Ecological Complexity 20 (2014) 107–115

Contents lists available at ScienceDirect

Ecological Complexity

journal homepage: www.elsevier.com/locate/ecocom

Comparing the influence of large- and small-scale disturbances on forest heterogeneity: A simulation study for mangroves

Juliane Vogt[a,*], Cyril Piou[b], Uta Berger[a]

[a] Department of Forest Biometry and Systems Analysis, Institute of Forest Growth and Forest Computer Sciences, Technische Universitaet Dresden, Postfach 1117, 01735 Tharandt, Germany
[b] CIRAD, UMR CBGP, F-34398 Montpellier, France

ARTICLE INFO

Article history:
Received 30 September 2013
Received in revised form 15 September 2014
Accepted 22 September 2014
Available online 10 October 2014

Keywords:
Conceptual mangrove model
Individual-based model
KiWi model
Lightning strikes
Hurricanes
Structural indices

ABSTRACT

Disturbances play a crucial role in various forest ecosystems and represent major shaping forces in forest succession and spatio-temporal processes. In this study, we simulated different disturbance regimes using the individual-based mangrove forest model KiWi. Frequent small-scaled gaps caused by lightning strikes and rare medium-sized patches caused by hurricanes were produced with varying size, severity and frequency. Additionally, a mixed regime including both lightning strikes and hurricanes was simulated. All three scenarios produced the same tree mortality rate over the simulation periods. We analyzed the temporal and spatial variations in these disturbances, taking into account their homogenizing or heterogenizing effects on the forest structure of a simulated area of 25 ha. All disturbance regimes produced significantly more homogenizing effects on the spatial forest structure than an undisturbed scenario. The hurricane regime produced a temporal heterogenization of the forest structure, while the small-scaled frequent lightning strike gaps were not able to contribute to additional heterogeneity. This shows that the explicit implementation of the disturbances generates different forest structures. The simulation results were integrated into an existing conceptual model for mangrove forest dynamics.

1. Introduction

Natural disturbances can be defined as discrete events in time that disrupt either an entire ecosystem or parts of it (Pickett and White, 2005). Disturbances are common phenomena in different types of forest ecosystems; they influence the spatial and temporal patterns of landscapes (Seidl et al., 2011) and can take the form of fires (Ratz, 1995), high winds (Jeltsch, 1992) or insect attacks (Coley and Barone, 1996). The sum of single time-discrete disturbance events forming patches in time and space is referred to as the disturbance regime and affects the ecosystem at a landscape level (Jentsch et al., 2002). Disturbance characteristics differ in their temporal and spatial variation and can produce homogenizing or heterogenizing and synchronizing or desynchronizing effects on the forest ecosystem. A homogenizing process results in large areas of the forest being in the same developmental stage. In contrast, a heterogenizing process leads to different developmental stages (Otto, 1994). Synchronizing processes are characterized by forces that lead trees to have temporally similar conditions.

The spatial and temporal scales of the structure of a studied landscape play a crucial role in evaluating the impacts to the landscape caused by the disturbances (Paluch, 2007; White and Jentsch, 2001). On one hand, small and frequent disturbances may contribute to a diversified vertical and horizontal forest structure (i.e., diverse tree size structure and spatial tree arrangement), thus producing a heterogenizing effect. On the other hand, large disturbed forest stands that have been differentially affected by disturbances create a mosaic of homogenous patches in different successional stages (Paluch, 2007).

Mangrove forests are distributed along tropical and subtropical coastlines and experience several different types of natural disturbances, from single tree falls and lightning strikes on a very local scale to medium- and large-scale disturbances such as hurricanes (Ward et al., 2006). Duke (2001) developed a conceptual mangrove forest model of these processes, integrating forest development states and forest gap processes. Fromard et al. (2004) enhanced this model with forest-shaping large-scale sedimentological processes. These models still lack the ability to model disturbances of different sizes and to characterize the forest structure.

* Corresponding author. Tel.: +49 35203 38 31612; fax: +49 35203 38 31632.
E-mail addresses: juliane.vogt@forst.tu-dresden.de (J. Vogt), cyril.piou@cirad.fr (C. Piou), uta.berger@tu-dresden.de (U. Berger).

http://dx.doi.org/10.1016/j.ecocom.2014.09.008
1476-945X/

The worldwide distribution of lightning flashes (NASA, 2011) shows that hot spots occur along subtropical and tropical coasts that enclose mangroves; such areas can be found in the Caribbean, Central West-Africa and Southeast Asia. In mangrove forests, lightning strikes create small gaps formed by a cluster of dead trees (Whelan, 2005) and are assumed to form the majority of small gaps in this forest system in Florida (Feller and McKee, 1999). Additionally, hurricanes directly impact sub-tropical and tropical coastal areas (NOAA, 2011) and consequently mangrove forests. The impacts of a hurricane can range from the defoliation of trees (Roth, 1992) to stem breakage to the uprooting of larger areas (Imbert et al., 1996). The relationship between forest damage, wind speed and duration is very complex and leads to different responses of the trees (Boose et al., 1994). The extent of the damage to forests depends on different factors such as the intensity of the disturbance (categorized by the Saffir–Simpson Scale), the distance to the eye track (Imbert and Portecop, 2008), the exposition to dominant winds (Piou et al., 2006), the topography of the landscape and the solidity of the soil layer (Canham et al., 2010). The response of the forest itself depends on the characteristics of the individual trees that influence the impacts of the disturbance (Canham et al., 2010).

Disturbances may act as catalysts for the succession of mangrove forests. For example, lightning strike gaps in homogenous areas confer more natural conditions to plantations (Vogt et al., 2011). In contrast, disturbances can halt the progress of a forest in a confined succession cycle (Lugo, 1980); this often occurs with devastating events such as hurricanes (Smith et al., 1994). Interactions of different disturbance types of, e.g., hurricanes and lightning strikes are quite common in mangrove forests and may have either beneficial or adverse effects. Thus, regenerating lightning strikes gaps created prior hurricane events remained as green patches within hurricane affected sites (Smith et al., 1994). This can be explained by the lower tree height of the regenerating green patches, which is less impacted by the hurricane (Vogt et al., 2012). Furthermore, the regeneration might be accelerated after hurricanes when these remaining green patches act as seed sources. The small number of species in the forest and the exposition of these forests to large- and small-scale disturbances render the mangrove forests very interesting systems in which to analyze the effect of different disturbance regimes on forest structure. However, field studies are quite limited for this topic due to the inability to accurately age mangrove trees (Robert et al., 2011; Menezes et al., 2003), the context-dependent speed of development of the trees (Feller, 1995) and the temporal scales needed to assess the long-term effects of hurricanes (Knapp et al., 2012). These constraints limit the ability of researchers to formally infer the implications of disturbance regimes on the history of mangrove stands. In this context, simulation models are helpful tools for testing the effects and interactions of disturbance.

In a previous study, Piou et al. (2008) used a simulation model to analyze the effect of perturbation frequency and intensity on the species composition of the three main neotropical mangrove species (Berger and Hildenbrandt, 2000). This model was developed to analyze neotropical mangrove forest dynamics and was successfully used to investigate the secondary succession trajectories of mangroves in abandoned rice fields (Berger et al., 2006) and the influence of lightning strike gaps on a forest plantation (Vogt et al., 2011). The individual-based spatially-explicit characteristics of this model make it a good tool for generalizing our understanding of the effects of disturbances on spatially-driven processes.

In the present study, we use the same model to analyze the effect of different disturbance regimes on forest structure and to evaluate the homogenizing and heterogenizing effects of disturbances of different sizes and frequency. Disturbance regimes consisting of lightning strikes and hurricanes are considered typical for mangroves and present different spatially-explicit and temporal characteristics. One of the objectives of this study was to integrate the effect of disturbance size and frequency on the conceptual models developed by Duke (2001) and Fromard et al. (2004), describing the characteristics of mangrove forest structures with a dynamical approach. Because of the relatively poor tree species richness of these forests, we focused on a monospecific system with homogenous environmental conditions to simplify the understanding of disturbance regimes effects. We also simulated a combined disturbance regime considering both disturbance types to check for potential non-linear interactions.

2. Material and methods

2.1. Model description

To analyze the effect of lightning strike gaps and hurricanes on mangrove forest structure we used the KiWi model, an individual-based spatially-explicit mangrove model developed by Berger and Hildenbrandt (2000). More specifically, we were interested in evaluating the homogenizing and heterogenizing effects of both disturbance types. As the effect of perturbation frequency and intensity on the species composition were analyzed in another study (Piou et al., 2008), we considered here a one-species system of *Rhizophora mangle*.

The model explicitly described individual trees that established, grew and eventually died of natural mortality. Each tree was characterized by its stem position in the simulation area (x,y), its age, its DBH (diameter at breast height), its height H and a scalar Field of Neighborhood (FON) that simulates inter-individual interactions. At each time step, the interaction level of trees was updated through the FON approach.

2.1.1. Plant interaction and growth

Trees interacted through their FON, and the growth of competing trees was reduced accordingly. The FON describes inter-individual spatial explicit competition for focal trees sharing resources with neighbors (Berger and Hildenbrandt, 2000).

The radius of the area considered for FON increased with DBH following:

$$R_{\mathrm{FON}} = a \times \left(\frac{\mathrm{DBH}}{2}\right)^{b} \qquad (1)$$

where a and b were scaling factors (Table 1). The optimal tree growth was calculated from the stem diameter increase over time:

$$\frac{\Delta \mathrm{DBH}}{\Delta t} = \frac{G \times \mathrm{DBH} \times (1 - \mathrm{DBH} \times \mathrm{H})/(\mathrm{DBH}_{\max} \times H_{\max})}{274 + 3 \times b_2 \times \mathrm{DBH} - 4b_3 \times \mathrm{DBH}^2} \times cF(\mathrm{comp}) \qquad (2)$$

where G, b_2, b_3, $D_{\max}$ and $H_{\max}$ were constants (Table 1), and H was the height of an individual tree. This equation ensured that tree grew asymptotically toward $\mathrm{DBH}_{\max}$ in function of competition. The tree height was calculated from the relationship $\mathrm{H} = 137 + b_2\mathrm{DBH} - b_3\mathrm{DBH}^2$ (Shugart, 1984). The cF(comp) was a correction factor reducing optimal growth under the influence of neighborhood competition (F_A) and computed as follows:

$$cF(\mathrm{comp}) = \left(\frac{1 - F_A}{\mathrm{shadTol}}\right) \qquad (3)$$

where ShadTol was a constant representing the shade tolerance of the simulated species. FA was computed for each kth tree as the mean value of the aggregate field strength F produced by all other trees on the tree's area A: