Propagation of local interactions create global gap structure and dynamics in a tropical rainforest

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Abstract

Gap dynamics in tropical forests are of interest because an understanding of them can help to predict canopy structure and biodiversity. We present a simple cellular automaton model that is capable of capturing many of the trends seen in the canopy gap pattern of a complex tropical rainforest on the Barro Colorado Island (BCI) using a single set of model parameters. We fit the global and local densities, the cluster size distributions, and two correlation functions, for gaps, gap formations, and gap closures determined from a spatial map of the forest (1983–1984). To the best of our knowledge, this is the first report that the cluster size distributions of gap formations and closures in the BCI are both power laws. An important element in the model is that when a transition from gap to non-gap (closure), or vice versa (formation), occurs, this transition is allowed to expand into adjacent cells in order to make different cluster sizes of transitions. Model results are in excellent agreement with reported field data. The propagation of local interactions is necessary in order to obtain the complex dynamics of the gap pattern. We also establish a connection between the global and local densities via the neighborhood-dependent transition rates and the effective global transition rates.

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1. Introduction

It is widely accepted in ecology that canopy gaps, which are low-level or open canopy areas, promote seedling recruitment, growth, and diversity among plant communities in forests (Canham, 1988; Hubbell et al., 1999; Schnitzer and Carson, 2001). A knowledge of gap dynamics in forests is thus important to understand forest ecology, and to effectively manage timber resources (Coates and Burton, 1997). Studies have shown that, although the growth rate of trees is highest in large gaps and clear-cut areas (Canham, 1988; Coates, 2000), both recruitment and survival rates are highest in mid-sized gaps (Coates, 2002; Paul et al., 2004; Zhu et al., 2003). This suggests that an accurate model of gap distribution would be useful in the formulation of optimal cutting and conservation strategies. A large majority of gap formation is caused by windthrow and windsnap. Other less frequent causes include limbfall, lightning, disease, and structural collapse due to epiphytes (Lawton and Putz, 1988; Worrall et al., 2005). Gaps recover to the canopy state via growth of new trees and branch extension (gap closure). Gaps are usually found to be aggregated and new gaps are likely to form adjacent to pre-existing gaps (Hubbell and Foster, 1986; Lawton and Putz, 1988; Runkle, 1984). This is consistent with the observation that gap expansion, which is caused by increased susceptibility to windthrow at gap edges, is more frequent than gap initiation, which is usually caused by disease, parasites, lightning, etc. (Worrall et al., 2005). Gap densities differ for different forest types. These densities display temporal variations, but are more or less...
constant over time. The gap size frequency distribution in many forests is well fit by a power law (Hubbell and Foster, 1986; Satake et al., 2004; Tanaka and Nakashizuka, 1997), and Solé and Manrubia (1995) suggested that a tropical rainforest is close to a critical state. No studies to date have considered the distributions of the gap disturbance events (for example, gap formation and closure). Previous attempts to model gap densities and size distributions did not succeed because the gap densities could not be fit when the power-law gap size distribution was fit and vice versa (Katori et al., 1998; Kubo et al., 1996; Solé and Manrubia, 1995; Manrubia and Solé, 1997; Pagnutti et al., 2005; Schlicht and Iwasa, 2004). Different sets of model parameters were required to reproduce each aspect of the data.

The focus of this work is to introduce a model that can simultaneously fit both the global and local densities of gaps (defined in Table 1) as well as the gap size distribution observed on the Barro Colorado Island (BCI) (Fig. 1(a)) using a single set of model parameters. Each square in Fig. 1(a)–(c) represents a 5 x 5 m² area. Gaps (0) are defined to be areas where the vegetation height is lower than the gap height threshold \( h_{th} = 20 \text{ m} \). Non-gaps (1) have a canopy above the threshold. Black indicates cells that were in the gap state for both years. This transition \( f \) is denoted by \( q \). Green indicates cells that were in the non-gap state for both years (i.e. \( 1 \rightarrow 1 \) transition denoted by \( n \)). Yellow indicates cells that were in the gap state in 1983 and in the non-gap state in 1984 (gap closure transition \( 0 \rightarrow 1 \) denoted by \( c \)). Red indicates cells that were in the non-gap state in 1983 and in the gap state in 1984 (gap formation transition \( 1 \rightarrow 0 \) denoted by \( f \)). In this paper, we use the term “transition” to refer to events of gap formations and/or gap closures. Our model is an extension of the KIF model (Kubo et al., 1996) with rules added to cause gap formations and closures to form in clusters. We also find that for the BCI, in addition to the gap size distribution, the distributions of gap formation and closure sizes are also fit by power laws. We discuss this later.

Many models of forest dynamics incorporate a striking level of ecological, biological, and physical detail (Bragg et al., 2004; Chave, 1999; Porté and Bartelink, 2002). Some of these models focus on interspecific interactions and environmental effects (e.g. habitat heterogeneity and light gradients). Some studies suggest that, although these factors are important among seedlings and saplings, they are not important to gap dynamics at the canopy level. For example, Hubbell et al. (2001) showed that total local stem density is more important than local conspecific density or local species richness when determining the survival probability of individual trees. Uriarte et al. (2004) devised a model to assess the importance of the specific identity of neighbors to sapling growth. They found that most species did not respond to the identity of neighbors (i.e. all species have the same effect), but the degree of crowding had a significant effect. Condit et al. (2000) found that most tree species have clustered spatial distributions, but Hardy and Sonké (2004) determined that limited dispersal and not habitat heterogeneity affected the clustering of species. Brokaw and Busing (2000) showed that gaps are filled by chance occupants rather than by best suited species, suggesting that chance is more important than niche partitioning to the maintenance of diversity. Harms et al. (2001) found that local habitat specialization plays only a limited role in the maintenance of species diversity. While recruitment seems to be significantly affected by light gradients, growth and survival, which are more important at the canopy level, are much less sensitive (Coates, 2000, 2002; Zhu et al., 2003). Dalling et al. (2004) found little evidence for niche partitioning along a gradient of gap sizes. Since species distinction and habitat structure are not likely to be important to gap dynamics at the canopy level, we use a model involving a single species in a homogenous environment.

2. Methods

In Section 2.1 we digitize the data in Fig. 1(a) taken from Satake et al. (2004) and calculate the densities, distributions, and correlation functions. Section 2.2 describes models that have had some success in fitting the BCI data (Solé and Manrubia, 1995; Manrubia and Solé, 1997; Pagnutti et al., 2005), but we prove that they are not sufficient to fit the data used in this work. In Section 2.3 we extend the KIF model (Kubo et al., 1996) to account for observations made from the data.

Table 1

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Name</th>
<th>Definition</th>
<th>Neumann</th>
<th>Moore</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \rho_0 )</td>
<td>Global density of gaps</td>
<td>The total fractional area of gaps</td>
<td>0.33</td>
<td>0.33</td>
</tr>
<tr>
<td>( q_0 )</td>
<td>Local density of gaps</td>
<td>The average fractional area of gaps among neighboring sites of gaps</td>
<td>0.63</td>
<td>0.39</td>
</tr>
<tr>
<td>( q_1 )</td>
<td>Local density of non-gaps</td>
<td>The average fractional area of non-gaps among neighboring sites of non-gaps</td>
<td>0.82</td>
<td>0.80</td>
</tr>
<tr>
<td>( \rho_f )</td>
<td>Global density of gap formations</td>
<td>The total fractional area of gap formations</td>
<td>0.059</td>
<td>0.059</td>
</tr>
<tr>
<td>( \rho_c )</td>
<td>Global density of gap closures</td>
<td>The total fractional area of gap closures</td>
<td>0.066</td>
<td>0.066</td>
</tr>
<tr>
<td>( q_f )</td>
<td>Local density of gap formations</td>
<td>The average fractional area of gap formations among neighboring sites of gap formations</td>
<td>0.23</td>
<td>0.20</td>
</tr>
<tr>
<td>( q_c )</td>
<td>Local density of gap closures</td>
<td>The average fractional area of gap closures among neighboring sites of gap closures</td>
<td>0.16</td>
<td>0.14</td>
</tr>
</tbody>
</table>

The subscript 0 refers to gaps, which are the transitions \( g \) and \( f \), and 1 refers to non-gaps, which are \( n \) and \( c \). Local densities were calculated using a von Neumann neighborhood and a Moore neighborhood.
2.1. Spatiotemporal forest data analysis

Hubbell and Foster (1986) constructed maps of a 50 ha plot on BCI, which were later presented, as shown in Fig. 1(a), by Satake et al. (2004). Gaps are defined to be areas where the vegetation height is less than the gap threshold height \( h_{th} = 20 \text{ m} \). A 5 m \( \times \) 5 m spatial grid is used over a 1000 m \( \times \) 500 m area. The cellular form of the data warrants the use of a cellular automaton to model the gap dynamics. We digitally processed the data (Fig. 1(a)) in order to calculate the observed densities, cluster size distributions, and correlation functions of gaps, as well as gap formations and closures. Table 1 defines the various densities of gaps and gap transitions (i.e. gap formation and closure). Some of the densities were previously calculated by Kubo et al. (1996); however, they used data from 1983 and a von Neumann neighborhood to calculate the local densities. We take the values from 1984 and use periodic boundary conditions and use both von Neumann and Moore neighborhoods and obtain slightly different results. In general, for a cell having made the transition \( x \) (where \( x \) assumes the index 0, 1, \( f \), or \( c \)), \( q_x > \rho_x \) indicates that cells of that type are clustered, and \( q_x < \rho_x \) indicates that these cells are dispersed more than what is predicted by chance. The case \( q_x \approx \rho_x \) implies a random distribution (Kubo et al., 1996). For a system fluctuating about equilibrium, we should have \( \rho_f \approx \rho_c \) on average. The probability that a given non-gap cell will become a gap depends linearly on the number of neighboring gap cells \( n(0) \) (Moore neighborhood) as \( P_f = P_f[n(0)] = 0.029 + 0.296n(0)/8 \). Likewise, the probability that a gap cell will close is \( P_c = P_c[n(1)] = 0.045 + 0.384n(1)/8 \), where \( n(1) \) is the number of neighboring non-gap sites. These regression lines were calculated by Satake et al. (2004). We may define the effective gap formation and closure rates to be \( R_f = \rho_f/(1 - \rho_0) = 0.090 \) and \( R_c = \rho_c/\rho_0 = 0.20 \), respectively. Now we take \( avg(n(0))/8 = q_{0/1} \) to be the average local density of gaps among non-gaps, and \( avg(n(1)/8) = q_{1/0} \) to be the average local density of non-gaps among gaps. We may write \( q_{0/1} = 1 - q_f \) and \( q_{1/0} = 1 - q_c \). If we plug these into the expressions for \( P_f \) and \( P_c \), we find that \( P_f \approx R_f \) and \( P_c \approx R_c \) within 1%. This is significant because it suggests that a Moore neighborhood interaction should suffice in order to obtain the global dynamics of the BCI. For example, if we repeat the above analysis using the von Neumann neighborhood we find that \( P_f \approx 0.07 \) (22% error) and \( P_c \approx R_c \), so the effective gap formation rate is underestimated.

The local density \( q_x \) defines the Moore neighbor correlation among cells having made the transition \( x \) (where \( x \in \{0, f, c\} \)). We extend this definition beyond the Moore neighbors by defining the correlation function \( C_x(r) \) to be the fraction of cells having made the transition \( x \) at a distance \( r \) from a focal cell having made the same
transition. This may be written as

$$C_x(r) = \frac{1}{|S_r|} \sum_{i=1}^{|S_r|} \rho(r) \rho(r_i),$$

(1)

where $S_r$ is the set of cells at a distance $r = |r_i - r'|$ from a focal cell located at $r'$, and $r_i$ is the position of the $i$th cell in the set $S_r$. The function $\rho(r) = 1$ for a cell at $r$ having made the transition $x$, and $\rho(r) = 0$ otherwise. Eq. (1) is the same as that used by Manrubia and Sole (1997), except that we use the normalization factor $1/|S_r|$ and they use $1/(|S_r|\rho_c)$. The function $C_x(r)$ is taken to be the average over all cells having made the transition $x$. We expect that $C_x(0) = 1$ and $C_x(1) = q_c$ for a Moore neighborhood, and also that $\lim_{r \to \infty} C_x(r) = \rho_c$ because at large distances where correlations disappear we expect to see the global (average) density. We also calculate another correlation function $G_x(r)$ defined in the same way as $C_x(r)$ but with the added restriction that correlated cells must be part of the same cluster. This definition can be found in Stauffer and Aharony (1992) within the context of percolation theory.

The gap size distribution, the gap formation size distribution, and the gap closure size distribution are all well fit by power laws, $p(k_x) \sim k_x^{-\alpha}$ (with scaling exponents, $\alpha_x \approx -1.6$, $\alpha_y \approx -2.1$, $\alpha_z \approx -2.8$, and maximum cluster sizes of about 1400, 30, 15, respectively. To the best of our knowledge, this is the first report that the distributions of the sizes of gap formation and closure events themselves (i.e. the gap formation pattern (red in Fig. 1) and the gap closure pattern (yellow in Fig. 1)) are power laws. The distributions, as well as the correlation functions, are important to characterize the pattern because they contain information about gaps and transitions at all scales, and not just at the global and local scales.

2.2. The need for a new model

We have mentioned that previous attempts to model the BCI dynamics did not succeed because different sets of parameters were used to fit both the densities and distributions. One set of parameters were used to fit the gap densities, and a different set was used to fit the distribution of gap sizes, but a single parameter set that reproduces both the densities and distribution could not be found. A model introduced by Sole and Manrubia (1995) called the forest game (FG) was able to reproduce several characteristics of the BCI data for a different gap height threshold of $h_{th} = 10$ m, but it was less successful in fitting the data described in the previous section (Manrubia and Solé, 1997; Pagnutti et al., 2005). Katori et al. (1998) and Schlicht and Iwasa (2004) used the Ising model to fit the gap size distribution for a threshold of 20 m. Although they improved the fit significantly, Schlicht and Iwasa give reasons why the Ising model is not a good model for forest gap dynamics. In this section we show, by calculating the phase diagram of the modified version of the FG model used by Pagnutti et al. (2005), that this model cannot reproduce the observed BCI data (gap densities and distributions) for a gap height threshold of $h_{th} = 20$ m using a single set of parameters. This justifies the need for a new model.

The FG model is characterized by four parameters: the birth rate $b$, the death rate $d$, the competition parameter $\gamma$ between neighboring trees, and the gap height threshold $h_{th}$, which is the height below which cells are considered to be gaps. For a detailed description of the FG model see Sole and Manrubia (1995). In Fig. 2(a)–(c) we show slices of the phase diagram for the FG model where we vary $b$ and $d$ while we hold $\gamma$ and $h_{th}$ fixed. At equilibrium the system displays one of the four distinct behaviors. The system is said to be in a state of percolation when there exists a gap cluster that extends from one end of the map to the other. Points in the phase diagram where the system is always in a state of percolation at equilibrium are colored in black (percolation). Points where the system is sometimes in a state of percolation are colored in blue (quasi-critical). Green (clustering) points indicate that there is no percolation, but significant clustering of gaps (i.e. $q_0 > \rho_0$). Red (non-clustering) indicates no percolation and no clustering of gaps ($|q_0 - \rho_0| < 0.05$). We ran a simulation using a $100 \times 100$ cell map for each point in the phase diagram for 1500 time steps. Equilibrium was reached within 1000 time steps for all parameter configurations. We monitored the system for the last 500 time steps by calculating the densities and the probability of gap percolation (i.e. the number of time steps where percolation is observed divided by 500). From percolation theory (Stauffer and Aharony, 1992) we expect that, in the case of an infinite lattice, the transition from the state of percolation to a state of non-percolation occurs at a well-defined surface in the phase diagram. Due to the finiteness of the lattice used in the simulation, the crossover surface becomes fuzzy.

Fig. 2(e) shows an example of the crossover from the percolation (black) state to a non-percolation (red) state. In Fig. 2(e) the probability of percolation is defined to be the number of time steps within which percolation was observed, divided by the total number of time steps within the observation period (Kubo et al., 1996). The crossover is the quasi-critical (blue) region in which the percolation (black) and non-percolation (green or red) regions overlap. It is in this region where the gap size distribution is scale invariant (i.e. power law). Clearly, in order to have scale invariance and gap clustering occurring simultaneously (i.e. for a single set of parameters), as in the BCI, we must have an overlap between the quasi-critical (blue) and clustering (green) regions. This only occurs if we have small $h_{th}$ and large $\gamma$ (Fig. 1(c)). However, at the blue–green boundary we cannot fit the correct BCI densities, $\rho_0 = 0.33$ and $q_0 = 0.63$. In Fig. 2(d) we show the global and local von Neumann densities of gaps for the same slice of the phase.
diagram as in (c). The square mesh and contour lines are colored to represent the value of the local density for any given values of $b$ and $d$. The solid color gradient under the mesh and contour lines represent the global density. The solid black lines in (d) delimit the quasi-critical (blue) region in (c). The vicinity of the thicker black line corresponding to the boundary between the quasi-critical (blue) and clustering (green) regions is where we have gap clustering $q_0 > \rho_0$ and scale invariance occurring simultaneously in the gap pattern. Around this line we have $q_0 \approx 0.6$ and $\rho_0 \approx 0.55$, so the local density is well fit, but the global density is not. In fact the local density is fit near the yellow contour line in Fig. 2(d), which is close to the thick black line, so scale invariance and the local density can be fit simultaneously. We can fit the global density only if we stray from the thick black line, but then we lose scale invariance. The global density ($\rho_0 \approx 0.3$) is fit near the magenta curve in Fig. 2(d), far from where the yellow contour line (for $q_0$) and the thick black line (for scale invariance) coincide. Thus the FG model cannot be used to fit all of the data. In the next section we introduce an alternative model capable of capturing the observed densities and distributions simultaneously.

Kubo et al. (1996) used a different model called KIF to illustrate an approximation technique and applied it to the BCI data. In the KIF model, each cell may be a gap (0) or a non-gap (1). At each time iteration, a gap becomes a non-gap with probability \[ b + n(1)\delta/z \] where $n(1)$ is the number of non-gap neighbors surrounding the original gap, and $z$ is the total number of neighbors. A non-gap becomes a gap with probability \[ d + n(0)\delta/z \] where $n(0)$ is the number of gap neighbors surrounding the original non-gap. The KIF model was made to explicitly account for the functions $P_f = P_f[n(0)]$ and $P_c = P_c[n(1)]$; however, the data for $P_c$ were not available at the time Kubo et al. introduced the model. The parameters that they used give poor fits to the densities $\rho_0 = 0.36$ and $q_0 = 0.44$, and the gap size distribution (Manrubia and Solé, 1997) was more like an exponential decay than a power law. We did an analysis similar to that in Fig. 2 for KIF and found again that no set of parameters gives the densities and distributions simultaneously.

Fig. 2. Two-dimensional slices of the phase diagram $\{b, d, \gamma; h^b\}$ for the FG model. (a) $\gamma = 0.01, h^b = 20 \text{ m}$. The yellow horizontal line indicates $b = 0.3$, and the yellow vertical lines indicate the region where the probability of percolation is between 0 and 1 in (e). (b) $\gamma = 0.01, h^b = 0 \text{ m}$. (c) and (d) $\gamma = 1.0$, $h^b = 0 \text{ m}$. (e) Probability of percolation as a function of the parameter $d$ with $b = 0.3, \gamma = 0.01, h^b = 20 \text{ m}$. In (d) the solid surface is the global density $\rho_0$ and the mesh and contour are the local density $q_0$. 
2.3. Transition expansion model (TEM)

The TEM is an extension of the KIF model (Kubo et al., 1996). It is a cellular automaton, which consists of a Euclidean space divided into cells ($5 \times 5$ m$^2$), each of which may be in one of two states (gap (represented by the value 0) and non-gap (represented by the value 1)) at a given time. Note that we disregard the actual height of the canopy, and focus only on whether a cell is a gap or a non-gap. We assume that these states arise solely through the processes of gap formation and closure. Every cell is updated simultaneously in discrete time iterations according to a set of transition rules that depend on the model parameters and the current states of the cell and its neighbors.

(i) **Gap formation**: $1 \rightarrow 0$ occurs with probability $d + n(0)\delta/d + n(1)\beta/z$, where $n(0)$ is the number of neighboring cells in the gap state. The parameter $d$ models low-rate random gap formation events that initiate new gaps (e.g. lightning, disease), and the $\delta$ term accounts for the increased susceptability to windthrow at the edge of gaps. Kubo et al. (1996) called $d$ the independent gap formation rate and $\delta$ the neighbor-dependent gap formation rate.

(ii) **Gap closure**: $0 \rightarrow 1$ occurs with probability $b + n(1)\beta/z$, where $n(1)$ is the number of neighboring cells in the non-gap state. The parameter $b$ models gap closure due to the vertical growth of a tree across the gap threshold height during 1 year. The $\beta$ term arises due to the fact that mature canopy branches may extend horizontally into the adjacent gap areas. Also, as much as 85% of new crowns emerge from the low brush canopy in gaps are found within 5 m of the gap edge (Paul et al., 2004). Kubo et al. (1996) called $b$ the independent gap closure rate and $\beta$ the neighbor-dependent gap closure rate.

(iii) **Gap formation expansion**: If a given cell $(i,j)$ undergoes the transition $1 \rightarrow 0$, then all of its non-gap neighbors undergo the same transition with probability $d_e + n(0)\delta_e/z$. Here $n(0)$ is calculated using the neighborhood of the non-gap neighbor of $(i,j)$. The parameter $d_e$ models the possibility that the falling crown is larger than one cell, i.e. $5 \times 5$ m$^2$ as seen in Fig. 1(d). The chances of gap formation increase if other crown elements are exposed to wind, hence the $\delta_e$ term. It has also been observed that tree deaths can produce “domino effects” over several months (Lin et al., 2004) implying that the effects of gap formation may persist after the event and range beyond its proximity. This is likely to occur because the underground disturbance weakens surrounding root systems (Casper et al., 2003). It is for this reason that we must distinguish the $\delta$ and $\delta_e$ parameters.

(iv) **Gap closure expansion**: If a given cell undergoes the transition $0 \rightarrow 1$, then all of its gap neighbors undergo the same transition with probability $b_e + n(1)\beta_e/z$. This rule accounts for the possibility that a growing crown is larger than one cell.

The TEM model is illustrated in Fig. 3 using a small example. The reader should note that rules (iii) and (iv) are defined recursively. In other words, if one of the rules is satisfied at a given site, then the same rule is re-applied to the neighbors of that site. The idea of recursive rule applications has been implemented previously (Drossel and Schwabl, 1992; Alonso and Solè, 2000; Wootton, 2004; Guichard et al., 2003). In Drossel and Schwabl’s model, the propagating disturbance is the spreading of forest fires. Alonso and Solè’s model incorporates gap formation propagation much like TEM; however, they consider the pattern of different tree species and do not focus on the gap pattern. Wootton and Guichard et al. created models of mussel bed dynamics in which disturbances can propagate via byssal threads that connect mussels in different clusters. It should be pointed out that multiple events cannot occur in a given cell during a single time step. Once a cell undergoes a transition at a given time step, that cell is no longer considered by any of the rules for the remainder of the time step.

We added the rules (iii) and (iv) as mechanisms for clustering both types of transitions, namely, gap formations and gap closures. Fig. 1(a) and (d) illustrate the clustering and thus that this is necessary to model the observed dynamics. We also considered the TEM model in the absence of recursion. In this case a transition due to rule (i) or (ii) may expand into the Moore neighborhood, but not beyond. The results from this model were quite good, but we chose to report on the recursive TEM model because it gives slightly better results than the non-recursive version. In the absence of rules (iii) and (iv), TEM reduces to the KIF model. In the following sections

![Illustration of the TEM model using a 5 x 5 cell example. Green squares are non-gaps and black squares are gaps. Red squares indicate possible gap formations. Consider applying the TEM model rules to the centermost cell. Since this cell is a non-gap, we are interested in gap formation. Gap formation (1) occurs with probability $d + 5\delta/z$ because there are 5 neighboring gaps. If (1) occurs, then the candidates (2), (3), and (4) may form gaps immediately (within the same time step) with probabilities $d_e + 5\delta_e/z$, $d_e + 4\delta_e/z$, and $d_e + 5\delta_e/z$, respectively. If (2) occurs, then (5) occurs with probability $d_e + 6\delta_e/z$. If (3) occurs, then (6) occurs with probability $d_e + 5\delta_e/z$. Note the use of periodic boundary conditions for (5) and (6). The process continues until either there are no more non-gap neighbors or the rule has failed for the last remaining candidates.](image)
we compare the results obtained using the TEM and KIF models to fit the BCI data.

The KIF model can be parameterized using the data because it explicitly accounts for the functions $P_f = P_f[n(0)]$ and $P_f = P_f[n(1)]$. Thus, we infer the parameters $b = 0.045$, $d = 0.029$, $\beta = 0.384$, $\delta = 0.296$ (Satake et al., 2004). However, using these parameters the global and local densities of gaps in KIF are $p_0 \approx 0.2$ and $q_0 \approx 0.3$, respectively, and are thus much smaller than the observed values, 0.33 and 0.59, respectively. Also, the gap size distribution in KIF is a power law with scaling exponent $-2.2$ and maximum cluster size of about 50, very different from the observed values, $-1.6$ and 1400, respectively. As such, we needed to find a different parameter set that gives a better fit to the densities. In doing so for KIF we lose the agreement with the observed $P_f[n(0)]$ and $P_f[n(1)]$. We empirically explored the phase diagrams of TEM and KIF in order to fit the densities listed in Table 1. The parameter sets that fit the densities well are $P_{TEM} = \{b = 0.003, d = 0.003, \beta = 0.336, \delta = 0.221, b_e = 0.011, d_e = 0.005, \beta_e = 0.210, \delta_e = 0.400\}$, and $P_{KIF} = \{b = 0.008, d = 0.008, \beta = 0.370, \delta = 0.353\}$. We found these parameters using an educated guess and trial and error. Starting from some reasonable values of the parameters, we manually adjusted them and assessed the fit to the data after each adjustment until good accuracy was achieved. The aspects of the data that were of primary concern to the goodness of fit were the global and local densities. It is evident from the data that $b$ and $d$ need to be small because transitions far from gap edges are scarce. We arbitrarily chose $b = d = 0.003$ for TEM and 0.008 for KIF which are reasonable (small) values. For the same reason, $b_e$ and $d_e$ should be small for TEM. These parameters were mainly used for fine tuning, in order to fit the densities, after settling on values for the remaining parameters, $\beta$, $\beta_e$, $\delta$, $\delta_e$, which control most of the dynamics and hence have the largest values. It is likely that $P_{TEM}$ and $P_{KIF}$ are not the optimal parameters to fit the BCI data; however, as we will see they are very good. In order to find the optimal parameters, one would have to analyze the entire phase diagram of the model. This would be an extremely difficult task because there are eight parameters that would need to be varied, and the goodness of fit to the data would need to be assessed for every parameter configuration. Actually, Satake et al. (2004) showed that the parameters are not constant, but may fluctuate in time, so the exact values of the parameters used in the models are not extremely important. In this work we hold all of the parameters fixed. In TEM, the parameters $b$, $d$, $\beta$, and $\delta$ cause single transitions to occur, while the parameters $b_e$, $d_e$, $\beta_e$, and $\delta_e$ may cause a cascade of local aggregated transitions. The latter parameters are mainly responsible for controlling cluster sizes of gap formations and closures (transitions). For the parameters in $P_{TEM}$ we note that $\beta > \beta_e$ and $\delta < \delta_e$. Gap closure occurs in many small patches, so we have $\beta > \beta_e$ but gap formation occurs in larger patches, hence $\delta < \delta_e$. This implies that gap closure occurs more slowly than gap formation on a local scale, but both processes are at equilibrium at the global scale (at least over a time span of 11 years; Satake et al., 2004). We use a regular square lattice with the same dimensions $(200 \times 100$ cells) as the BCI map (Fig. 1(a)), and periodic boundary conditions. The initial condition is a random pattern with $\rho_0 = 0.5$ unless specified otherwise. Our results were processed from different statistical ensembles, as well as from the snapshots of TEM and KIF in Fig. 1B and C, which were taken after 500 iterations at which time both models have reached equilibrium (Fig. 4). Due to the stochastic nature of the models, there is some variation in the results derived from individual snapshots of a particular model. However, the snapshot results presented herein are typical of the TEM and KIF models.

3. Results

For the density estimation, we calculated one average over configurations and another one over time to see if

![Fig. 4. Time evolution of densities for different initial conditions. (a) TEM model using the parameters $P_{TEM}$ and (b) KIF model using the parameters $P_{KIF}$ starting from randomly distributed configurations of gaps with global densities $\rho_0(t = 0) = q_0(t = 0) = 0, 0.5, $ and $1$.](image_url)
there was a difference. We found that, within the uncertainties, the averages are the same. We considered an ensemble of 500 individual snapshots from different runs each taken after 500 iterations at which time equilibrium is well established. Each snapshot produces a different spatial configuration of the forest. We calculated the densities for each snapshot and averaged over all snapshots. For the time average, we executed a single run of 1000 time steps and calculated the average densities over the last 500 iterations, neglecting in this way the transients at early times. We also calculated the densities from the single snapshots in Fig. 1. Table 2 summarizes the results for the densities. The average densities and standard deviations from each sample were found to be approximately equal. Thus, an average over time and an average over configurations are statistically equal, suggesting ergodicity. The parameters $P_{\text{TEM}}$ and $P_{\text{KIF}}$ were specifically chosen to fit the densities. In fact, almost any two-state cellular automaton, like TEM, KIF, FG, etc., can be made to fit the global densities. However, problems arise when we want to fit the local densities. In comparison with the BCI data we see that TEM gives the better agreement for the local densities $q_0$, $q_1$, and $q_2$. Fig. 4 shows that the densities in both systems achieve equilibrium between 300 and 400 time steps, regardless of the initial condition. The time to reach equilibrium does, however, depend on the model parameters. There are temporal fluctuations in the densities, which are greater for TEM than for KIF; however, the standard deviations are small for both. For TEM they are about 6% for the global density and 3% for the local density. For KIF they are both about 3% and 2%, respectively. Since the statistics do not fluctuate radically, any given snapshot would serve to give typical results from the model. For the BCI, only small temporal density fluctuations are evident (Satake et al., 2004); however, the data are limited to a short period of time (~10 years).

The distributions of gap sizes, gap closure sizes, and gap formation sizes are given in Fig. 5. We present results for the individual snapshots as well as for averages over 100 configurations each taken at the 500th iteration. The error bars on the average curves are calculated as the standard deviation of the results from the 100 configurations. The uncertainty becomes larger as gap size increases. We found that taking larger samples did not change the results significantly. The average distributions are smoother than the snapshot distributions due to better statistics, but this does not compare well with the BCI data which are taken from an individual snapshot. Both models give a good fit to the gap size distribution; however, larger-sized gaps are more likely to occur in TEM, as can be seen from the snapshot data in Fig. 5. TEM and KIF both give scaling exponents of about $\alpha_0 \approx -1.7$ for the gap size distribution, which is in good agreement with the observed value of $-1.6$. For the gap formation and closure size distributions, the TEM model gives a much better fit to the data. The scaling exponents are $\alpha_f \approx -2.1$ and $\alpha_c \approx -2.8$, respectively, which are in perfect agreement with the observed values. The scaling exponents for the KIF model are $\alpha_f \approx -4.4$ and $\alpha_c \approx -4.3$, very different from the observed values.

Fig. 6 shows the probabilities of gap formation and gap closure as functions of the number of neighboring gaps $n(0)$ and non-gaps $n(1)$, respectively. The results are for the individual snapshots as well as for averages over 100 configurations each taken at the 500th iteration. We do not

Table 2

<table>
<thead>
<tr>
<th>Density</th>
<th>TEM</th>
<th>TEM avg.</th>
<th>KIF</th>
<th>KIF avg.</th>
<th>BCI</th>
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<td></td>
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<td></td>
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<td>0.32</td>
<td>0.33,0.33 ± 0.023,0.023</td>
<td>0.32</td>
<td>0.33,0.32 ± 0.011,0.011</td>
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<tr>
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<td>0.51</td>
<td>0.51,0.50 ± 0.012,0.010</td>
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<td>0.061</td>
<td>0.063,0.062 ± 0.002,0.002</td>
<td>0.059</td>
</tr>
<tr>
<td>$p_c$</td>
<td>0.067</td>
<td>0.066,0.066 ± 0.004,0.004</td>
<td>0.059</td>
<td>0.063,0.062 ± 0.002,0.002</td>
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<tr>
<td>$q_f$</td>
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<td>0.062,0.062 ± 0.005,0.005</td>
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<td>0.068,0.068 ± 0.005,0.005</td>
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<td>0.063,0.062 ± 0.002,0.002</td>
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<td>0.067,0.066 ± 0.004,0.005</td>
<td>0.14</td>
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</table>

The local densities in the first seven rows are calculated using a von Neumann neighborhood and a Moore neighborhood is used in the last seven rows. Results for the single snapshots in Fig. 1 and the averages are shown. For the averages, the first value is for the average over configurations and the second one is over time.
present error bars in these plots because they would be smaller than the size of the markers, and therefore not visible. The KIF model, in fact, was designed specifically to account for this observed trend. Consequently, the average gives a perfect linear relationship that depends only on the KIF parameters. Thus, for KIF we
have \( P_f = 0.008 + 0.35n(0)/8 \), which is a fair fit to the data, and \( P_c = 0.008 + 0.37n(1)/8 \) which, however, does not fit the data well. The snapshot results for TEM compare well with the data, but the average curve is clearly not linear. The bow-like shape for TEM is due to the effects of rules (iii) and (iv). The bulging becomes more extreme as \( \delta_c \) and \( \beta_r \) are increased. We believe that this effect is the result of some cells being subjected to rule (iii) or (iv) many times due to recursion. In other words, when a given cell is tested to undergo a transition, the probability that that cell undergoes a transition depends linearly on \( n(0) \) or \( n(1) \). However, if that cell is tested many times in a time step, because several of its neighbors made the same transition, then the dependence is no longer linear; there is some kind of mixing of the linear rules. We plan to investigate whether some non-linear dependence on \( n(0) \) or \( n(1) \) results in mixing that gives a more linear trend.

Despite the deviation from linearity, it may be verified that the model results lie within a tolerance allowed by observed statistical fluctuations. Satake et al. (2004) showed that the observed slope and intercepts of the function \( P_f[n(0)] \) fluctuate significantly from year to year. The broken lines in Fig. 6 delimit the maximum slope and intercept and the minimum slope and intercept. The results from both models easily fit within the large tolerance allowed by observation.

The regression lines for TEM are \( P_f = 0.22 + 0.28n(0)/8 \) and \( P_c = 0.035 + 0.35n(1)/8 \). As we discussed in Section 2.1, the observed gap formation (closure) rate \( R_f \approx 0.090 \) (\( R_c \approx 0.20 \)) and the observed average probability of gap formation (closure) \( P_f \approx 0.090 \) (\( P_c \approx 0.20 \)) are equal. By interpolating the average curve, we find that for TEM we get \( R_f = 0.10 \) and \( P_f = 0.11 \), which are off by 10%, and \( R_c = 0.20 \) and \( P_c = 0.19 \), off by only 5%. For KIF we get \( R_f = 0.094 \) and \( P_f = 0.092 \), and \( R_c = 0.19 \) and \( P_c = 0.19 \), both within 5%. For both models, the fact that \( R_c \approx P_f \) (\( x = f \) or \( c \)) tells us that the local dependence of \( P_f \) on \( n(0) \) or \( n(1) \) is enough to account for the global rates of transitions \( R_c \). Therefore, the assumption of the dependence of the gap formation and closure rates (in rules (i)-(iv)) on the Moore neighborhood is justified.

Fig. 7 shows the correlation functions \( C_x(r) \) and \( G_x(r) \) for gaps (\( x = 0 \)), gap formations (\( x = f \)), and gap closures (\( x = c \)). Results are for the snapshots and for averages over 100 configurations each taken at the 500th iteration. The error bars on the average curves are calculated as the standard deviation of the results from the 100 configurations. These functions allow us to compare the patterns at any length scale, and to estimate the correlation lengths. We see that \( C_x(r) \) saturates to a value of \( \rho_x \), as \( r \to \infty \), and \( C_x(1) \approx q_x \), as expected. TEM and KIF can produce significant gap correlations because they both have rules (i) and (ii) that tend to create and close gaps near the edges. However, KIF gives almost no correlations between transition cells, while TEM gives significant correlations, which compare well to the BCI data. This is because KIF has no explicit rule for clustering transitions while TEM does. TEM clearly gives a better fit to the observation than KIF, but TEM over-estimates the fraction of gaps, and underestimates the fraction of gap formations and closures. This means that there are too many large gaps (or large gaps are too close together), and there are not enough large gap formations and closures (or large gap formations and closures are too far apart). If we define the correlation length \( \xi_x \) (where \( x = 0, f, \) or \( c \)) to be the distance before which \( C_x(r) \approx \rho_x \), then we find that \( \xi_0 \approx 30, \xi_f \approx 15, \) and \( \xi_c \approx 10 \) for BCI, \( \xi_0 \approx 20, \xi_f \approx 10, \) and \( \xi_c \approx 6 \) for TEM, and \( \xi_0 \approx 8, \xi_f \approx 0, \) and \( \xi_c \approx 0 \) for KIF.

4. Discussion

The gap size distribution in the BCI forest has been well studied. Its power-law behavior has been well fit by several models: the Ising model works well for a gap height threshold of 20 m (Katori et al., 1998). The FG works well for a gap height threshold of 10 m (Solé and Manrubia, 1995) and a modified version (Pagnutti et al., 2005) works well for a threshold of 20 m. Here, we discuss not only the gap size distribution, but also, for the first time, the gap closure and formation size distributions, which we find to be power laws as well. To the best of our knowledge this is the first study of the BCI gap pattern in which close attention has been paid to the dynamical transitions that create the pattern. Although the size distributions of gap formations and closures are both scale invariant, we observe that even the largest clusters of gap formations or closures are very small (\( \sim 1\% \)) in comparison to the largest gaps. This may be related to the fact that the scaling exponents for the gap formation and closure size distributions are significantly smaller than that for the gap size distribution; that is, occurrences of large gap formations or closures are far less likely than occurrences of large gaps. The implication is that large gaps are neither created nor filled by single events but rather by a slow propagation of many events near gap edges over several years.

The observed scale invariance in the gap size distribution suggests that the gap pattern is close to the percolation threshold (Stauffer and Aharony, 1992; Guichard et al., 2003) which is the global gap density at which a single gap cluster connects one edge of the map to the opposite edge. In the absence of local interactions, percolation theory predicts that the global density of gaps should be about 0.59 at the percolation threshold when scale invariance is realized. However, since we observe scale invariance and a global density of about 0.5 in the BCI, then some non-random phenomenon driving the transitions must be at work. Local interactions cause gaps to be more aggregated than those in a purely random pattern, which allows us to have a percolating gap cluster in the system with less total gap area (i.e. global density). In other words, the aggregation of gap cells makes a large contiguous percolating gap more likely to occur, so a smaller global gap area is required to reach the percolation threshold. This can be easily verified by comparing the pure
The percolation model to the KIF model, which has local interactions; the KIF model can produce more aggregated gap patterns because it can give $g_0 > \rho_0$ and scale invariance is realized for smaller values of $\rho_0$. However, the degree of aggregation and the transition rates in the BCI are too high to be captured by KIF. This suggests that transition expansion, as in TEM, is necessary to create strong enough aggregation to fit the BCI pattern.

Fig. 7. Left panel: (a) correlation function $C_0(r)$ for gaps. (c) Correlation function $C_f(r)$ for gap formations. (e) Correlation function $C_c(r)$ for gap closures. Right panel: (b) correlation function $G_0(r)$ for gaps. (d) Correlation function $G_f(r)$ for gap formations. (f) Correlation function $G_c(r)$ for gap closures.
In TEM, the most important ingredient is that transitions are allowed to propagate to adjacent cells which can, in turn, create large gap formations and closures. The expansion of transitions is related to the fact that the observed individual crown size and interaction length are larger than one cell (5 × 5 m²) (Casper et al., 2003; Lin et al., 2004). This has been discussed previously (Manrubia and Solé, 1997; Satake et al., 2004; Schlicht and Iwasa, 2004), but only little has been done to incorporate long-range interactions into a model of forest gap dynamics; a study by Molofsky et al. (2002) addresses the importance of scale in cellular automata; they examine all ranges of dispersal and frequency-dependent interactions. Another study by Chen and Mynett (2003) considers the effects of neighborhood size and shape. They consider long-range interaction in a predator–prey model but not beyond what they call the extended Moore neighborhood (z = 12). By counting the number of empty patches (gaps), they concluded that longer-ranged interaction results in a more aggregated system because the predators can jump over an empty patch. Likewise, the transition expansion in TEM is a long-range interaction that results in a much more aggregated pattern than the KIF model where there is no transition expansion. The main difference, however, is that the long-range interactions used by Molofsky et al. and Chen and Mynett do not propagate the transitions at all; i.e. TEM may allow a cascade of transitions around a given cell that undergoes a transition, but in the aforementioned models only single transitions occur. The FG model (Solé and Manrubia, 1995; Manrubia and Solé, 1997; Pagnutti et al., 2005) incorporates a gap formation expansion rule, but the transitions are restricted only to the Moore neighborhood. The FG model yields a slightly better gap size distribution than the KIF model, but it cannot capture the other aspects of the BCI data.

Some models of other systems represent transitions (usually just one type; i.e. gap formation) as explicit states in addition to the empty (gap) and occupied (non-gap) states, where a cell in this third state may propagate the transition to its neighbors in each time step. Examples of these models include the self-organized forest fire model (FFM) (Drossel and Schwabl, 1992) and mussel bed models (Wootton, 2004; Guichard et al., 2003). However, these models are sometimes implemented such that an initial transition is allowed to complete its entire propagation, all within the time step in which it appeared (Drossel and Schwabl, 1992; Wootton, 2004). This is very similar to how transitions can propagate in TEM. The FFM has been implemented such that it becomes the same as TEM if we use a von Neumann neighborhood for interactions and we let \( \beta = \delta = b_c = \beta_c = \delta_c = 0 \) and usually \( d_e = 1 \). Schenk et al. (2002) define the FFM, as follows:

Each site is either occupied by a tree, or is empty. At each time step, all sites are updated in parallel according to the following rules:

(i) An empty site becomes occupied by a tree with probability \( p \),

(ii) A tree is struck by lightning with probability \( f \).

This tree and the whole cluster of trees connected to it (by nearest-neighbour coupling) burn down and become empty sites.

Replace the terms “tree” and “empty” in the FFM by “non-gap” and “gap”, respectively, and replace the symbols \( p \) and \( f \) in the FFM by \( b \) and \( d \). Now, rule (i) in FFM is identical to rule (ii) in TEM if we let \( \beta = 0 \). The first part of rule (ii) in FFM, “A tree is struck by lightning with probability \( f \). This tree... burn[s] down and become[s] an empty site.”, is identical to rule (i) in TEM if we let \( \delta = 0 \). The second part of rule (ii) in FFM, “...the whole cluster of trees connected to [the tree struck by lightning]... burn down and become empty sites.”, is identical to rule (iii) in TEM if we let \( d_e = 1 \) and \( \delta_c = 0 \). The FMM has no realization of rule (iv) in TEM, so we can remove it by letting \( b_c = \beta_c = 0 \). Drossel and Schwabl (1992) briefly consider this version of the FFM by assuming “that a whole forest cluster is burned down... during one time step when one of its trees is struck by lightning.” The critical gap density for the FFM is \( p_0 = 0.59 \), but this refers to the density at which the pattern of fires is critical. The scaling exponent for the fire size distribution is \(-1.45\) (Schenk et al., 2002). Alonso and Solé (2000) used a model of forest dynamics that had gap formation expansion much like TEM. They found a power-law gap size distribution with a scaling exponent of approximately \(-1.8\). Also, in Wootton’s model the transitions were allowed to propagate as in TEM. From his results we calculate a scaling exponent of approximately \(-1.2\) for the gap size distribution. He also investigated various forms of his model, including some without transition propagation, and found that the strong gap aggregation that is characteristic of mussel beds could only be fit if the transitions were allowed to propagate. We plan to study these models in a comparative manner to determine how the differences in scaling exponents reported can be linked to the specific rules of the models. However, at this point, it is interesting to note that only TEM is able to reproduce the scaling exponents calculated from the BCI data.

Now we need to further understand when it is warranted to have propagation of local interactions, in particular for the BCI dynamics. In order to accurately model the BCI dynamics, we must consider the densities of gap formations and closures because they tell us the rates at which transitions occur and are thus crucial to understand the overall gap dynamics. Using the KIF model, the location of each gap formation (or closure) is independent of the others, so there is no reason for the transitions to be non-randomly aggregated and we get \( p_l \approx q_g \) and \( p_c \approx q_c \). In the BCI data, however, we observe that \( p_l < q_g \) and \( p_c < q_c \), suggesting that there must be local interactions that cause the transitions to be aggregated. Since there is no way of knowing a priori where the transitions will occur, we need some explicit mechanism to cause them to form in
aggregated clusters. We have achieved this in TEM by allowing transitions to propagate into neighboring cells. Thus, transition propagation is warranted whenever the local density of a transition is greater than the global density. In order to achieve the necessary aggregation of transition events we added the rules (iii) and (iv). These require four new parameters $b$, $d$, $\beta$, and $\delta$, in addition to the KIF parameters $b$, $d$, $\beta$, and $\delta$. Perhaps it is not surprising that adding complexity to the KIF model, by adding new rules and parameters, should improve the fit to the data. However, we have argued that the particular mechanisms of our new rules, namely the expansion of transitions, are indeed justified on physical grounds, and the improvements to the fit support our claims.

In TEM gap formation (or closure) patches are often partially replaced (or removed) at the next iteration. The gap edges migrate slowly and large gaps may persist for long periods of time. This seems consistent with a study by Young and Hubbell (1991). They report a significant re-disturbance in large gaps caused by treefalls into these gaps, and suggest that gaps, especially large ones, are more persistent than previously thought. They report that repeated gap formations occur because gap-edge crowns grow asymmetrically towards the gap and fall on the heavy side into the gap. This suggests that the dynamics displayed by TEM may be quite realistic. This may be readily verified when more data become available for comparison.

5. Conclusion

In this work we have introduced a model that can capture very well the canopy dynamics observed in the BCI forest. To the best of our knowledge, TEM is the first model that is able to simultaneously account for the following aspects of the BCI data using a single set of model parameters: global and local densities, size distributions, and correlation functions for gaps, gap formations, and gap closures, as well as the neighborhood-dependent transition rates. All but the last aspect of the data were fit very well. The non-linearity of the neighborhood-dependent transition rates is likely due to the recursive nature of the linear rules of TEM. However, the strict linearity in the BCI data is debatable on the grounds of poor statistics, and the parameters defining the equations of the lines may fluctuate from year to year (Kubo et al., 1996; Satake et al., 2004). Nevertheless, because TEM can simulate the BCI gap pattern with such detail and accuracy, we think it is a useful model for studying gap dynamics. An effective model for predicting gap dynamics will become increasingly useful as advancements in remote sensing make high-resolution plots of canopy architecture more accessible (Blair et al., 1999; De Wasseige and Defourny, 2002; Drake et al., 2002).

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References


