–F). Due to its main application in tropical forests lacking any pronounced seasonal cycle, the model architecture is based on a time step of one year. In the following, we discuss the main processes included in FORMIND.

Tree growth. Tree biomass growth is determined by a physiology-based tree carbon balance that includes leaf photosynthesis, maintenance and growth respiratory costs. An increase in tree biomass results in increments in height, stem diameter, stem volume and leaf area through the use of allometric relationships (see Appendix G for details).

Tree mortality. In FORMIND, background mortality is generally calculated stochastically from a mean annual mortality rate. Alternatively, the model also allows calculating mortality as a function of tree size or stem diameter growth. In addition, trees compete for space. Crowded stands are thinned, i.e., mortality rate is increased if crowns of trees overlap. If large trees die, they have a certain probability of falling over into neighboring patches, in which their crowns smash smaller trees and create canopy gaps. Thus, trees might die for various reasons (age, growth rate, space competition, tree fall damage; see also Appendix E for details). All individual tree mortalities are determined stochastically.

Recruitment. In FORMIND, trees emerge from seeds, which can originate either from a surrounding forest (constant seed rain) or from mother trees within the same forest stand. As seeds need a certain amount of light to germinate, their development might be hindered by shading effects on the forest ground. In that case, seeds are accumulated in the soil of a patch (seedbank) for a certain time until the light conditions are appropriate for germination. While waiting for better light conditions, a fraction of the seeds die (seed mortality). As soon as the light conditions change (e.g., through

Fig. 1. The basic concept of FORMIND (white) and its extensions required for certain applications (blue). Boxes show physiological and demographic processes with numbers in brackets representing their scheduled flow. Parallelograms indicate important information needed as input for the model. Light gray boxes refer to sections in this manuscript that provide more details of the extensions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

gap creation), seeds can receive sufficient light to germinate (see Appendix D for more details).

Tree competition. In FORMIND, the competition between individual trees is threefold. First, tree growth is mainly driven by light. Large trees in a patch receive most of the incoming radiation and gradually shade smaller trees, causing asymmetric light competition. Second, trees compete symmetrically for space. Trees in crowded patches are thinned by increasing mortality (Köhler et al., 2001). Third, between neighboring patches, the gap created by the falling of large trees increases the local mortality rates. Furthermore, seed dispersal from mother trees leads to interactions among patches (see Appendix F for more details).

Each modeled process is flexible enough to be parameterized for a specific study site. It takes a site specific forest inventory (including stem diameter measurements) and stem diameter increment measurements to obtain values for model parametrization. For site-specific adaptation of the model additional information is helpful. Uncertain parameter values can be determined by a calibration process using as reference inventory data of mature forests (e.g. in some studies this has been done for the recruitment rates). However, many parameters used in the model are known from literature (at least their typical ranges). For example, in tropical forests, approximately 1–2% of the standing trees die annually (Phillips and Gentry, 1994). In the case of site specific measurements, these parameters can be adapted.

Beside the modeled processes, three important aspects are incorporated into FORMIND which are intended to be applicable to tropical forest sites. This distinguishes FORMIND from classical forest gap models:

(1) The high tree species-richness in tropical forests is accounted for by the concept of plant functional types (PFTs), i.e., grouping of tree species (see Section 2.1).
(2) Disturbances, both on small and large scale, caused by either natural reasons (e.g. tree falling, edge effects) or anthropogenic

activity (e.g. tree logging) are investigated on their effects on forest structure and dynamics (see Section 2.2).
(3) The simulation of the carbon balance of individual trees is based on a detailed process-based approach that enables upscaling to forest-wide carbon balances (see Section 2.3).

2.1. Consideration of tree species-rich forests: Plant functional types

Tropical forests have high tree species richness with up to 300 tree species per hectare (Whitmore, 1998; Slik et al., 2015). Modeling complex interactions between multiple tree species is important to reproduce typical emerging forest structures such as tree size distribution, species composition and aboveground forest biomass (Köhler and Huth, 1998). However, including this complexity (1) increases the effort for model parameterization, and (2) increases model uncertainty for the lack of empirical data for most tree species. To reduce model complexity, it is necessary to aggregate the hundreds of tree species into a few classes or types in a meaningful way. Field studies revealed that species often show similar attributes (e.g., growth rate, seed production rates, mortality rates), making it possible to classify similar tree species of highly diverse tropical forests into species groups known as plant functional types (PFT; Smith and Shugart, 1997). Following this knowledge, in one of the first FORMIND studies, all recorded tree species were aggregated into five or 22 PFTs to analyze the impact of species aggregation on tree competition and forest dynamics (Köhler and Huth, 1998). Although five PFTs were considered sufficient to reproduce more aggregated variables such as stem size distribution or basal area (Köhler et al., 2001), a higher number of PFTs is needed to represent interspecific competition and extinction processes. The initial concept of grouping tropical tree species into PFTs was later-on generalized in Köhler et al. (2000) based on the two physiological attributes maximum tree height at maturity and light requirement (or shade tolerance), that are assumed to be independent from each other. In the application of this grouping

concept for tropical lowland rainforest in South–East Asia, three different shade tolerance levels (shade-intolerant, intermediate and shade-tolerant species) and five different height groups of adult trees (shrubs, understory, lower and upper canopy, and emergent species) have been distinguished leading finally to 13 PFTs that can be found in tree species inventories (Köhler et al., 2000).

Note that finding a suitable number of PFTs for a specific research question of a simulation study is not completely resolved (Kazmierczak et al., 2014) and there are challenges to transfer the PFT classification to other regions (Bugmann, 1996a; Picard and Franc, 2003). Additionally, species classifications might not be unique for a certain study region as shown by Picard et al. (2012). In this study five different classification schemes were compared for the same tropical forest in French Guiana: the schemes agreed on the tree height classification but differed with respect to the light requirements of the trees.

Köhler and Huth (2007) showed that this PFT grouping might also be used to investigate questions on tropical tree species richness. They simulated the forest dynamics and species competition of a tropical rainforest in South–East Asia with more than 400 tree species using the PFT-based parameterization as published before (Köhler and Huth, 2004). However, tree regeneration including seed production was determined not for PFT, but tree species specific. The study explored how recruitment limitation (Hubbell et al., 1999) and disturbance intensity (i.e. intermediate disturbance hypothesis; Connell, 1978) influence tropical tree species richness. Köhler and Huth (2007) demonstrated that both processes are important for species richness in tropical forest. In addition, both processes interact, and should therefore not be analyzed separately. At a local level, an increase in recruitment limitation promotes species richness, whereas the overall richness at the forest level declines.

In general, to tackle the high tree species richness in tropical forests, species grouping offers a powerful technique to reduce complexity. In applications with FORMIND, we have shown that this approach allows a realistic description of species dynamics in forests (e.g., Köhler and Huth, 1998). The creation of these functional groups is flexible enough to include relevant differences and to avoid functional redundancy between species (Kazmierczak et al., 2014). Future research could tackle the question of how many PFTs are appropriate to describe a specific forest (e.g., Picard et al., 2012). The results of future research in the field of functional biodiversity can be used to improve the species grouping concept of forest models.

2.2. The impact of disturbances and logging on forest dynamics

Disturbance regimes and forest management play an important role for forests dynamics. Disturbances can occur on varied spatial scales. Large-scale disturbances occur across several hectares (e.g., wildfire) and small-scale (local) disturbances occur within a few meters (e.g., falling trees). Most gap models incorporate natural disturbances, e.g., the falling of large trees, which creates new forest gaps. This tree fall process was included in FORMIND, including physical damages caused to surrounding trees. Surrounding trees (in the same or neighboring patches) are damaged depending on the crown size of the falling tree and their own height (for details see Appendix E.3).

In addition to natural disturbances, logging poses a major threat to tropical forests. One challenge is to evaluate whether a certain forest management practice is sustainable. Logging has been included in FORMIND, allowing users to simulate different logging strategies and to explore their long-term impacts on forest dynamics (Kammesheidt et al., 2001; Köhler and Huth, 2004). The individual-based approach easily allows selecting single trees and removing them from the forest. Such a selection of single trees
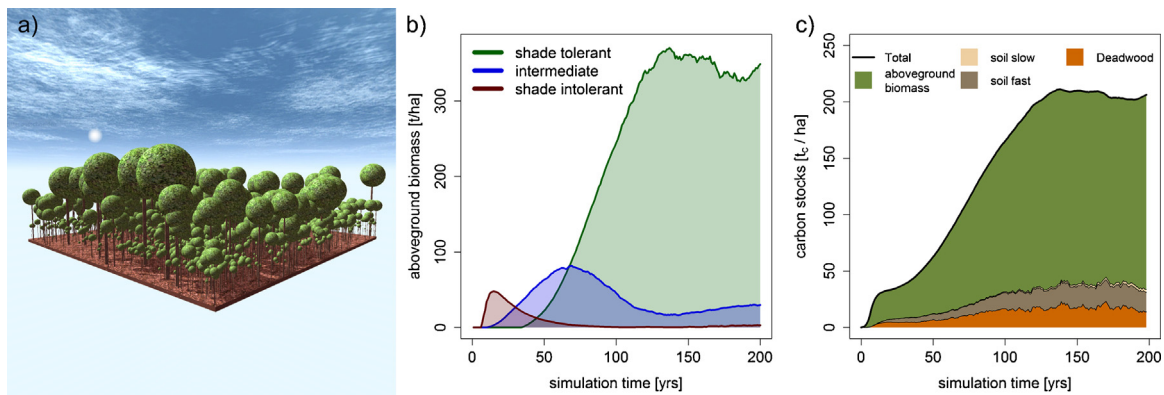
for logging typically depends on species group and stem diameter (cutting limits). FORMIND provides two logging strategies: conventional logging and reduced impact logging (RIL). RIL takes into account substantial planning of the logging event. This refers mainly to the direction in which the logged tree falls, i.e., toward the largest gap, which reduces the damage and thus death of other trees. Consequently, the falling tree causes the least amount of damage to surrounding trees. The damage caused to surrounding trees is similar to the natural tree falling (see above), but includes an additional damage due to road building efforts etc. (for details see Appendix I).

Using FORMIND, simulation studies conducted in Venezuela (Kammesheidt et al., 2001) and Malaysia (Köhler and Huth, 2004; Huth et al., 2004, 2005) showed the impact of different management strategies on the yield and forest state. It was shown that long logging cycles (>60 years) in combination with reduced-impact logging strategies could significantly reduce the negative long-term impact of logging on forest carbon stocks. This strategy might be applied as a compromise between economic and ecological interests (Huth et al., 2005). The results from another study conducted in rainforests in South America demonstrated that legal logging strategies (i.e., strip cuttings) severely altered the structure and composition of old-growth stands (Rüger et al., 2007). Alternative logging strategies that compromise between ecological and economic interests have been proposed, for example, reliance on native species and retention of an uneven-aged forest structure. This proposed strategy promotes the maintenance of native biodiversity and tree reproduction, and protects the forest ecosystem from exotic species invasion (Rüger et al., 2007). Similar studies have been conducted to investigate logging for forest sites in Mexico (Rüger et al., 2008), Malaysia (Ditzer et al., 2000; Glauner et al., 2003; Tietjen and Huth, 2006; Huth and Ditzer, 2001), Venezuela (Kammesheidt et al., 2001) and Paraguay (Kammesheidt et al., 2002). Based on these simulation experiments, an attempt was made to estimate thresholds for logging intensities to maintain a stable forest structure and species composition.

While logging can affect forest structure, forest conversion into agricultural land leads to forest fragmentation (Skole and Tucker, 1993; Laurance et al., 1998). Empirical studies showed that forest fragments suffer from edge effects up to 300 m into the forest (Laurance et al., 2002). These edge effects induce changes in the microclimate, resulting in higher tree mortality (Laurance et al., 2002). Therefore, such edge effects, i.e., higher mortality rates in the edge area of a fragment, have been introduced into FORMIND by increasing the background mortality and introducing extra mortality for large trees within the first 100 m of the forest edge to represent changes in micro-climatic conditions and the impact of wind turbulence (see Appendix E.4 for more details). Simulations of forest fragmentation using FORMIND for forest stands in French Guiana and the Mata Atlantica showed that standing forest biomass was significantly reduced by up to 60% compared with non-fragmented forests (Pütz et al., 2011; Köhler et al., 2003).

Simulating small isolated forest fragments instead of continuous forests requires a concept of local tree regeneration. In this context, we differentiate between two seed dispersal modes: (1) local dispersal, i.e. all seedlings are originated from fertile trees within the simulated area and (2) external seed rain. Furthermore, Groeneveld et al. (2009) found that negative density regulation for seedlings was necessary to match empirical data from the Brazilian Atlantic rainforest. We have found that moderate density regulation is essential to achieve coexistence for a broad range of regeneration parameters. This ecological process is essential to increase structural realism when analyzing the impacts of forest fragmentation. Without density regulation coexistence would be only possible in the model for a small range of the regeneration parameters, which

Fig. 2. Forest succession and carbon stocks simulated using FORMIND. (a) Exemplary visualization of a simulated forest stand showing all trees with a stem diameter >10 cm for a forest area of 1 ha. (b) Simulated forest succession of a tropical forest with a size of 1 ha on Mt. Kilimanjaro, Tanzania. We distinguished between shade-tolerant tree species (climax species), shade-intolerant tree species (pioneer species) and intermediate shade-tolerant species (Fischer et al., 2015). (c) Simulated amount of carbon in the living biomass, in the deadwood, and in the soil (fast and slow decomposing soil stock) for a tropical forest on Mt. Kilimanjaro, Tanzania (Fischer et al., 2015).

seems to be unrealistic and does not reflect the large variability in field measurements.

A study of the long-term degradation trajectory of initially undisturbed forest fragments within the Atlantic Forest showed that increased tree mortality is the most important fragmentation process acting on forest edges (e.g., due to changes in seed dispersal and micro climate; Pütz et al., 2011). Simulations with FORMIND showed that the degradation process occurring in fragmented forests might last for approximately a century, and might result in aboveground carbon losses of more than $5\,\mathrm{Mg\,C\,ha^{-1}\,y^{-1}}$, and changes in evapotranspiration (43% loss) and surface runoff (57% gain) at forest edges (Dantas de Paula et al., 2015).

In a nutshell, as the impact of disturbance events in forests is mainly quantified at the tree level, an individual-based structure is a huge advantage for simulating disturbances. This structural realism was the key driver for the successful application of the gap model FORMIND for questions on forest management and fragmentation. Other types of disturbances, such as landslides, forest wildfires, and windstorms, have also been found important to increase structural realism of FORMIND (e.g., Rüger et al., 2007; Gutiérrez and Huth, 2012; Dislich and Huth, 2012). An unanswered question remains on how to upscale the forest gap models to larger areas. For fragmentation one approach to link forest gap models to remote sensing data for the whole Amazon rainforest has been developed (see below). There is a strong need to develop methods for a further integration of remote sensing and the simulation of forest dynamics (Shugart et al., 2015).

2.3. Simulating the carbon balance of tropical forests

The carbon balance of a tropical forest depends on its successional stage and the environmental conditions. Hence, the carbon budget is variable at the local scale and forests might be a source or a sink of atmospheric CO_2 (Gatti et al., 2014; Morton et al., 2014). To simulate the carbon balance of an entire forest, a physiological approach based on the growth of every single tree is essential. Including this approach into FORMIND, it offers the possibility for simulating the forest carbon balance at different successional stages and under variable climate conditions as the model calculates the carbon balance for each individual tree.

2.3.1. Carbon balance in a forest gap model

In contrast to many other forest gap models, FORMIND calculates the biomass increment via a tree carbon balance based explicitly on photosynthetic production and respiratory losses (Thornley and Johnson, 1990). Biomass production leads to tree
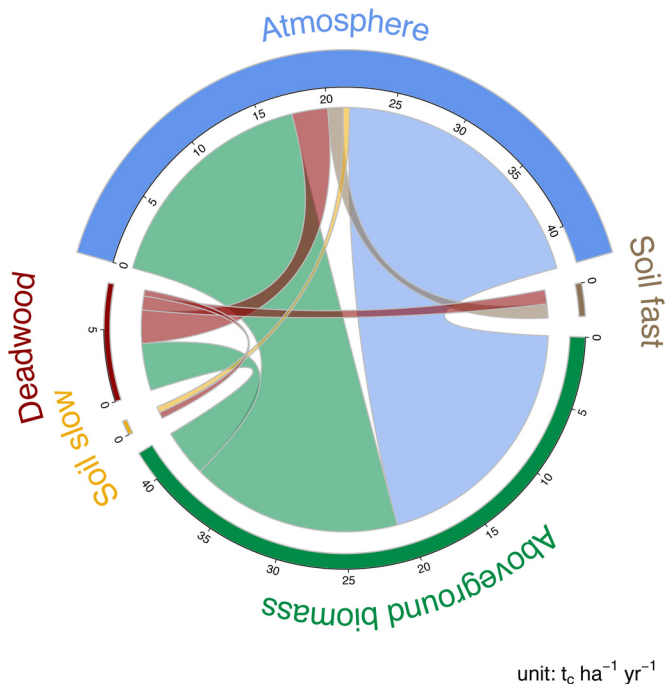
growth, which is predominantly driven by light in FORMIND (details in Appendix G). Photosynthesis is calculated based on light availability within the forest canopy (Thornley and Johnson, 1990), whereby large trees shade smaller ones that grow in the same forest patch. This assumption differs from biogeochemical models in which the assimilation of atmospheric CO_2 is based on carbon pools at the ecosystem level (e.g., dynamic global vegetation model LPJ, Sitch et al., 2003). In FORMIND, respiratory costs are assumed to be tree-size dependent. Recently, the model was extended to incorporate the decomposition processes of deadwood and soil carbon (see Fig. 2; Details see Appendix H; Gutiérrez, 2010; Fischer et al., 2014, 2015). The sum of these above- and belowground fluxes contributes to a more complete assessment of the carbon balance in forest ecosystems (Figs. 2 and 3) and helps to identify the role of successional stages in the local and regional carbon cycle and how it might contribute to the global carbon budget. This approach allows simulation experiments and complements complex field measurements (e.g., based on eddy-covariance techniques).

2.3.2. The impact of climate change on tropical forests

The influence of climate changes on forest carbon stocks and fluxes remains highly uncertain (Wang et al., 2014). The physiological approach, as used in FORMIND, enables investigation of the influence of variable climate conditions on the carbon balance of forest ecosystems. Several modules were implemented in FORMIND by adopting the growth of single trees with respect to climatic changes: temperature limitations of photosynthesis and respiration (approaches from: Haxeltine and Prentice, 1996; Prentice et al., 1993) and the influence of the soil water content on photosynthesis (Details see Appendix F.2; Fischer et al., 2014; Gutiérrez et al., 2014). The effect of changes in precipitation on tropical forests was analyzed in a case study conducted in Madagascar (Fischer et al., 2014). A decline in rainfall by more than 30% reduced biomass by 20% and drought-intolerant species almost went extinct. These effects can be amplified by additional stress factors, such as rising temperatures or tree harvesting. For rainforests in South America, FORMIND simulations suggested that primary old-growth forests will be reduced in aboveground biomass by 11% whereas the net primary productivity might decrease by 30% in the year 2100 due to increased drought conditions (Gutiérrez et al., 2014).

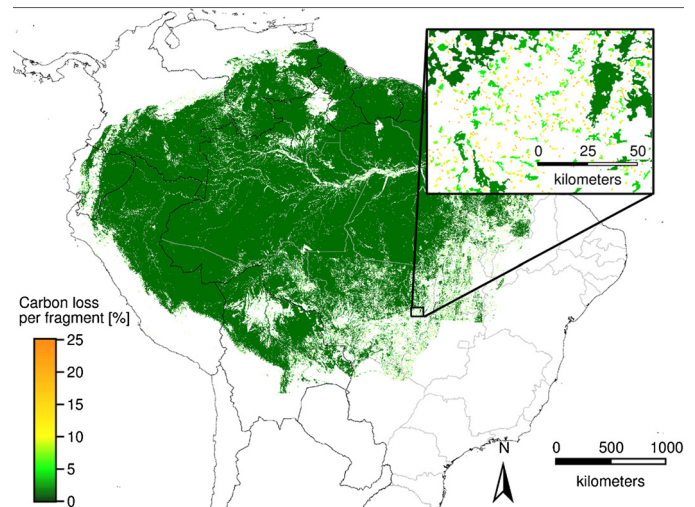#### 2.3.3. The carbon balance of tropical forests at a biome scale

Given the increasing availability of remote sensing data (e.g. Ribeiro et al., 2009), FORMIND was recently applied at a regional scale (i.e., the Amazon forest) by combining local ecological

unit: t_c ha^{-1} yr^{-1}

Fig. 3. Example of simulated forest carbon fluxes. The mean carbon fluxes of a simulated old-growth tropical forest on Mt. Kilimanjaro, Tanzania, are presented (Fischer et al., 2015). The colors indicate the different stocks and fluxes. The color of the fluxes indicates the source of the flux. From the atmosphere (blue), the greatest flux goes to aboveground biomass (forest gross primary productivity). Aboveground biomass (green) emits carbon back to the atmosphere due to tree respiration, and biomass mortality to the deadwood pool. From the deadwood pool (red), carbon is emitted to the atmosphere or to a slow (yellow) or fast (brown) decomposing soil carbon stock. Carbon is emitted to the atmosphere from both soil stocks. The amount of carbon in the different fluxes is indicated by the thickness of the colored links; the amount of carbon stored in the different stocks is indicated by the thickness of the circle frame pointing inwards. The circle frame of the atmosphere points outwards because carbon moves from the atmosphere to the forest. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

knowledge with remote sensing data on forest patch structures (Pütz et al., 2014). This analysis of the long-term dynamics of forest fragments in South America (i.e., long-term carbon loss per fragment for different fragment sizes) revealed that small fragments lose approximately 50–60% of the aboveground carbon stored in living trees. This study provides a first estimate of land carbon losses of about 0.25 Pg C per year due to forest fragmentation in the tropics (see Fig. 4; Pütz et al., 2014). Losses caused by fragmentation contribute approximately 25% to the total carbon loss due to land use change and are therefore important for a comprehensive understanding of the role of vegetation dynamics within the global carbon cycle (Pütz et al., 2014).

The example of FORMIND shows how additional process-based elements can be implemented into forest gap models. To conclude, the structural realistic description of tree-related processes has various advantages: (1) processes and parameters have a physical or physiological interpretation, (2) model parameters can be measured in field experiments, and (3) model structure is flexible enough to adapt processes to new circumstances (e.g., climate change) or to include new processes (e.g., logging). The process-based and individual-based approach of FORMIND allows the calculation of gross primary production and respiration of forests, which is not possible with classical gap models. This offers the possibility of quantifying the carbon fluxes of forests at different scales and linking these fluxes to dynamics in the forest. This is a result of the individual-based structure of forest gap models, which is the basis for linking forest carbon balance to tree competition. In

Fig. 4. Spatial distribution of tropical forest fragments in the Amazon Forest and their estimated carbon loss due to fragmentation. Color ranges indicate the relative carbon loss due to fragmentation, which was estimated using the FORMIND model (Pütz et al., 2014).

addition, the individual-based approach allows integrating various types of disturbance regimes.

3. Current and future applications of forest gap models

Having summarized how a forest gap model has been developed for the tropics over the last decades, we now provide a brief outlook on new applications.

Forest gap models can be used to study the relationship between forest productivity and tree species diversity (Morin et al., 2011). Recent studies have shown that forest productivity typically increases with increasing tree species diversity (e.g., Morin et al., 2011; Zhang et al., 2012; Vilà et al., 2007). However, several studies show unchanged or even inverse relationships between productivity and diversity (e.g., Jacob et al., 2010; Cavard et al., 2010). Following the study of Morin et al. (2011), we extended this method to study a broader range of diversity-productivity relationships. Instead of long-term simulations, thousands of different virtual forest stands have been generated, combining different species mixtures with various forest structures (e.g., different basal area values or heterogenic tree heights). For each of these virtual forest stands, forest productivity can be calculated using forest gap models. The obtained diversity - productivity relationships can then be compared to field studies. This new way of using a forest gap model as an analysis tool of virtual forest stands enables a much faster analysis of numerous forests compared with the classical method of simulating forest successions.

Parameter estimation in forest gap models is a challenging process. Manual calibration and sensitivity analysis of these models require a large number of simulations, leading to a time-consuming computational demand. Thus, for the automatic calibration of uncertain parameters, when direct measurements are missing or made under specific conditions (e.g., climate, soil), a collection of rapid stochastic search methods have been developed (Tolson and Shoemaker, 2007) and applied in FORMIND (Lehmann and Huth, 2015). These methods automatically minimize the difference between simulation results and field observations by running the model a thousand times. Additionally, for the assessment of parameter uncertainty, approximate Bayesian methods can be used in combination with a Markov chain Monte Carlo approach (Hartig et al., 2011). These methods can also be used for forest sites where a limited number of observations in time and space are available.

After careful examination of the model and available observation data, a combination of manual and automatic calibrations leads to the successful parameterization of forest gap models.

A very recent and promising application of forest models is in combination with remote sensing data. Techniques such as Radar (Radio detection and ranging) and Lidar (Light detection and ranging) are capable of measuring the 3D-structures of forests. However, the intrinsic attributes of the forests, such as biomass, can only be estimated indirectly with remote sensing based on empirical relationships (e.g., Drake et al., 2002; Asner, 2009; Lefsky et al., 2002). The calibration of such relationships has long been limited by the availability of field data and the spatial resolution of remote sensing data, especially in the tropics. Synthetic forest inventory data generated by forest models provide a novel approach to explore forest structures and develop new concepts for remote sensing (Palace et al., 2015). To this end, the full functionality of an individual-based forest model might be used, including the simulation of disturbances, topographic variability and carbon fluxes (Shugart et al., 2015). The classical method is to use remote sensing data to set the initial state of forest models. Here, forest gap models are used the other way around to calibrate remote sensing products by creating virtual remote sensing flights over simulated forests. So far, FORMIND has served to investigate the relationship between canopy height and aboveground biomass as a function of spatial scale (Köhler and Huth, 2010). In the near future, FORMIND will also be used to improve the understanding of the relationship between forest structure and other ecosystem functions, e.g., forest productivity. Until now, remote sensing efforts toward the detection of changes in biomass content in the tropics have been restricted to a few sites (Dubayah et al., 2010; Englhart et al., 2013; Meyer et al., 2013). By using forest models, general principles might be found, on which one might base new remote sensing applications.

4. Discussion

Finding an acceptable balance between model simplicity and required complexity is a classic challenge in ecological modelling (Grimm et al., 2005; Evans et al., 2013). In this review, we showed how the FORMIND model could achieve this balance by combining the gap approach with fundamental ecological processes. The individual-based structure of forest gap models allows the modeling of structural realistic concepts that are based on field measurements at different organizational levels (e.g., leaves, trees, forests). Forest ecosystem functions (e.g., productivity) and forest structure (e.g., tree size distribution) emerge from individual trees and their interactions. Using the forest gap model FORMIND as an example, it was demonstrated that whenever a new ecological pattern was investigated, the basic concept of the model did not change; rather, a new module was added. The use of the same model, but with the addition of modules instead of the construction of new models for different applications, allowed a rigid comparison of results and fostered theory development. In particular, we highlighted the advances that have been made in the fields of (1) species aggregation using PFTs, (2) modeling the impact of natural and anthropogenic disturbances on ecosystem functions and forest dynamics, and (3) upscaling carbon dynamics from photosynthesis at the leaf level to the forest ecosystem level.

Such extensions have led to a modular architecture of forest gap models, which allowed FORMIND to be successfully applied to different forest sites worldwide during the last two decades (Fig. 5). This modular architecture began with the development of logging routines to simulate the impact of tree harvesting on forest structure. Later applications provided insights into the role of forest fragmentation within the global carbon cycle. In particular, the individual-based structure of gap models facilitates modelling the impact of disturbances, such as logging, on forest dynamics. Studies on the effects of human activities and recently, changing climatic conditions, have motivated extensions of FORMIND toward a complete forest carbon balance model.

In summary, during the last two decades, FORMIND has shown that forest gap models can be applied to tropical forest sites and that such models are capable tools to provide answers to questions related to species richness, natural and anthropogenic disturbances, and carbon balance (Fig. 6; a full list of all FORMIND related publications can be found in Appendix A). We envision a strong potential of forest gap models in the future, i.e., with respect to the coupling of these models to remote sensing data due to the increasing availability of various products and new missions.

Forest gap models such as FORMIND, ForClim (Bugmann and Solomon, 2000), FAREAST (Yan and Shugart, 2005), and ZELIG (Urban et al., 1991) are usually applied at the local scale (e.g., hundreds of hectares), although most of them can simulate forest dynamics for a wide range of different environmental conditions. In contrast, dynamic global vegetation models (DGVMs) have been designed to simulate forest dynamics at a regional to global scale (e.g. LPJ-DGVM or SEIB–DGVM: Sitch et al., 2003; Sato et al., 2007), but are limited by necessary simplification of ecological processes. Note that forest gap models and DGVMs have been developed to address different research questions. While forest gap models focus
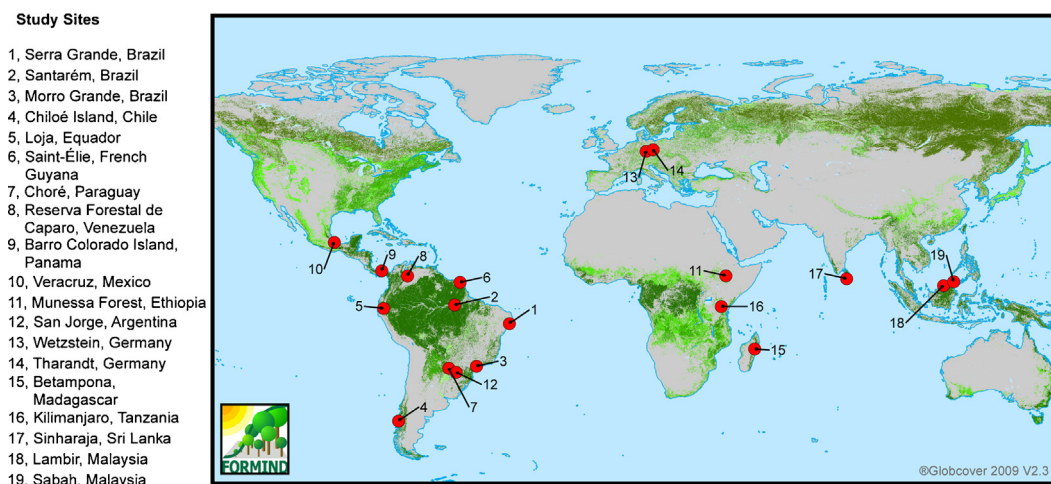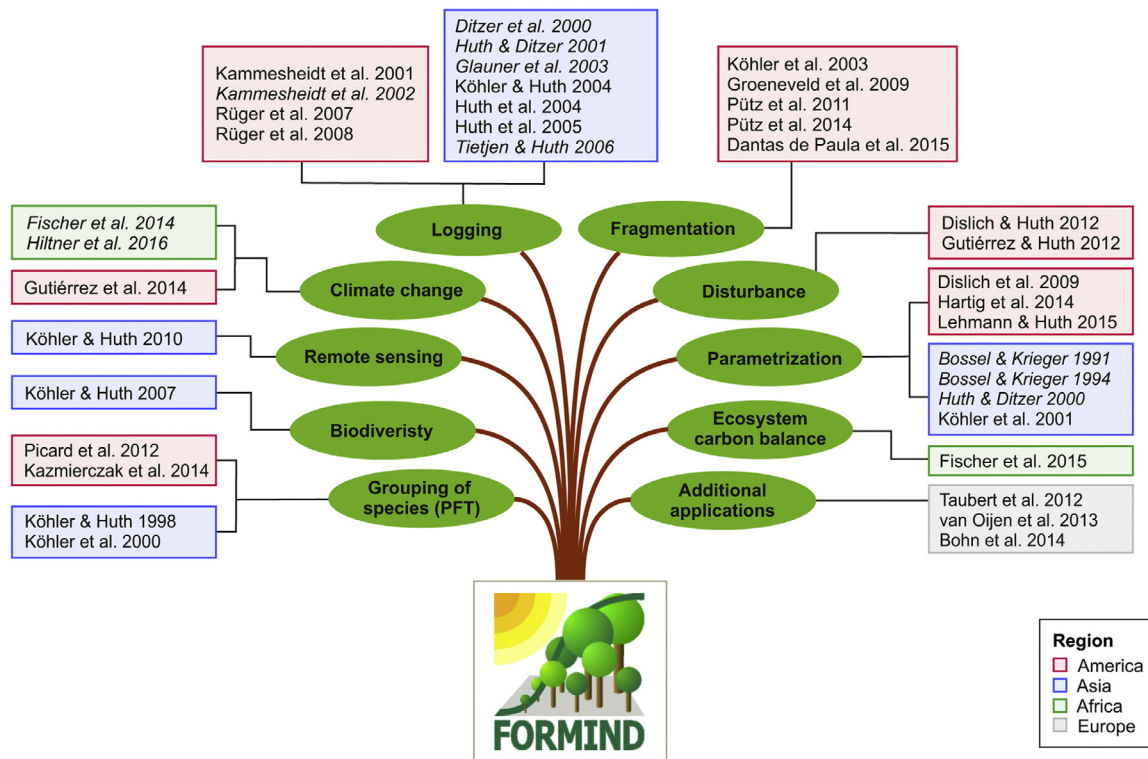

Study Sites

1, Serra Grande, Brazil
2, Santarém, Brazil
3, Morro Grande, Brazil
4, Chiloé Island, Chile
5, Loja, Equador
6, Saint-Élie, French Guyana
7, Choré, Paraguay
8, Reserva Forestal de Caparo, Venezuela
9, Barro Colorado Island, Panama
10, Veracruz, Mexico
11, Munessa Forest, Ethiopia
12, San Jorge, Argentina
13, Wetzstein, Germany
14, Tharandt, Germany
15, Betampona, Madagascar
16, Kilimanjaro, Tanzania
17, Sinharaja, Sri Lanka
18, Lambir, Malaysia
19, Sabah, Malaysia

Fig. 5. Study sites to which the FORMIND model family has been applied (including also applications beyond the tropics).

Fig. 6. Overview of studies using models of the FORMIND model family. Publications are ordered by research field and study region. A full list with all publications can be found in the Appendix A including the specific research topic, study region and forest type. 'Additional applications' include FORMIND model versions developed for temperate forests and grasslands. Publications of the related FORMIX model are shown in italics.

on reproducing forest structure and dynamics at the local scale, DGVMs have been used to project global change in vegetation cover and aboveground carbon stocks at coarse resolution (Sitch et al., 2003). At the global scale, DGVMs have to reduce species diversity to a few broadly classified plant functional types (PFTs). For example, in most DGVMs, only one dominating PFT is used to describe tropical forests at the cost of a realistic reproduction of forest succession. Attempts to include the individual-based approach into DGVMs have already been made, for example, in the SEIB-DGVM model (Sato et al., 2007) and the LPJ-GUESS model (Hickler et al., 2012; Wårlind et al., 2014). However, large-scale applications could still benefit from embedding more concepts of forest gap models into the DGVM framework. Landscape forest models such as LandClim (Schumacher et al., 2004; Schumacher, 2004) try to transfer the gap model concept to landscapes (e.g., for 10,000 ha) including explicit position of gaps and seed dispersal (similar to FORMIND). This type of approach has potential to be applied also on larger scales at the cost of increasing simulation times. To describe the impact of disturbances (e.g., fire, logging) or land-use change on forests across spatial scales the individual-based approach of gap models is a strong advantage. For future model developments and large-scale applications, we suggest developing methods for upscaling local gap models or embedding forest gap models in DGVMs (see also Snell et al., 2014).

The individual-based approach of forest gap models offer a high degree of flexibility to be adapted to different environments (e.g., temperate, sub-tropical, cloud forests) or even other ecosystem types (e.g., temperate grassland; Taubert et al., 2012; Coffin and Lauenroth, 1990). This high flexibility has motivated the increasing number of simulation studies using forest gap models like the FORMIND model (Fig. 5). During the development of forest gap models, extensive knowledge has been gathered on modelling processes in forests, their parameterization and resulting model behavior. For the evolution of such complex simulation models, this learning process has been highly relevant. As a side effect, future model applications have already been initiated (e.g., link to remote sensing), which in turn might feed back into the design of new field experiments and monitoring studies, or hypothesis building in forest ecology. Therefore, both field experiments as well as theoretical forest ecology might benefit from the application of forest gap models. This closer connection promotes a better understanding of the role of complex forest ecosystems on Earth, which in future will become more relevant to a society under global change.

Acknowledgements

Appendix A-J. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2015.11.018.

References

Anderson-Teixeira, K.J., Davies, S.J., Bennett, A.C., Gonzalez-Akre, E.B., Muller-Landau, H.C., Wright, J.S., Abu Salim, K., Almeyda Zambrano, A.M., Alonso, A.,

Baltzer, J.L., Basset, Y., Bourg, N.A., Broadbent, E.N., Brockelman, W.Y., Bunyavejchewin, S., Burslem, D.F.R.P., Butt, N., Cao, M., Cardenas, D., Chuyong, G.B., Clay, K., Cordell, S., Dattaraja, H.S., Deng, X., Detto, M., Du, X., Duque, A., Erikson, D.L., Ewango, C.E.N., Fischer, G.A., Fletcher, C., Foster, R.B., Giardina, C.P., Gilbert, G.S., Gunatilleke, N., Gunatilleke, S., Hao, Z., Hargrove, W.W., Hart, T.B., Hau, B.C.H., He, F., Hoffman, F.M., Howe, R.W., Hubbell, S.P., Inman-Narahari, F.M., Jansen, P.A., Jiang, M., Johnson, D.J., Kanzaki, M., Kassim, A.R., Kenfack, D., Kibet, S., Kinnaird, M.F., Korte, L., Kral, K., Kumar, J., Larson, A.J., Li, Y., Li, X., Liu, S., Lum, S.K.Y., Lutz, J.A., Ma, K., Maddalena, D.M., Makana, J.R., Malhi, Y., Marthews, T., Mat Serudin, R., McMahon, S.M., McShea, W.J., Memiaghe, H.R., Mi, X., Mizuno, T., Morecroft, M., Myers, J.A., Novotny, V., De Oliveira, A.A., Ong, P.S., Orwig, D.A., Ostertag, R., den Ouden, J., Parker, G.G., Phillips, R.P., Sack, L., Sainge, M.N., Sang, W., Sri-Ngernyuang, K., Sukumar, R., Sun, I.F., Sungpalee, W., Suresh, H.S., Tan, S., Thomas, S.C., Thomas, D.W., Thompson, J., Turner, B.L., Uriarte, M., Valencia, R., Vallejo, M.I., Vicentini, A., Vrška, T., Wang, X., Wang, X., Weiblen, G., Wolf, A., Xu, H., Yap, S., Zimmerman, J., 2015. CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. Global Change Biol. 21, 528–549.
Asner, G.P., 2009. Tropical forest carbon assessment: integrating satellite and airborne mapping approaches. Environ. Res. Lett. 4, 4.
Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320, 1444–1449.
Bossel, H., Krieger, H., 1991. Simulation model of natural tropical forest dynamics. Ecol. Modell. 59, 37–71.
Bossel, H., Krieger, H., 1994. Simulation of multi-species tropical forest dynamics using a vertically and horizontally structured model. For. Ecol. Manage. 69, 123–144.
Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60, 849–873.
Bugmann, H., 1996a. Functional types of trees in temperate and boreal forests: classification and testing. J. Veg. Sci. 7, 359–370.
Bugmann, H., 1996b. A simplified forest model to study species composition along climate gradients. Ecology 77, 2055–2074.
Bugmann, H., 2001. A review of forest gap models. Clim. Change 51, 259–305.
Bugmann, H., Solomon, A.M., 2000. Explaining forest composition and biomass across multiple biogeographical regions. Ecol. Appl. 10, 95–114.
Cavard, X., Bergeron, Y., Chen, H.Y.H., Paré, D., 2010. Mixed-species effect on tree aboveground carbon pools in the east-central boreal forests. Can. J. For. Res. 40, 37–47.
Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. Sci. Adv. 1, e1400253.
Coffin, D.P., Lauenroth, W.K., 1990. A gap dynamics simulation model of succession in a semiarid grassland. Ecol. Modell. 49, 229–266.
Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.
Dantas de Paula, M., Groeneveld, J., Huth, A., 2015. Tropical forest degradation and recovery in fragmented landscapes—Simulating changes in tree community, forest hydrology and carbon balance. Global Ecol. Conserv. 3, 664–677.
Debinski, D.M., Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. Conserv. Biol. 14, 342–355.
Dislich, C., Huth, A., 2012. Modelling the impact of shallow landslides on forest structure in tropical montane forests. Ecol. Modell. 239, 40–53.
Ditzer, T., Glauner, R., Forster, M., Köhler, P., Huth, A., 2000. The process-based stand growth model Formix 3-Q applied in a GIS environment for growth and yield analysis in a tropical rain forest. Tree Physiol. 20, 367–381.
Doyle, T.W., 1981. The role of disturbance in the gap dynamics of montane rain forest: an application of a tropical forest succession model. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), Forest Succession: Concepts and Application. Springer, New York, Heidelberg, Berlin, pp. 56–73.
Drake, J.B., Dubayah, R.O., Clark, D.B., Knox, R.G., Blair, J.B., Hofton, M.A., Chazdon, R.L., Weishampel, J.F., Prince, S.D., 2002. Estimation of tropical forest structural characteristics using large-footprint lidar. Remote Sens. Environ. 79, 305–319.
Dubayah, R.O., Sheldon, S.L., Clark, D.B., Hofton, M.A., Blair, J.B., Hurtt, G.C., Chazdon, R.L., 2010. Estimation of tropical forest height and biomass dynamics using lidar remote sensing at La Selva, Costa Rica. J. Geophys. Res. Biogeosci. 115, G00E09.
Englhart, S., Jubanski, J., Siegert, F., 2013. Quantifying dynamics in tropical peat swamp forest biomass with multi- temporal LiDAR datasets. Remote Sens. 5, 2368–2388.
Evans, M.R., Grimm, V., Johst, K., Knuuttila, T., de Langhe, R., Lessells, C.M., Merz, M., O'Malley, M.A., Orzack, S.H., Weisberg, M., Wilkinson, D.J., Wolkenhauer, O., Benton, T.G., 2013. Do simple models lead to generality in ecology? Trends Ecol. Evol. 28, 578–583.
Fischer, R., Armstrong, A., Shugart, H.H., Huth, A., 2014. Simulating the impacts of reduced rainfall on carbon stocks and net ecosystem exchange in a tropical forest. Environ. Modell. Softw. 52, 200–206.
Fischer, R., Ensslin, A., Rutten, G., Fischer, M., Schellenberger Costa, D., et al., 2015. Simulating carbon stocks and fluxes of an african tropical montane forest with an individual-based forest model. PLoS ONE 10 (4), e0123300, http://dx.doi.org/10.1371/journal.pone.0123300.
Gatti, L.V., Gloor, M., Miller, J.B., Doughty, C.E., Malhi, Y., Domingues, L.G., Basso, L.S., Martinewski, A., Correia, C.S.C., Borges, V.F., Freitas, S., Braz, R., Anderson, L.O., Rocha, H., Grace, J., Phillips, O.L., Lloyd, J., 2014. Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. Nature 506, 76–80.
Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378-+.

Glauner, R., Ditzer, T., Huth, A., 2003. Growth and yield of tropical moist forest for forest planning: an inquiry through modeling. Can. J. For. Res. 33, 521–535.
Grace, J., Mitchard, E., Gloor, E., 2014. Perturbations in the carbon budget of the tropics. Global Change Biol. 20, 3238–3255.
Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310, 987–991.
Groeneveld, J., Alves, L.F., Bernacci, L.C., Catharino, E.L.M., Knogge, C., Metzger, J.P., Pütz, S., Huth, A., 2009. The impact of fragmentation and density regulation on forest succession in the Atlantic rain forest. Ecol. Modell. 220, 2450–2459.
Gutiérrez, A.G., 2010. Long-Term Dynamics and the Response of Temperate Rainforests of Chiloé Island (Chile) to Climate Change. Technische Universität München, Lehrstuhl für Waldwachstumskunde, pp. 170.
Gutiérrez, A.G., Armesto, J.J., Díaz, M.F., Huth, A., 2014. Increased drought impacts on temperate rainforests from southern South America: results of a process-based, dynamic forest model. PLoS ONE 9, e103226.
Gutiérrez, A.G., Huth, A., 2012. Successional stages of primary temperate rainforests of Chiloé Island. Chile Perspect. Plant Ecol. Evol. Syst. 14, 243–256.
Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. Science 342, 850–853.
Hartig, F., Calabrese, J.M., Reineking, B., Wiegand, T., Huth, A., 2011. Statistical inference for stochastic simulation models—theory and application. Ecol. Lett. 14, 816–827.
Haxeltine, A., Prentice, I.C., 1996. A general model for the light-use efficiency of primary production. Funct. Ecol. 10, 551–561.
Hickler, T., Vohland, K., Feehan, J., Miller, P.A., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T.R., Cramer, W., Kuhn, I., Sykes, M.T., 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecol. Biogeogr. 21, 50–63.
Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J., de Lao, S.L., 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283, 554–557.
Huston, M., DeAngelis, D., Post, W., 1988. New computer models unify ecological theory—Computer simulations show that many ecological patterns can be explained by interactions among individual organisms. BioScience 38, 682–691.
Huth, A., Ditzer, T., 2001. Long-term impacts of logging in a tropical rain forest—a simulation study. For. Ecol. Manage. 142, 33–51.
Huth, A., Drechsler, M., Köhler, P., 2004. Multicriteria evaluation of simulated logging scenarios in a tropical rain forest. J. Environ. Manage. 71, 321–333.
Huth, A., Drechsler, M., Köhler, P., 2005. Using multicriteria decision analysis and a forest growth model to assess impacts of tree harvesting in Dipterocarp lowland rain forests. For. Ecol. Manage. 207, 215–232.
IPCC, 2013. Climate change 2013: the physical science basis. In: Stocker, T.F., et al. (Eds.), Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, p. 1535.
Jacob, M., Leuschner, C., Thomas, F.M., 2010. Productivity of temperate broad-leaved forest stands differing in tree species diversity. Ann. For. Sci. 67, 503.
Kammesheidt, L., Köhler, P., Huth, A., 2001. Sustainable timber harvesting in Venezuela: a modelling approach. J. Appl. Ecol. 38, 756–770.
Kammesheidt, L., Köhler, P., Huth, A., 2002. Simulating logging scenarios in secondary forest embedded in a fragmented neotropical landscape. For. Ecol. Manage. 170, 89–105.
Kazmierczak, M., Wiegand, T., Huth, A., 2014. A neutral vs. non-neutral parametrizations of a physiological forest gap model. Ecol. Modell. 288, 94–102.
Köhler, P., Chave, J., Riéra, B., Huth, A., 2003. Simulating the long-term response of tropical wet forests to fragmentation. Ecosystems 6, 114–128.
Köhler, P., Ditzer, T., Huth, A., 2000. Concepts for the aggregation of tropical tree species into functional types and the application on Sabah's dipterocarp lowland rain forests. J. Trop. Ecol. 16, 591–602.
Köhler, P., Ditzer, T., Ong, R.C., Huth, A., 2001. Comparison of measured and modelled growth on permanent plots in Sabahs rain forest. For. Ecol. Manage. 144, 101–111.
Köhler, P., Huth, A., 1998. The effects of tree species grouping in tropical rainforest modelling: simulations with the individual-based model FORMIND. Ecol. Modell. 109, 301–321.
Köhler, P., Huth, A., 2004. Simulating growth dynamics in a South–East Asian rainforest threatened by recruitment shortage and tree harvesting. Clim. Change 67, 95–117.
Köhler, P., Huth, A., 2007. Impacts of recruitment limitation and canopy disturbance on tropical tree species richness. Ecol. Modell. 203, 511–517.
Köhler, P., Huth, A., 2010. Towards ground-truthing of spaceborne estimates of above-ground life biomass and leaf area index in tropical rain forests. Biogeosciences 7, 2531–2543.
Laurance, W.F., Camargo, J.L.C., Luizao, R.C.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., Stouffer, P.C., Williamson, G.B., itez-Malvido, J., Vasconcelos, H.L., van Houtan, K.S., Zartman, C.E., Boyle, S.A., Didham, R.K., Andrade, A., Lovejoy, T.E., 2011. The fate of Amazonian forest fragments: a 32-year investigation. Biol. Conserv. 144, 56–67.
Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M., Laurance, S.G., 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology 79, 2032–2040.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G., Sampaio, E., 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv. Biol. 16, 605–618.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S., Watt, A.D., 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391, 72–76.

Le Quéré, C., Moriarty, R., Andrew, R.M., Peters, G.P., Ciais, P., Friedlingstein, P., Jones, S.D., Sitch, S., Tans, P., Arneth, A., Boden, T.A., Bopp, L., Bozec, Y., Canadell, J.G., Chevallier, F., Cosca, C.E., Harris, I., Hoppema, M., Houghton, R.A., House, J.I., Jain, A., Johannessen, T., Kato, E., Keeling, R.F., Kitidis, V., Klein Goldewijk, K., Koven, C., Landa, C.S., Landschützer, P., Lenton, A., Lima, I.D., Marland, G., Mathis, J.T., Metzl, N., Nojiri, Y., Olsen, A., Ono, T., Peters, W., Pfeil, B., Poulter, B., Raupach, M.R., Regnier, P., Rödenbeck, C., Saito, S., Salisbury, J.E., Schuster, U., Schwinger, J., Séférian, R., Segschneider, J., Steinhoff, T., Stocker, B.D., Sutton, A.J., Takahashi, T., Tilbrook, B., van der Werf, G.R., Viovy, N., Wang, Y.P., Wanninkhof, R., Wiltshire, A., Zeng, N., 2015. Global carbon budget 2014. Earth Syst. Sci. Data 7, 47–85.

Lefsky, M.A., Cohen, W.B., Harding, D.J., Parker, G.G., Acker, S.A., Gower, S.T., 2002. Lidar remote sensing of above-ground biomass in three biomes. Global Ecol. Biogeogr. 11, 393–399.

Lehmann, S., Huth, A., 2015. Fast calibration of a dynamic vegetation model with minimum observation data. Ecol. Modell. 301, 98–105.

Meyer, V., Saatchi, S.S., Chave, J., Dalling, J.W., Bohlman, S., Fricker, G.A., Robinson, C., Neumann, M., Hubbell, S., 2013. Detecting tropical forest biomass dynamics from repeated airborne lidar measurements. Biogeosciences 10, 5421–5438.

Morin, X., Fahse, L., Scherer-Lorenzen, M., Bugmann, H., 2011. Tree species richness promotes productivity in temperate forests through strong complementarity between species. Ecol. Lett. 14, 1211–1219.

Morton, D.C., Nagol, J., Carabajal, C.C., Rosette, J., Palace, M., Cook, B.D., Vermote, E.F., Harding, D.J., North, P.R.J., 2014. Amazon forests maintain consistent canopy structure and greenness during the dry season. Nature 506, 221–224.

Moser jr., J.W., 1980. Historical chapters in the development of modern forest growth and yield theory. In: Brown, K.M., Clarke, F.R. (Eds.), Forecasting Forest Stand Dynamics. School of Forestry, Lakehead University, Thunder Bay, ON, pp. 42–61.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Palace, M.W., Sullivan, F.B., Ducey, M.J., Treuhaft, R.N., Herrick, C., Shimbo, J.Z., Mota-E-Silva, J., 2015. Estimating forest structure in a tropical forest using field measurements, a synthetic model and discrete return lidar data. Remote Sens. Environ. 161, 1–11.

Phillips, O.L., Gentry, A.H., 1994. Increasing turnover through time in tropical forests. Science 263, 954–958.

Picard, N., Franc, A., 2003. Are ecological groups of species optimal for forest dynamics modelling? Ecol. Modell. 163, 175–186.

Picard, N., Köhler, P., Mortier, F., Gourlet-Fleury, S., 2012. A comparison of five classifications of species into functional groups in tropical forests of French Guiana. Ecol. Complex. 11, 75–83.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344, 987.

Prentice, I.C., Leemans, R., 1990. Pattern and process and the dynamics of forest structure: a simulation approach. J. Ecol. 78, 340–355.

Prentice, I.C., Sykes, M.T., Cramer, W., 1993. A simulation model for the transient effects of climate change on forest. landscapes. Ecol. Modell. 65, 51–70.

Pretzsch, H., 2009. Forest Dynamics, Growth and Yield. Springer, Berlin, pp. 664.

Pütz, S., Groeneveld, J., Alves, L.F., Metzger, J.P., Huth, A., 2011. Fragmentation drives tropical forest fragments to early successional states: a modelling study for Brazilian Atlantic forests. Ecol. Modell. 222, 1986–1997.

Pütz, S., Groeneveld, J., Henle, K., Knogge, C., Martensen, A.C., Metz, M., Metzger, J.P., Ribeiro, M.C., Dantas de Paula, M., Huth, A., 2014. Long-term carbon loss in fragmented neotropical forests. Nat. Commun. 5, art. 5037.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biol. Conserv. 142, 1141–1153.

Rüger, N., Gutiérrez, A.G., Kissling, W.D., Armesto, J.J., Huth, A., 2007. Ecological impacts of different harvesting scenarios for temperate evergreen rain forest in southern Chile—a simulation experiment. For. Ecol. Manage. 252, 52–66.

Rüger, N., Williams-Linera, G., Kissling, W.D., Huth, A., 2008. Long-term impacts of fuelwood extraction on a tropical montane cloud forest. Ecosystems 11, 868–881.

Sato, H., Itoh, A., Kohyama, T., 2007. SEIB-DGVM: a new dynamic global vegetation model using a spatially explicit individual-based approach. Ecol. Modell. 200, 279–307.

Schumacher, S., 2004. The Role of Large-Scale Disturbances and Climate for the Dynamics of Forested Landscapes in the European Alps. Swiss Federal Institute of Technology Zurich, Switzerland, pp. 149.

Schumacher, S., Bugmann, H., Mladenoff, D.J., 2004. Improving the formulation of tree growth and succession in a spatially explicit landscape model. Ecol. Modell. 180, 175–194.

Shugart, H.H., 1984. A Theory of Forest Dynamics. The Blackburn Press, New York, pp. 278.

Shugart, H.H., 1998. Terrestrial Ecosystems in Changing Environments. Cambridge University Press, Cambridge, pp. 537.

Shugart, H.H., 2003. A Theory of Forest Dynamics. The Blackburn Press, New York, pp. 278.

Shugart, H.H., Asner, G.P., Fischer, R., Huth, A., Knapp, N., Le Toan, T., Shuman, J.K., 2015. Computer and remote-sensing infrastructure to enhance large-scale testing of individual-based forest models. Front Ecol. Environ. 13, 503–511.

Shugart, H.H., West, D.C., 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. J. Environ. Manage. 5, 161–179.

Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K., Venevsky, S., 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Global Change Biol. 9, 161–185.

Skole, D., Tucker, C., 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. Science 260, 1905–1910.

Slik, J.W.F., Arroyo-Rodríguez, V., Aiba, S.-I., Alvarez-Loayza, P., Alves, L.F., Ashton, P., Balvanera, P., Bastian, M.L., Bellingham, P.J., van den Berg, E., Bernacci, L., da Conceição Bispo, P., Blanc, L., Böhning-Gaese, K., Boeckx, P., Bongers, F., Boyle, B., Bradford, M., Brearley, F.Q., Breuer-Ndoundou Hockemba, M., Bunyavejchewin, S., Calderado Leal Matos, D., Castillo-Santiago, M., Catharino, E.L.M., Chai, S.-L., Chen, Y., Colwell, R.K., Chazdon, R.L., Clark, C., Clark, D.B., Clark, D.A., Culmsee, H., Damas, K., Dattaraja, H.S., Dauby, G., Davidar, P., Dewalt, S.J., Doucet, J.-L., Duque, A., Durigan, G., Eichhorn, K.A.O., Eisenlohr, P.V., Eler, E., Ewango, C., Farwig, N., Feeley, K.J., Ferreira, L., Field, R., de Oliveira Filho, A.T., Fletcher, C., Forshed, O., Franco, G., Fredriksson, G., Gillespie, T., Gillet, J.F., Amarnath, G., Griffith, D.M., Grogan, J., Gunatilleke, N., Harris, D., Harrison, R., Hector, A., Homeier, J., Imai, N., Itoh, A., Jansen, P.A., Joly, C.A., de Jong, B.H.J., Kartawinata, K., Kearsley, E., Kelly, D.L., Kenfack, D., Kessler, M., Kitayama, K., Kooyman, R., Larney, E., Laumonier, Y., Laurance, S., Laurance, W.F., Lawes, M.J., Leao do Amaral, I., Letcher, S.G., Lindsell, J., Lu, X., Mansor, A., Marjokorpi, A., Martin, E.H., Meilby, H., Melo, F.P.L., Metcalfe, D.J., Medjibe, V.P., Metzger, J.P., Millet, J., Mohandass, D., Montero, J.C., de Morisson Valeriano, M., Mugerwa, B., Nagamasu, H., Nilus, R., Ochoa-Gaona, S., Page, O.N., Parolin, P., Parren, M., Parthasarathy, N., Paudel, E., Permana, A., Piedade, M.T.F., Pitman, N.C.A., Poorter, L., Poulsen, A.D., Poulsen, J., Powers, J., Pasad, R.C., Pyravaud, J.P., Razafimahaimodison, J.C., Reitsma, J., dos Santos, J.R., Spironello, W.R., Romero-Saltos, H., Rovero, F., Rozak, A.H., Ruokolainen, K., Rutishauser, E., Saitert, F., Saner, P., Santos, B.A., Santos, F., Sarker, S.K., Satdichanha, M., Schmitt, C.B., Schöngart, J., Schulze, M., Suganuma, M.S., Sheil, D., da Silva Pinheiro, E., Sist, P., Stevart, T., Sukumar, R., Sun, I.-F., Sunderland, T., Suresh, H.S., Suzuki, E., Tabarelli, M., Tang, J., Targhetta, N., Theilade, I., Thomas, D.W., Tchouto, P., Hurtado, J., Valencia, R., van Valkenburg, J.L.C.H., Van Do, T., Vasquez, R., Verbeeck, H., Adekunle, V., Vieira, S.A., Webb, C.O., Whitfeld, T., Wich, S.A., Williams, J., Wittmann, F., Wöll, J., Yang, X., Yao, C.Y.A., Yap, S.L., Yoneda, T., Zahawi, R.A., Zakaria, R., Zang, R., de Assis, R.L., Garcia Luize, B., Venticinque, E.M., 2015. An estimate of the number of tropical tree species. Proc. Natl. Acad. Sci. U.S.A. 112, 7472–7477.

Smith, T.M., Shugart, H.H., 1997. Plant Functional Types. In Their Relevance to Ecosystem Properties and Global Change. Cambridge University Press, Cambridge.

Snell, R.S., Huth, A., Nabel, J.E.M.S., Bocedi, G., Travis, J.M.J., Gravel, D., Bugmann, H., Gutiérrez, A.G., Hickler, T., Higgins, S.I., Reineking, B., Scherstjanoi, M., Zurbriggen, N., Lischke, H., 2014. Using dynamic vegetation models to simulate plant range shifts. Ecography 37, 1184–1197.

Taubert, F., Frank, K., Huth, A., 2012. A review of grassland models in the biofuel context. Ecol. Modell. 245, 84–93.

Thornley, J.H.M., Johnson, I.R., 1990. Plant and Crop Modelling. Claredon Press, Oxford.

Ticktin, T., 2004. The ecological implications of harvesting non-timber forest products. J. Appl. Ecol. 41, 11–21, 1990.

Tietjen, B., Huth, A., 2006. Modelling dynamics of managed tropical rainforests—an aggregated approach. Ecol. Modell. 199, 421–432.

Tolson, B.A., Shoemaker, C.A., 2007. Dynamically dimensioned search algorithm for computationally efficient watershed model calibration. Water Resour. Res. 43, 43.

Urban, D.L., Bonan, G.B., Smith, T.M., Shugart, H.H., 1991. Spatial applications of gap models. For. Ecol. Manage. 42, 95–110.

Vilà, M., Vayreda, J., Comas, L., Ibanez, J.J., Mata, T., Obon, B., 2007. Species richness and wood production: a positive association in Mediterranean forests. Ecol. Lett. 10, 241–250.

Wang, X.H., Piao, S.L., Ciais, P., Friedlingstein, P., Myneni, R.B., Cox, P., Heimann, M., Miller, J., Peng, S.S., Wang, T., Yang, H., Chen, A.P., 2014. A two-fold increase of carbon cycle sensitivity to tropical temperature variations. Nature 506, 212-+.

Wårlind, D., Smith, B., Hickler, T., Arneth, A., 2014. Nitrogen feedbacks increase future terrestrial ecosystem carbon uptake in an individual-based dynamic vegetation model. Biogeosciences 11, 6131–6146.

Whitmore, T.C., 1998. An Introduction to Tropical Rain Forests. Oxford University Press, Oxford, pp. 296.

Yan, X.D., Shugart, H.H., 2005. FAREAST: a forest gap model to simulate dynamics and patterns of eastern Eurasian forests. J. Biogeogr. 32, 1641–1658.

Zhang, Y., Chen, H.Y.H., Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. J. Ecol. 100, 742–749.