Estimating gap lifetime and memory from a simple model of forest canopy dynamics

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ABSTRACT

Gap formation and closure represent important disturbance events in forests, but the processes involved are still poorly understood. We use models, which we and others previously developed, to make long-term predictions of tropical forest gap dynamics based on Barro Colorado Island data. We first fit the models to the data by comparing their discrete Fourier transforms, and we propose a definition for the lifetime of a gap and predict a large-gap lifetime typically to be less than 50 years. We find that the gap lifetime diverges logarithmically for large-gap sizes. We examine the 'memory' of spatial gap patterns via spatiotemporal correlations and find a correlation time of about 160 years, suggesting that present gap patterns could have long-lasting effects on forest spatial patterns.

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1. Introduction

In recent decades, canopy gaps in rainforests have been considered to be one of the key factors involved in the recruitment and growth of seedlings, and in the ability of these forests to support their great diversity of species (Schnitzer and Carson, 2001; Zhu et al., 2003; Menges et al., 2008). The study of gap dynamics in ecology is not new (Watt, 1947), but still today ecologists continue to question the mechanisms and patterns generated by gap disturbances (e.g., Jansen et al., 2008; Kellner and Asner, 2009). As the importance of canopy gap dynamics becomes better understood, and data more readily available, models of these dynamics will become increasingly useful to predict the effects of logging, climate change, natural disasters, and other sources of disturbance.

Although several attempts to model rainforest gap dynamics have been made (e.g., Kubo et al., 1996; Manrubia and Solé, 1997; Alonso and Solé, 2000; Pagnutti et al., 2007), most studies analyze and fit only current data and have had various degrees of success in doing so. These models have, however, not been used to make long-term predictions about forest gap dynamics. Indeed, Kubo et al. (1996) derived the global and local densities of a stationary state of their model. However, there are dynamical processes taking place on all spatial scales within this stationary state. Although the gap densities

and distributions are stationary, the gap pattern changes with time. These are the dynamics that interest us in this paper.

Pagnutti et al. (2007) introduced a model, called the transition expansion model (TEM), capable of capturing the structure and dynamics observed in the gap pattern on the Barro Colorado Island (BCI) (Hubbell and Foster, 1986; Satake et al., 2004). Here we use the TEM model to make long-term predictions about the BCI gap dynamics that are not easily measured in the field due to the time required to get reliable statistical data. More specifically, we estimate the maturation time for a rainforest starting from a state that is far from equilibrium, and propose a definition for the lifetime of a gap, which we calculate as a function of the gap's initial size. To the best of our knowledge, no previous modelling studies have given estimates of gap lifetimes. We note that the gap lifetime is not equivalent to gap age (time since gap formation), which is a variable that is equally difficult to measure in the field, particularly in tropical forests (Iwasa, 1995). We also calculate a spatiotemporal correlation function that allows the prediction of the amount of time for which the gap-gap correlations persist at a given distance. We loosely refer to this amount of time as the *memory* of the gap pattern.

2. Methods

2.1. Review of the TEM model

The TEM model is a cellular automaton that was designed to reproduce the BCI gap dynamics. Cells are either gaps or non-gaps. At

each time step, gaps may become non-gaps and non-gaps may become gaps according to the rules specified below. The novel feature of TEM is that it allows single-cell disturbances to propagate within a single time step. TEM was shown to reproduce many different aspects of the observed data with very good accuracy (Pagnutti et al., 2007). In Section 2.2 we will offer yet another, albeit more powerful, fit of the model to the data in the form of a discrete Fourier transform (DFT). The excellent agreement between the TEM model results and the BCI data gives credibility to the use of TEM (as compared to the KIF model; Kubo et al., 1996) to make long-term predictions about rainforest gap dynamics, which is the main purpose of this paper.

It is important to note that a gap is defined here, as in most cases in ecology, as a relatively lower local average height of trees in the canopy (Brokaw, 1982a). The BCI data provided by Hubbell and Foster (1986) represents a two-dimensional horizonal slice of the canopy, where gaps are areas with canopy height less than 20 m. The TEM and KIF models simulate the canopy dynamics across this slice, so they are effective two-dimensional models. The problem of modelling the full three-dimensional structure is a much more challenging problem and will not be addressed here. Solé et al. (2005) studied the gap-size distribution in the BCI data for several slices taken at different heights, thereby probing the three-dimensional canopy structure.

For convenience, we restate the rules of the TEM model here. For more detail see Pagnutti et al. (2007). This model reads as:

(i) Gap formation: $1 \to 0$ occurs with probability $d + n(0)\delta/z$, where $n(0)$ is the number of neighbouring cells in the gap state, and z is the number of neighbouring cells. The parameter d initiate random gap formation events, and δ accounts for susceptibility to windthrow at gap edges.

(ii) Gap closure: $0 \to 1$ occurs with probability $b + n(1)\beta/z$, where $n(1)$ is the number of neighbouring cells in the non-gap state. The parameter b creates random gap closure events due to vertical growth across the gap/non-gap height threshold, and β accounts for the outward growth of mature trees.

(iii) Gap formation expansion: if a given cell (i,j) undergoes the transition $1 \to 0$, then all of its non-gap neighbours undergo the same transition with probability $d_e + n(0)\delta_e/z$. Here $n(0)$ is calculated using the neighbourhood of the non-gap neighbour of (i,j).

(iv) Gap closure expansion: if a given cell undergoes the transition $0 \to 1$, then all of its gap neighbours undergo the same transition with probability $b_e + n(1)\beta_e/z$. Rules (iii) and (iv) account for the possibility that a single disturbance event may affect an area larger than one cell.

Using this model we were able to fit many aspects of the observed data (power-law scaling exponent of gap-size distributions, local and global densities of gaps, spatial correlation function, neighbourhood dependence of gap formation) provided that the parameters were set equal to the values given in Table 1. Like in Pagnutti et al. (2007), we will compare the results of the TEM model to those obtained using the KIF model (Kubo et al., 1996), which is obtained by setting the parameters to the values in Table 1. The values of these parameters were chosen by coarsely scanning regions of the parameter spaces of the models to find parameter values that roughly reproduce the gap-size distribution, and the global and local densities of gaps, gap closures and gap formations. Finer adjustments to the parameters were made by trial and error to improve on the fits, and to reproduce the other aspects of the data reported in Pagnutti et al. (2007). The main difference between the TEM and KIF models is that, in KIF, rules (iii) and (iv) are turned off, so it does not allow disturbance events to propagate within a given time step. We also compare our results to a NULL model, in which all local interactions are turned off. The parameters used in the NULL model are given in Table 1. The values

Table 1
Parameter values used for the models.

	TEM	KIF	NULL
d	0.003	0.008	0.146
δ	0.221	0.353	0
b	0.003	0.008	0.100
β	0.336	0.370	0
d_e	0.005	0	0
δ_e	0.400	0	0
b_e	0.011	0	0
β_e	0.210	0	0

for b and d were chosen to fit the power-law gap-size distribution as well as the global density of gap formations and closures observed in BCI. Note, however, that it is not possible to simultaneously fit the gap-size distribution and gap density using the NULL model. We compare these three models in order to observe the effects that the strength of local interactions has on the spatiotemporal gap dynamics.

2.2. Model fitting: discrete Fourier transform

Before we can use the TEM model to predict the spatiotemporal dynamics of the BCI gap pattern, we should ensure that it can reproduce the short-term dynamics that have already been observed. Pagnutti et al. (2007) used TEM to reproduce many different aspects of the data. Here we offer another more powerful test of the fit of the model to the data: the DFT. In short, the DFT transforms a spatial pattern into a spectrum of frequencies. This spectrum, in a sense, quantifies the spatial structure of the pattern. The DFT test for the fit of the model to the data offers several advantages over those used previously (Kubo et al., 1996; Manrubia and Solé, 1997; Satake et al., 2004; Pagnutti et al., 2007). First, it allows us to compare the gap patterns as a whole, rather than comparing very specific aspects of the data (e.g., the global and local densities of gaps). Also, using the DFT we can compare single snapshots of gap patterns and get good insight into the patterns' similarities and differences without resorting to averaging over long times or over many configurations. Although the averaging process is not difficult in a simulated environment, it is not convenient when doing field observations due to the time required in order to get good statistics. For this reason we think that the DFT is the best way to check if simulation results fit the field observations directly.

The DFT is defined by

$$F(k,l) = \frac{1}{MN} \sum_{x=0}^{M-1} \sum_{y=0}^{N-1} f(x,y) \exp\left[-2\pi i \left(\frac{kx}{M} + \frac{ly}{N} \right) \right], \quad (1)$$

where M and N are the numbers of cells along the length and width of the map respectively, and $f(x,y) = 1$ for a gap at the cell (x,y) and zero otherwise, and i is the imaginary unit. The function $F(k,l)$ is complex-valued, so it can be schematically represented as $F = |F|e^{i\theta}$ where r is the magnitude of F and θ is its phase. The phase of F is usually only required when one wishes to reconstruct the original image from the DFT. Since we will not need to reconstruct the original spatial images, we will only be interested in the magnitude of F. To calculate the magnitude, simply replace i with $(-i)$ in F to find the complex conjugate F^*; the magnitude is calculated as $|F| \equiv \sqrt{F^*F}$. When we refer to the DFT, we will always mean the magnitude of F, i.e. we use $F \equiv |F|$ and ignore the phase altogether. The value of $F(0,0)$ turns out to be the global density of gaps. This value has been calculated explicitly in Pagnutti et al. (2007). Since it is by far the dominant component of the DFT, it makes the remainder of the function look flat