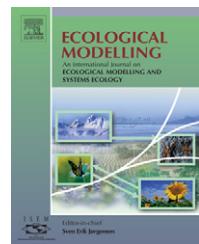


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Short communication

Impacts of recruitment limitation and canopy disturbance on tropical tree species richness

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ARTICLE INFO

Article history:

Received 24 October 2006

Received in revised form

20 November 2006

Accepted 20 November 2006

Published online 26 December 2006

Keywords:

Tropical rain forest

Forest growth model

Species richness

Recruitment limitation

Intermediate disturbance

hypothesis

ABSTRACT

We used the process-based forest growth model FORMIND2.0 to show that recruitment limitation and the intermediate disturbance hypothesis which proposes maximum diversity in forests of intermediate disturbance intensity or frequency are both processes which impact on tropical tree species richness. Both processes influence each other and should therefore not be analyzed separately. While on a local level a rise in recruitment limitation promotes species richness, the overall richness of the whole forest declines. Disturbance levels are more important for species richness in forests which are highly limited by recruitment. This study supports previous field data investigations from the Americas. It also highlights the lack of consensus regarding the definition of disturbance and recruitment limitation, which makes inter-study comparisons difficult.

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1. Introduction

One often discussed question in ecology is which processes define species diversity in the species rich tropical rain forest flora (Hubbell et al., 1999; Vandermeer et al., 2000; Molino and Sabatier, 2001). Besides an intensive analysis of field data now available from large long-term rain forest plots (Condit et al., 1996; Hubbell et al., 1999) quite simplistic conceptual models were used to highlight the influence of various processes and mechanisms on species abundance and diversity in the past

(Hubbell, 1979, 2001; Yu et al., 1998; Alonso and Solé, 2000; McGill, 2003; Chave et al., 2002; Bampfylde et al., 2005). Only in a few case studies were more elaborated forest growth models used to assess the dynamics of tree species diversity (Liu and Ashton, 1999; Chave, 2001).

Besides classical concepts describing species richness – e.g. the number of species increases, generally with area size (MacArthur and Wilson, 1967; Plotkin et al., 2000b) – other theories are still a matter of debate (Brokaw and Busing, 2000; Wright, 2002). For the case of tropical tree species richness, particularly the intermediate disturbance hypothesis IDH

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(Connell, 1978; Sheil, 1999; Vandermeer et al., 2000; Molino and Sabatier, 2001; Roxburgh et al., 2004; Sheil and Burslem, 2003; Johst and Huth, 2005) and the concept of recruitment limitation (Hurt and Pacala, 1995; Hubbell et al., 1999; Chazdon et al., 1999; Hubbell, 1999) acting as the main mechanisms for maintenance of tree species diversity have been discussed within recent years.

Here, we attempt to add a few new aspects to the discussion regarding which mechanisms promote tropical tree species richness from a modeling perspective by using, for the first time, a complex process-based forest growth model. We used the model FORMIND2.0 which has been used to assess the impacts of tree harvesting (Kammesheidt et al., 2001; Huth et al., 2004, 2005; Köhler and Huth, 2004) and forest fragmentation (Köhler et al., 2003) on tropical forest dynamics. FORMIND2.0 calculates the carbon cycle of individual trees which belong to different plant functional types. We expanded the model to distinguish all the different 468 species found at our study site, a lowland dipterocarp rain forest in Sabah, Malaysia. We believe that a detailed process-based model like FORMIND2.0 which does not only consider seed dispersal and establishment (Hubbell, 1979), but also succession by including processes such as competition and reasonable tree growth rates will give new insights and is a valuable tool for questioning current ecological theories.

2. Material and methods

2.1. Area description

Our study area is the Deramakot Forest Reserve (DFR) in Sabah (North Borneo, Malaysia, 117°30'E, 5°25'N, 130–300 masl). Deramakot has a per-humid climate typical of the inner tropics. The mean annual temperature is 27 °C with little seasonal variation. The average annual precipitation is about 3500 mm, with no pronounced dry season. The geology of Deramakot is characterized by tertiary sediments, mostly sandstone. The soils are low in nutrients and prone to erosion once left devoid of tree cover. The prevailing forest type is lowland dipterocarp forest (Schlensog, 1997). We took a primary forest stand (plot 1) for our stand initialization from a research inventory in DFR (Schlensog, 1997).

2.2. Species grouping

The shrub and tree species found in DFR (total number: 468 species) are assigned to 13 different plant functional types (PFT) based on their successional status and maximum height at maturity (Köhler et al., 2000). The successional status (early, mid, or late) is determined by their growth rates under various light regimes, as well as through a survey of wood densities, which are good indicators of growth rates for most species. A species list including grouping is available online (<http://www.usf.uni-kassel.de/usf/archiv/dokumente.en.htm>). In addition to former applications of the model, each tree, seed and seedling of the initial site distribution is assigned randomly to one of the 468 species following the abundance pattern in our field

data. During simulation fecund trees produce only offsprings of their species and not of the more general PFT. Species richness is defined by the number of different tree species within the tree population.

2.3. Description of the model

We used the individual-oriented process-based forest growth model FORMIND (Köhler and Huth, 1998) in its updated version (2.0) (Köhler, 2000) – which has been proven suitable to simulate a wide range of forest sites in Sabah (Köhler et al., 2001), Venezuela (Kammesheidt et al., 2001) and French Guiana (Köhler et al., 2003) – to simulate the species composition of an uneven-aged mixed tropical rain forest. The site-specific model adaptation and parameterization to DFR in Sabah as used here were published elsewhere (Huth et al., 2004, 2005; Köhler and Huth, 2004).

The model describes forest dynamics as a mosaic of interacting forest patches (20 m × 20 m), which have the typical crown size of emergent trees in our observation area. Within these patches trees are not spatially explicitly distributed, and thus all compete for light and space following the gap model approach (Botkin, 1993). Allometric relationships connect the above-ground biomass of a tree with its stem diameter, the tree height, the bole volume and the crown dimensions. Using these relationships, the distribution of individual tree crowns and their leaf area in the canopy is calculated in horizontal canopy layers with a width of 0.5 m.

The growth of an individual tree is based on a carbon balance. Calculations include the photosynthesis of the trees and assimilate losses due to respiration, litter-fall and fine root decay. Within a patch, vertical light attenuation in the canopy is calculated from light intensity above the canopy with respect to the absorption of tree crowns. The dependence of specific photosynthetic productivity on irradiance is modeled using a Michaelis–Menten-type light response curve. Photosynthetic production is calculated from the tree's leaf area. We assume an increasing limitation effect of water transport deficiencies with increasing tree height. Thus, actual productivity is calculated by applying a size-dependent limitation factor. Assimilation losses are estimated in relation to tree biomass. We distinguish between biomass-dependent maintenance respiration and growth respiration. Tree growth is calculated in annual time steps. Competition is modeled in terms of competition for light and space, the latter resulting in self-thinning.

Mortality is modeled as a stochastic event. Senescent trees die and collapse with a certain probability, knocking down smaller trees in neighboring patches and creating gaps of a size depending upon their crown size. Recruitment takes into account the production and explicit dispersal of individual seeds produced by local mother trees. Thus, the recruitment rate lumps together several regeneration stages: fecundity, seed survival, germination and possible predation upon young seedlings. Incoming seeds update a seed pool, taking into account the dormancy variability across functional groups. Seeds from the seed pool per patch will be established as saplings at dbh = 1 cm, when specific light conditions are fulfilled. The initial seed pool is filled with average seed numbers from long-term simulations.

If not stated otherwise, each simulation is run over 9 ha and repeated five times to average stochastic effects. No immigration of species from outside the simulation area is assumed. This assumption implies that the number of species over time is decreasing, because without new immigrating species the species richness declines due to extinction. We have therefore to select a time period for analysis, in which the effects of the different mechanisms are already detectable, but in which the results are not converging towards similar species numbers (in the light of the stochastic uncertainty of the mortality and seed dispersal processes) due to the declining species richness. From tests the dynamics after 200 simulated years have been shown to fulfill these requirements. Differences in species richness caused by our investigated mechanisms are then detectable. Cumulative species numbers as function of cumulative stem numbers are averages of 500 randomly resampled data sets (100 random resamples for each of the five repeated simulations) using thus the same methodology as in Vandermeer et al. (2000).

2.4. Recruitment limitation and local disturbance

We first tested whether our model was able to reproduce well-known diversity patterns. It is known that species richness increases with area size (MacArthur and Wilson, 1967). Thus, we investigated the species-area-relationship for simulations with different area size (1–49 ha). We then focused on the role of recruitment limitation and disturbance. After the IDH one finds maximum species richness at sites of intermediate disturbance intensity or frequency (Connell, 1978). We therefore simulated forests with different degree of local disturbances by varying the probability W of a dying tree to fall over, smash down smaller trees and create large canopy gaps ($W = 0, 20, 40, 60, 80, 100\%$). Through recruitment limitation not only the best competitor but the one, which is at the right time at the right place will be established (Hurt and Pacala, 1995; Hubbell et al., 1999). We have chosen to distinguish between low and high recruitment limitation by reducing the number of dispersed seeds for all species by one order of magnitude (divided by a factor of 10).

3. Results

Our model evaluation of the species-area-relationships (Fig. 1) shows that species richness increased with area size and followed the classical relationship $S = cA^z$ with $z = 0.29$ corresponding well to typical values for tropical rain forests around $z \sim 0.25$ (Plotkin et al., 2000a). The species-area-relationship of our simulations also follows the new function $S = cA^z e^{kA}$ proposed after the reanalysis of different large tropical forest plots (Plotkin et al., 2000b).

At the maximum investigated simulation size (49 ha), 85% of all possible tree species were established in the simulation area. Because of the neglected species immigration this ratio depended on the simulation time selected for the analysis (here $t = 200$ years).

To come to unbiased estimates of species richness independent of stem density (Denslow, 1995) cumulative species

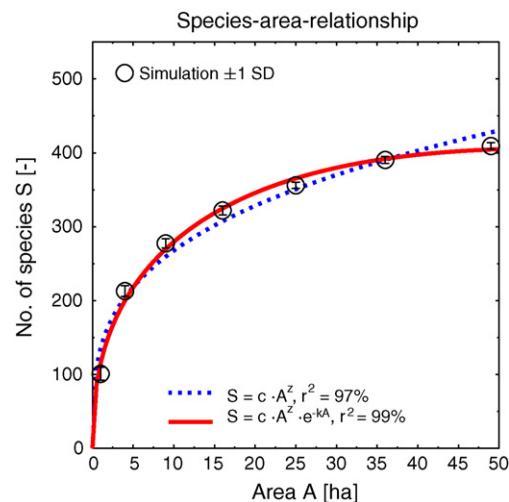


Fig. 1 – Testing model performance with species-area-relationships (SAR). Two different models of SAR are tested against our simulation data (± 1 S.D.). The fitted functions are $S = 136A^{0.29}$ and $S = 116A^{0.41} e^{-0.00736A}$. In this reference run recruitment limitation is low and disturbance of average intensity (tree falling probability $W = 0.4$).

numbers S is plotted as a function of cumulative stem numbers N (Fig. 2A and B) as done in other studies (Chazdon et al., 1999; Vandermeer et al., 2000). In our reference case (low recruitment limitation) the difference in species numbers for different disturbances was small, but already detectable. Species number per stem was largest in simulations with no disturbances for high stem numbers ($N > 1500$) (Fig. 2A). The species numbers decreased with increasing disturbance level with indistinguishable effects for a disturbance level of 80% and higher. For small stem numbers ($N < 1500$) the species numbers in forests with intermediate disturbance levels (20% tree fall probability) was largest.

In scenarios with high recruitment limitations (Fig. 2B) the disturbance level had a higher impact on the species richness. For a given cumulative stem number the cumulative species number for different disturbance regimes spanned a wider range compared to the low recruitment case. This difference was especially pronounced for low stem numbers ($N < 1000$). The highest species number was found for a disturbance level of 20% for stem numbers N larger than 520. Species richness for high stem numbers ($N = 4000$) was smallest for no disturbance or for high disturbance levels (Fig. 2C).

These modeling results support to a certain extent the IDH which proposes maximum species diversity in areas with intermediate disturbance regimes. In our study a maximum in species richness occurs only at intermediate disturbance levels if recruitment in the forest is limited (Fig. 2C). Our study suggests that species richness is generally more influenced by disturbance than by recruitment limitation.

We further investigated the IDH at a local level (here areas of 20 m × 20 m) with pioneer species abundances as the indicator for disturbance intensity (Molino and Sabatier, 2001). Species richness is significantly enhanced by recruitment

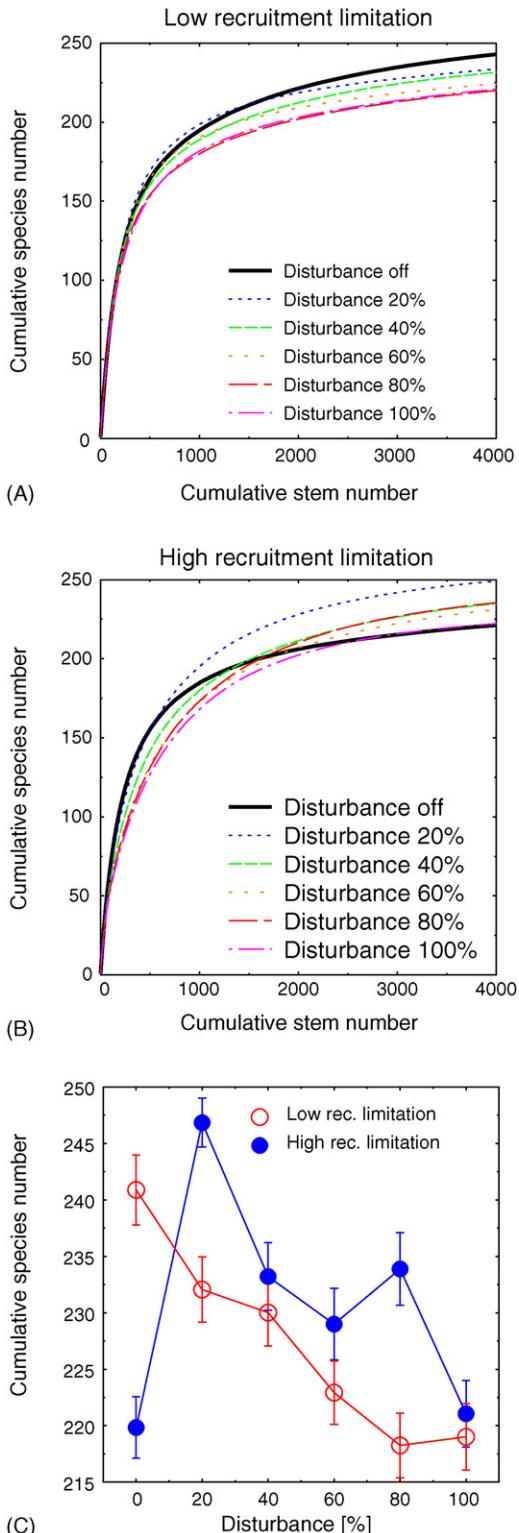


Fig. 2 – Cumulative species numbers as function of cumulative stem numbers for $t = 200$ years. We compare six levels of disturbance defined by the gap creating probability of dying trees $W \in (0, 20, 40, 60, 80, 100\%)$. (A) Reference case with low recruitment limitation. (B) High recruitment limitation. (C) Cumulative species richness as function of disturbance at cumulative stem number $N = 4000$. Data sets are averages of 500 random resamplings. Error bars in sub-figure C are ± 1 S.D.

limitation here (Fig. 3A). A maximum in species richness at intermediate disturbance levels is not very pronounced and situated at a small share of pioneers (pioneers $\sim 20\%$). Since the selected time of analysis might lay outside a potential maximum in species richness over time as proposed by the IDH we additionally focused on different time periods after a heavy disturbing impact, here realized by a clear cut of all trees in the simulation area and a regrowth of secondary forest recruited out of the existing seed/seedling pool only (Fig. 3B–E). The maxima in tree species richness were only found after 100 years of secondary forest regrowth and always found at small pioneer fraction (pioneers $< 20\%$). Younger secondary forest showed either a strong rise in stem number normalized species numbers for low recruitment limitations or a switch from a small rise (year 50) to a moderate decline (year 100) for forests with high recruitment limitations. High recruitment limitation leads in young forests (year 50) to a broad range of different pioneer abundances.

4. Discussion

In our model trees compete for light and space leading to the succession dynamics in the simulated forest including the creation of canopy gaps. The results of this succession process in terms of increased mortality were compared with field data (van der Meer and Bongers, 1996; Köhler and Huth, 1998) and should thus mimic the basic dynamics of forest succession in a rain forest ecosystem. The IDH is to a certain extent supported by our results, although the dependence of species richness on recruitment limitation is also apparent and seems to have significance.

Analyzing species richness in two different ways as done here (cumulative species numbers over cumulative stem numbers versus stem number normalized species richness as a function of pioneer abundance) does not result in conflicting conclusions. Both methods support the theory that recruitment limitation and disturbance are two main processes which determine tree species richness in the tropics. In forest sites with high recruitment limitation disturbance intensity is more important for species richness than in an area with low recruitment limitation and a maximum at intermediate disturbance level can be observed. But it has to be kept in mind that cumulative investigations (Vandermeer et al., 2000) interpret overall species richness of the whole forest site while the second method (Molino and Sabatier, 2001) analyzes species diversity on the local level. Furthermore, by combining both approaches not only the identification of mechanisms seems possible, difficulties in the comparison of studies using different methodologies become apparent. For the analyses of both mechanisms reliable definitions of either recruitment limitation or disturbance intensity are still missing. Therefore, it is difficult to generalize from single site investigations to ecological theories. Additionally, the time of observation considerably influences the results. For example, species composition changes quickly after extreme events such as the impact of a hurricane (Vandermeer et al., 2000). Here, models give the opportunity to test theories proposed after the investigation of single forest invento-

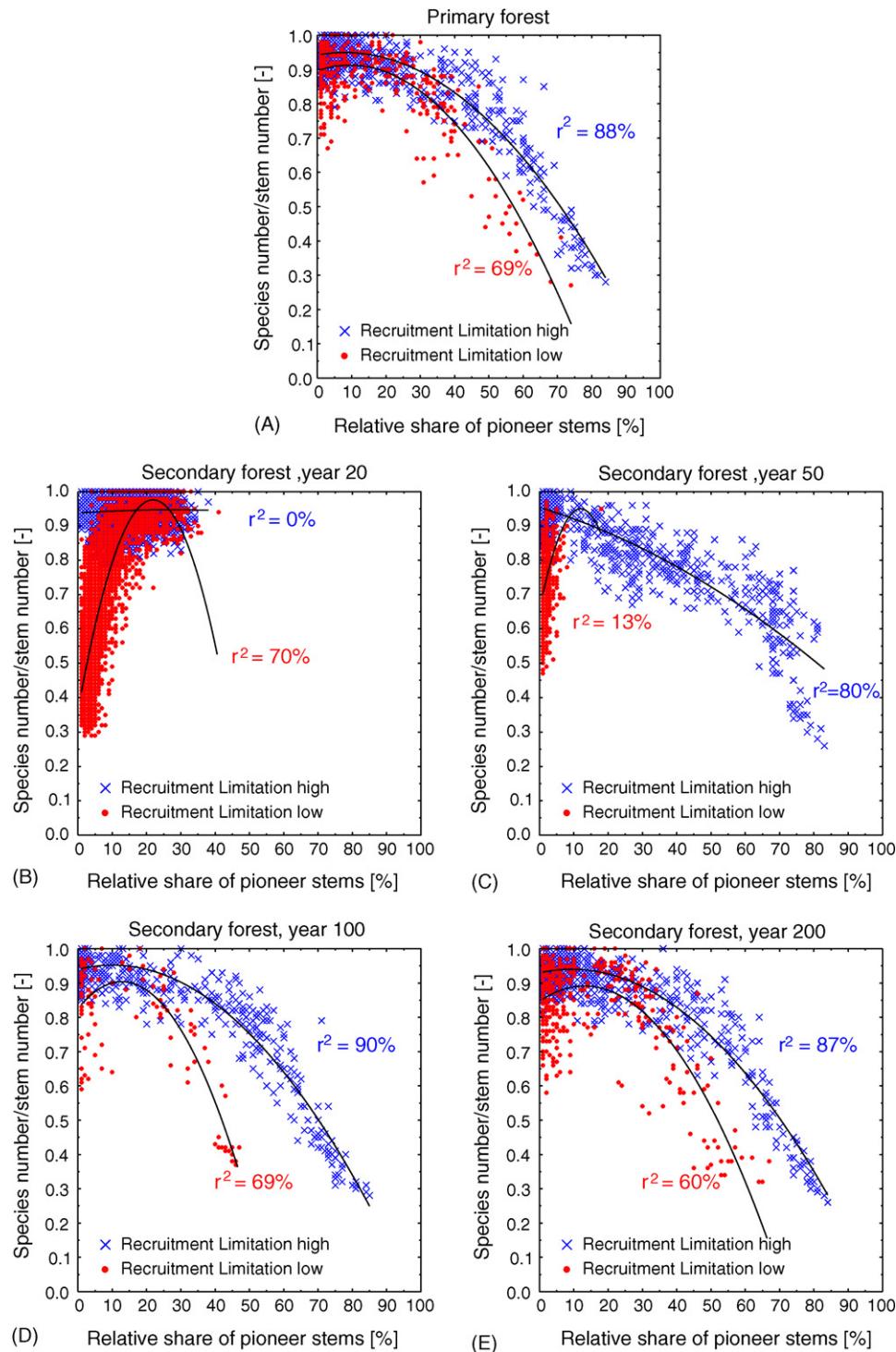


Fig. 3 – Relative species number in single patches ($20 \text{ m} \times 20 \text{ m}$) as a function of pioneers (early successional species) similar previous field data analysis (Molino and Sabatier, 2001). (A) Primary forest site at $t = 200$ years. (B-E) Different times after the regrowth of secondary forest from a clear-cut area are analyzed ($t = 20, 50, 100, 200$ years).

ries or short time series. As the carbon storage in tropical forest was analyzed recently to be a function of species composition (Bunker et al., 2005) a better understanding of processes influencing the tree species composition would also improve estimates of future carbon storage capacities in tropical forests.

The approach of Hubbell et al. (1999) differs further from these studies as they counted species richness in selected areas with or without forest gaps. We argue that results based on the division of the field site are difficult to interpret and will require more discussion (Chazdon et al., 1999). A process-based modeling approach such as ours here might be, to a

certain extent, suitable for analyzing the impact of different processes on species richness and for testing various hypothesis.

It was shown recently (Roxburgh et al., 2004), that the IDH is not one mechanism of coexistence, but rather summarizes a set of similar phenomena that can arise from the action of several different coexistence mechanisms, such as the storage effect or relative nonlinearity. Coexistence under the storage effect (Warner and Chesson, 1985) is obtained by species which 'store' certain attributes (e.g. biomass or seeds/seed production) under favorable growth periods, which can then be used during suboptimal environmental conditions. The concept of relative nonlinearity implies that competing species respond differently (nonlinear) to a given environmental disturbance. It was furthermore highlighted that the quantification of the disturbance itself is important to understand the system, but the effect and response of this disturbance is what will determine coexistence in the system (Shea et al., 2004). In our model setup the disturbance, which is the gap creation by falling large trees, causes uniform effects of increased mortality in the struck area without the preference of any species. The response to the disturbance, however, differs throughout the spectrum of different PFT and both above-mentioned mechanisms are at work and thus responsible for the observation of pattern which are characterizing the IDH. Different recruitment strategies in terms of different seed numbers per adult plant and year for a different successional status result in a different number of seeds which are 'stored' in the seed pool. On the other hand, the variable light conditions generated by a canopy disturbance create various different 'nonlinear' responses. Germination of seeds of different PFT differs with light intensity at the forest floor, photosynthetic production and tree growth are a function of incoming radiation. To move from the observed pattern (IDH) to the underlying processes (causes and effects of the disturbances) is an important step towards system understanding. As various different processes which generate the emerging patterns typically for the IDH are at work we relied on the phenomenological description (Is the IDH supported or not?) here. However, an identification of the relative importance of the different processes summarized under the IDH for the results would be a next step. For this purpose hypothetical parameterizations of the model are necessary, e.g. with PFT which differ only in those parameters which generate the storage effect. This was not performed here as we concentrated on possible comparisons with field data and relied on our well tested and most plausible model parameterization.

In conclusion, our modeling study suggests that both disturbance and recruitment limitation influence tropical tree species richness and they have to be considered together, especially at sites of high recruitment limitation. At the stand level, limited recruitment enhances species richness, while the IDH is supported in general.

Acknowledgement

We thank Karin Johst for valuable comments.

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