Are Rainforests Self-organized in a Critical State?

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The spatial distribution of low-canopy gaps in the Barro Colorado Island rainforest (Panama) is shown to exhibit fractal properties. A simple cellular automata model (the "Forest Game") was constructed in order to simulate the gap dynamics of such forests as well as the observed macroscopic spatial regularities. Generalized fractal dimensions are studied as a function of several relevant parameters. The observed and simulated fractal behaviour is shown to be related to self-similar dynamics of biomass. This result is interpreted as related to the emergence of a class of "self-organized critical state".

1. Introduction

1.1. FRACTALS AND MULTIFRACTALS

Following the pioneering studies of Mandelbrot (see e.g. Mandelbrot, 1982), fractal objects have become a familiar class of structures in almost all areas of scientific knowledge. Today, it is clear that self-similarity is widely present in nature. Biological systems are not excluded from the fractal world: blood vessels, neural structures and plant growth have been shown to be fractal-like objects (Burrough, 1981).

As recently discussed by Sugihara & May (1990), different scales of observation are necessarily related to different aspects of structure, and fractal methods can be applied in order to detect self-similar hierarchies in ecology. Such hierarchical scaling has been observed, for instance, in coral reefs (Bradbury *et al.*, 1984), from patch perimeter measures in deciduous forests (Krummel *et al.*, 1987), vegetation patterns (Morse *et al.*, 1985) and landscapes (Wiens & Milne, 1989; Scheuring, 1991).

The aim of this paper is to show how a non-linear dynamical process—gap formation—in forest ecosystems can generate such fractal structures. Treefall and gap formation (and regeneration) in rainforests has

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been shown to be a major force in tropical ecosystems (Whitmore, 1991). From time to time, old trees fall down, leaving a gap in the canopy, giving new plants the chance to develop. The gap torn through the forest is often large, even for a single tree, due not only to the size but also to the strong link with neighboring trees through elastic lianas. The opening of a gap shakes the forest equilibrium to the starting point and recurrent successional phases are observed. In this way, gaps are known to contribute to the maintenance of high diversity levels in tropical rainforests (Jonsson & Esseen, 1990). Such high diversity is particularly clear in relation to bryophyte populations, and species richness has been shown to be highest at intermediate patch ages. Consequently, treefall disturbances are important for the persistence of colonists. Even in grassland ecosystems, gaps are known to be very important (Silvertown & Smith, 1988).

As an example, consider the Barro Colorado Island (BCI) forest, a remnant of rainforest isolated after the formation of the Panama's canal. Figure 1 shows a map of a 50-ha plot showing 2582 canopy survey points, where the height of the canopy was less than 10 m in 1982, 1983 or in both years (Wendel *et al.*, 1991; see also Brokaw, 1985). Such low-canopy sites generally correspond to gap formation (after some recent recolonization has been produced).
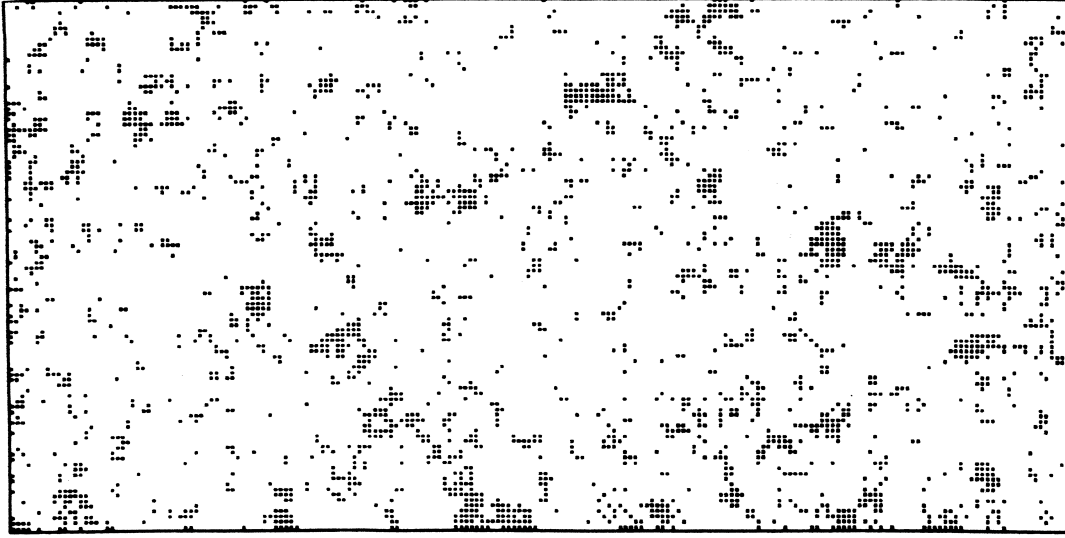
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FIG. 1. Map of 50-ha plot on Barro Colorado Island, Panama. Here 2582 low canopy survey points are shown, as block dots. These points indicate that the eight of the canopy was <10 m in 1982, 1983 or in both years.

Furthermore, the distribution of fallen trees is not significantly associated with topographic features (Lieberman *et al.*, 1985) and the spatial distribution of gaps is known to be non-random and independent of site factors. A first step in our understanding of these spatial structures can be obtained from fractal theory.

Using the BCI map, self-similar structures can be detected. In this sense, we can calculate the fractal dimension D_g of the low-canopy gap distribution. If we divide our fractal into a set of boxes of edge size ϵ, using $N(\epsilon)$ boxes to cover the set, $N(\epsilon)$ is expected to scale as

$$N(\epsilon) \approx \epsilon^{-D_g}, \qquad (1)$$

where D_g can be estimated in several ways (see, for example, Barnsley, 1988). Explicitly,

$$D_g = -\lim_{\epsilon \to 0} \frac{\log(N(\epsilon))}{\log(\epsilon)}. \qquad (2)$$

For the BCI ecosystem, we found $D_g \approx 1.86$—clearly a non-integer. In this sense, the BCI forest is a very large living fractal. The existence of self-similar behaviour here is suggestive of self-organization near a phase transition, where large-scale correlations can emerge. In an equilibrium state, correlations are limited to local scales (Bak & Creutz, 1994). To sum up, the BCI plot, which at first appears featureless, is actually remarkably correlated.

However, D_g is only one of an infinite spectrum of the so-called correlation dimensions of order q.

Equation (2) is the particular case $q = 0$ of the general expression (see, for example, Schuster, 1989):

$$D_q = \lim_{\epsilon \to 0} \frac{1}{(q-1)} \cdot \frac{\log[X(q)]}{\log(\epsilon)}, \qquad (3)$$

where

$$X(q) = \sum_{i=1}^{N(\epsilon)} p_i^q,$$

with $-\infty < q < +\infty$. The probability of every i-th box (p_i) can be arbitrarily defined over the set, with the only requirement being normalization: $\sum_{i=1}^{N(\epsilon)} p_i = 1$. In the particular case of BCI (Fig. 1), we have assigned equal probability to every black dot, $p_d = 1/2582$. Therefore, $p_i = N_{bd} \times p_d$, where N_{bd} stands for the number of black dots inside the box. This is called a "mass measure". For $q = 0$ we have again $D_g = D_0$. It can be shown that the inequality $D_{q'} \leqslant D_q$ holds for $q' \geqslant q$. For $q = 1$, the so-called information dimension is merely the Shannon entropy:

$$D_1 = \lim_{\epsilon \to 0} \sum_{i=1}^{N(\epsilon)} p_i \log(p_i), \qquad (4)$$

and for $q = 2$ the correlation dimension is defined by:

$$D_2 = \lim_{\epsilon \to 0} \frac{\log\left[\sum_{i=1}^{N(\epsilon)} = 1 \, p_i^2\right]}{\log(\epsilon)}. \qquad (5)$$

Here D_2 is in fact a measure of correlations: p_j^2 give the probability of finding at least two points

inside the j-th cell. Thus, D_1 is sensitive to binary correlations in the probability distribution. These dimensions and the whole spectrum of them provide an enormous amount of additional information about the geometric structure of the underlying fractal set.

Another important function is defined in relation to $D(q)$: the spectrum of fractal dimensions, $f(\alpha)$. α is a scaling exponent defined by

$$p_k \approx \epsilon_k^\alpha,$$

representing the divergency of the measure. $f(\alpha)$ is the fractal dimension corresponding to the set with diverging exponent α. They can be calculated from $D(q)$ in the following way:

$$\alpha(q) = \frac{\mathrm{d}}{\mathrm{d}q}[(q-1)D_q], \qquad (6)$$

$$f(\alpha(q)) = D_q(q-1) - q\alpha(q) \qquad (7)$$

(A detailed study of $D(q)$ and $f(\alpha)$ can be found in Halsey *et al.*, 1986).
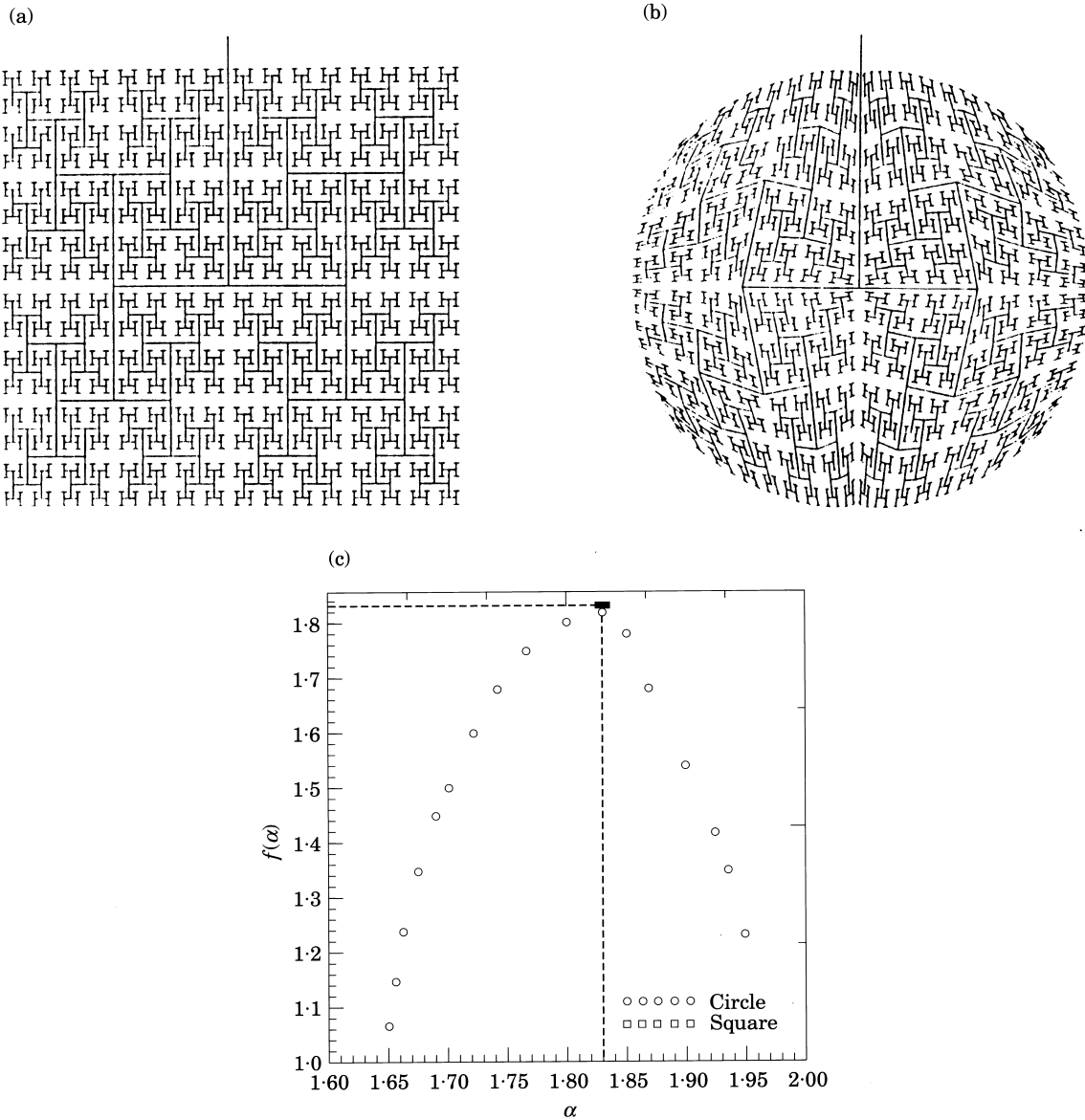
(a)

(b)

(c)

FIG. 2. Two examples of fractal objects: (a) an homogeneous square and (b) a multifractal circle. They were obtained by progressively branching with square and circular boundaries, respectively (from Nelson, 1992). (c) Their spectrum of fractal dimensions, $f(\alpha)$. $f(0) = 1.83$ (square) and ($f(0) = 1.82$ (circle). There exists a single-valued point for $f(\alpha)$ for the square boundary which spreads into a continuous function for the circle.

For a pure fractal, there exists no basic length which can be used as a unit of length; the whole spectrum of dimensions collapses into the usual fractal dimension, i.e. the $f(\alpha)$ spectrum reduces to a point, and the $D(q)$ to a straight line. This is related to the non-existence of subsets of different density in the fractal. The diverging exponent is thus the same for every part of the set. On the other hand, real fractals are, in fact, multifractals: the measure (or equivalently the density, if we are dealing with a mass measure) is not the same in every subset, and each of them has a different fractal dimension ($f(\alpha)$) and a different associated diverging exponent (α). In the limit, this represents the continuous multifractal spectrum. An example of both cases is depicted in Fig. 2. The square has $D_0 = 1.83$, and the circle $D_0 = 1.82$—roughly the same. It is worth noting that the spread of $f(\alpha)$ when a change in the homogeneity of the square is introduced by means of a change in the boundaries (from Nelson, 1992).

For the problem under consideration, it is well known that the effects of small and large gaps on the colonizer species are quite different. In this sense, multifractal measures can give us a better quantitative characterization of these differences. If we calculate the spectrum of fractal dimensions for the BCI forest, the set $\{D_q\}$ clearly shows a wide distribution of fractal dimensions, as shown in Fig. (3). The BCI is then a multifractal, at least in relation to the spatial structure of gaps. As can be observed, $D_0 \approx 1.86$, i.e. roughly the same as before.

To gain insight into the origin of such a self-similar spatial structure, we can try to construct a simple model able to retain the basic mechanisms of gap formation, competition and treefall. Using simple, spatially extended models, we can expect to

capture the essential mechanisms (Ruthen, 1993). This approach is particularly well-known from studies on competition in plant communities (for a recent study, see Silvertown *et al*., 1992, and references therein). As a dramatic example, complex, macroscopic patterns of wave regeneration in *Abies* forests can be very well reproduced by means of very simple CA rules (Iwasa *et al*., 1991). In the following sections, a CA is described as well as several numerical simulations. The resulting dynamics is shown to be related in several ways with the so called "self-organized criticality" phenomenon.

1.2. GAP DYNAMICS AND CRITICALITY

Recent studies on the behaviour of non-linear systems far from equilibrium with extended spatial degrees of freedom have shown that these systems often spontaneously evolve towards a so-called "self-organized critical state" (Bak *et al*., 1988; Bak & Chen, 1991). Under these conditions, the system is organized in a well-defined way (there is some kind of "attractor") which is characterized by the existence of order at all length scales and where small perturbations evolve creating objects of all sizes. This essential result provides in fact a physical explanation for some fractal objects and some natural power laws as the one observed for the so-called $1/f$ noise (Bak & Chen, 1989).

The standard example of self-organized criticality is the pile of sand. As the pile grows by adding grains of sand, the slope grows until the "angle of repose" is reached.

Now, if new grains are added avalanches occur with a wide range of sizes. The only limitation is linked to the absolute size of the pile. A cellular automata model can be constructed in order to
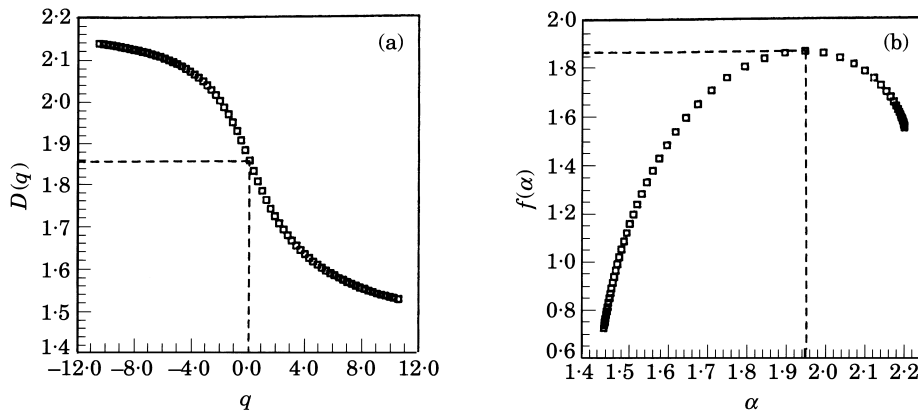

FIG. 3. The BCI of Fig. (1) was covered with a grid of 1250 boxes, in order to obtain the mass measure for the forest. (a) Spectrum of correlation dimensions, $D(q)$. (b) Spectrum of fractal dimensions, $f(\alpha)$. $f(0) = D_0 \approx 1.86$, the fractal dimension of BCI.

simulate this process (Bak *et al.*, 1988). The dynamical and structural properties of this state can be characterized through several scaling laws. In the special case of the sand pile, the number of grains $N(r)$ falling a distance r at the same time step follows the exponential law:

$$N(r) \approx r^{-D},$$

where D is a fractional quantity: the "fractal dimension" of the avalanches. Several applications of self-organized criticality have been developing the study of $1/f$ noise (Bak *et al.*, 1988), earthquakes, large scale structures in the Universe, and a simple ecosystem model: the well-known "game of life" (Bak *et al.*, 1989).

The game of life is just a caricature of reality, but as Chen and Bak pointed out, it ". . .serves to demonstrate how large-scale structures can arise in complex extended dynamical systems". Using numerical perturbation experiments (adding individuals to a stationary configuration), they analysed the corresponding power laws related to the distribution of clusters (avalanches) of size s, $D(s)$, and the distribution of the duration of perturbations $D(T)$. They found two well-defined scaling laws: $D(s) \approx s^{-\tau}$ with $\tau \approx 1.4$ and $D(T) \approx T^{-b}$ with $b \approx 1.6$. In spite of the artificiality of this model, the authors claimed that the general properties of the critical state are common to other more realistic situations. The validity of this scheme was recently shown by means of Monte Carlo simulation studies (Solé, 1991; Solé *et al.*, 1992). The interesting fact is that the spatial distribution of automata in the lattice at the critical state was also shown to exhibit fractal behaviour. The link between both spatial and temporal domains is self-similarity: $1/f$ noise is merely the expression of the existence of an underlying self-similar spatial structure. Conversely, the spatial structure is the result of scale-invariant dynamical processes. For the BCI example (and others) we know that fractality is present, that not all gap sizes are equally probable and that non-linear interactions take place along the forest succession. If we calculate from the Barro Colorado map the frequency distribution of gap sizes, we find only an additional fingerprint of a critical state. Figure 4 depicts a power-law distribution of gap sizes, i.e.

$$N(G) \approx G^{-\phi}$$

with $\phi = 1.74$. Power laws for cluster sizes are typical when a system is operating out of equilibrium at or near a threshold of instability. A wide spectrum of
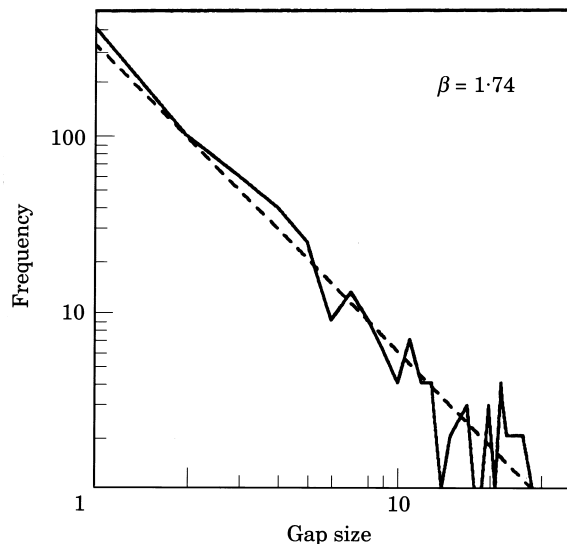

FIG. 4. Power-law distribution of gaps from the BCI forest. A critical exponent $\phi = 1.74$ is obtained.

possibilities in patches of habitat is spontaneously generated by means of this mechanism.

Following Bak's theory, we can conjecture that the system evolves automatically to this critical state without any fine-tuning (Bak & Chen, 1989). Now the question is: can the fractal structure of the BCI ecosystem be generated as the result of self-organization near some kind of critical state? A cellular automata model can give us an answer to this question.

2. The Forest Game

The cellular automaton (the "forest game") is a forest growth model running on a two-dimensional lattice of $L \times L$ points. Cellular automata (see Wolfram, 1984) are mathematical models for complex natural systems with local interactions, and the value of each automaton is determined in some way by the previous values of a neighbourhood of sites around it. Trees (our automata) grow and compete for resources (light, nutrients, etc). A given tree can grow from a minimum size S_0 to a maximum value S_c. As the $S = S_c$ state is reached (or the tree becomes too old), treefall occurs. This treefall will occur in accordance with some given probability. The state of each tree is then determined by $S_n(i, j, \tau_{ij})$ with $i, j \in \{1, 2, \ldots, L\}$ and $n = 0, 1, 2, \ldots$ the corresponding time step. The actual age of the (i, j)-th tree is defined by τ_{ij}. For simplicity, we will use the notation $S_n(i, j)$, without (explicitly) taking into account the age of the tree. The automata rules are defined by:

(i) *Growth*. A given tree will grow if the screening from nearest trees (here we take the eight nearest neighbours) is weak enough. Explicitly, the tree size is updated following:

$$S_{n+1}(i,j) = S_n(i,j) + \Delta_n(i,j)$$

where $\Delta_n(i,j)$ include the way in which nearest trees interact. Here we take a simple screening between trees and in this case $\Delta_n(i,j)$ is defined as:

$$\Delta_n(i,j) = \Theta\left[\mu - \frac{\gamma}{8} \sum_{\langle r,s \rangle} S_n(r,s) \right],$$

where $\Theta(z) = z$ if $z > 0$ and $\Theta(z) = 0$, otherwise. Here $\langle r,s \rangle$ indicates the restriction to nearest trees (obviously $(r,s) \neq (i,j)$). We take $\mu = 1$ in all our simulations. γ gives us the interaction strength. For $\gamma = 0$, no interaction takes place (trees are independent) and for γ very high growth will not be possible. Here we take $\gamma = 1$.

(ii) *Death*. A given tree will die randomly with some probability p_d and treefall will take place. Additionally, no trees beyond some specified size S_c can exist. Thus, if $S_n(i,j) \geqslant S_c$, treefall will also occur (here we take $S_{n+1}(i,j) = 0$ if $S_n(i,j) \geqslant S_c$). The study of mortality patterns in tropical forests gives us an estimate of $p_d \in (0.1–0.3)$ (Lieberman *et al*., 1985).

(iii) *Birth*. A new tree can appear at any empty lattice point with some probability p_b. The size of the new tree is the smallest one, i.e. $S_0(i,j) = S_0$. In all our simulations we take $S_0 = 0.1$.

(iv) *Gap formation*. Finally, a canopy gap formation rule needs to be defined. In our model, the canopy gap will be formed each time a tree dies, and
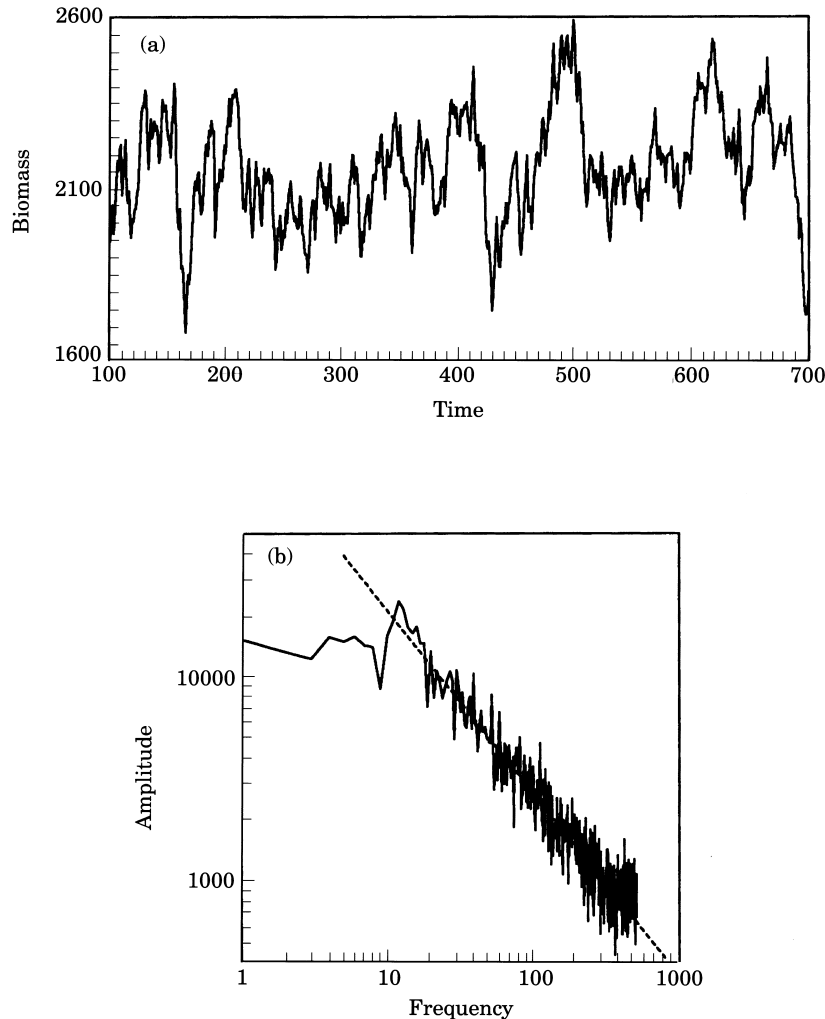

FIG. 5. (a) Dynamics of the forest biomass at the critical state for a 40×40 lattice. Parameters are $p_b = 0.3$ and $p_d = 0.01$. (b) Fourier transform (here, $\beta \approx 0.93$), averaged over five samples.

the gap size will be proportional to the size $S_n(i, j)$ of the dying tree. In order to make the rule as simple as possible, we create a circular gap of radius R around the (i, j) point. All nearest trees such that

$$\sum_{\langle r, s \rangle} S_n(r, s) \leqslant S_n(i, j),$$

(verifying $(r - i)^2 + (s - j)^2 \leqslant i^2 + j^2$) will be removed (i.e. $S_{n+1}(r, s) = 0$) and clearly R is determined through the previous inequality.

As we can see, no fine details about interactions are included. Other more realistic rules could be used, but, as previously mentioned, only the basic skeleton of interactions is considered here.

3. Results

Many computer simulations have been performed, using several lattice sizes (up to $L = 256$ in order to avoid finite-size effects). Typically, $L = 80 - 100$ have been used as those shown in this paper.

An example of the dynamics of the total biomass $B(t)$ is shown in Fig. 5(a). A wide spectrum of fluctuation sizes, as in other self-organized critical phenomena, can be observed. If the Fourier spectrum is calculated for $m = 2^9$ points (after 200 transients are discarded, and averaging over five simulations) we can clearly appreciate a $1/f^\beta$-like shape, which oscillates in our simulations between $0.87 \leqslant \beta \leqslant 1.02$ [Fig. 5(b)]. As discussed before in relation to the sandpile model, self-organized spatial structures emerge from the non-linear competition
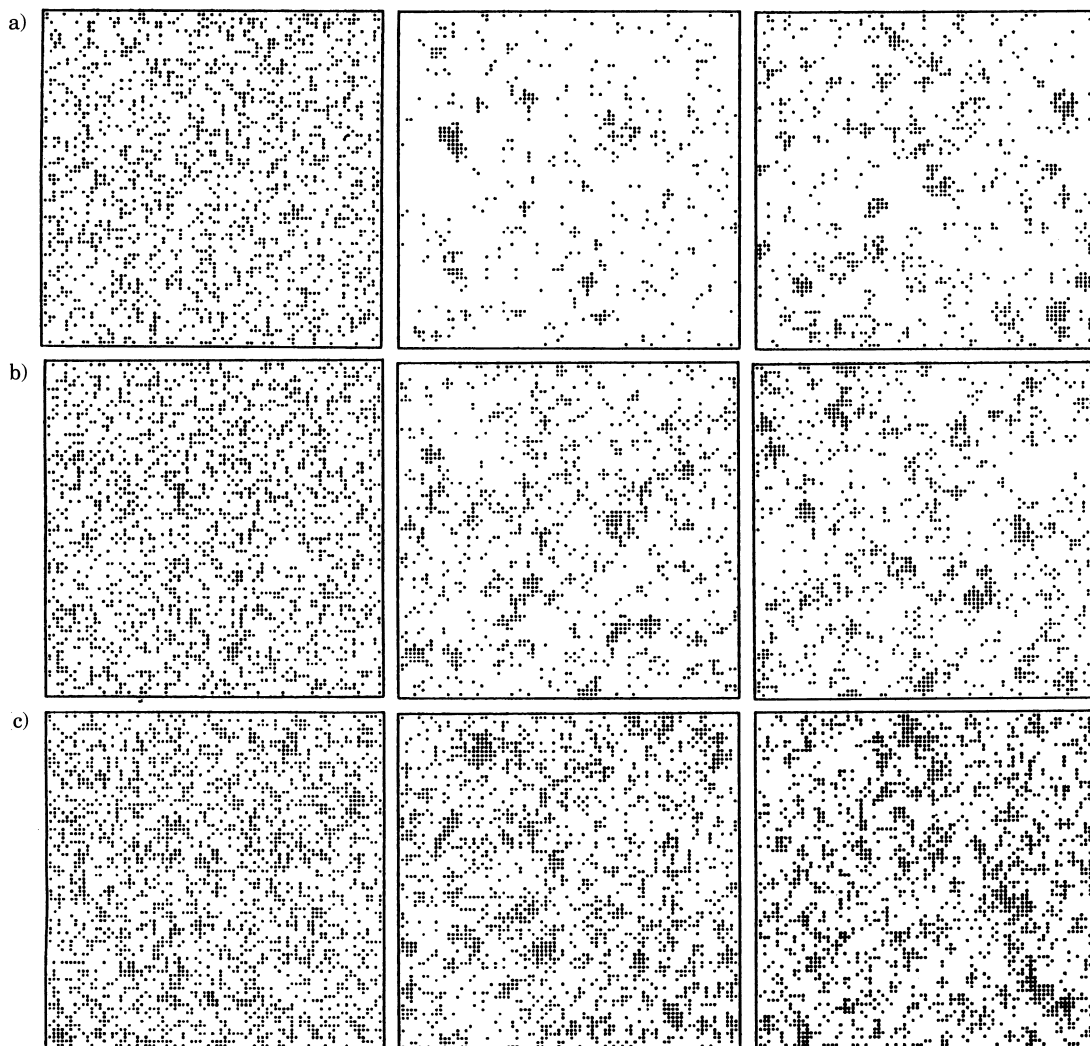

FIG. 6. Simulation model. Here a 81×81 lattice has been used, with $p_b = 0.3$ and $S_c = 30$. Probability of death is (a) $p_d = 0.01$ (b) $p_d = 0.025$ and (c) $p_d = 0.05$. Three time steps are shown. From left to right, $t = 5$, $t = 50$, and $t = 150$.
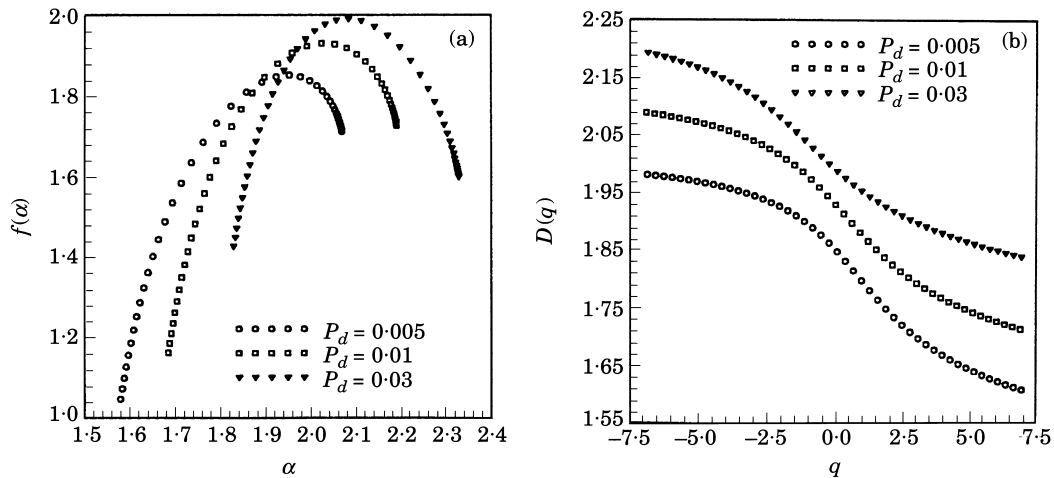
FIG. 7. (a) Multifractal spectrum $f(\alpha)$ and (b) correlation dimensions $D(q)$, for three simulated ecosystems. Here we have used 80×80 lattices, $p_b = 0.3$ and several values of p_d, as indicated.

process between nearest trees, and they reflect the kind of dynamical pattern involved.

Now, let us analyse the spatial structure. Nine snapshots of our simulated forest are also shown in Fig. 6(a–c), starting from a low-density lattice (with only $0.5L^2$ trees of minimum size S_0). Black points indicate low canopy points, where $S_n(i, j) = 0$. For $n = 5$, many disperse gap points are present, and for $n = 25$ the birth and growth of trees has reduced the number of such points and the first small gaps appear. Later in the simulation, the distribution of gap sizes reaches a stable state and the forest shows a dynamical evolution with self-similar structure (corresponding to the last three snapshots). The total biomass and fractal dimensions are stable for $n \geqslant 50$. The biomass grows faster in the first steps (when only small trees are present) and less fast for $7 - 8 \leqslant n \leqslant 38 - 40$ steps, as a consequence of the increasing competition. Treefall and gap formation becomes dominant after $n \approx 50$ time steps and several statistical measures (density, diversity, etc) now remain stable in time. For that particular case, the fractal dimension for both biomass and gap distribution appears to be stationary. Starting from $D_g \approx 2$ (i.e. totally random) the fractal dimension of gaps evolves towards a characteristic value linked with the self-organized state.

We can easily show that this state is not dependent on initial conditions, i.e. that the fractal structure and self-similar dynamics are "attractors" of the model. To probe this point, we have performed several simulations starting from different initial densities of trees. In this sense we can analyse to what extent the random-like rules can destroy the initial information leading to the same class of final pattern. All

simulations show a characteristic convergence to such a final state.

At this state, the multifractal spectrum can be calculated from our model. Using different p_d values, which lead to different densities of low canopy points, the D_q spectrum was estimated. Figure 7 shows the spectrum for $p_d = 0.005$, 0.01 and 0.03. As the extinction probability is raised, the fractal dimension ($D_0 = f(0)$) grows towards $D_0 = 2$, as expected: the system is more random in generating gaps. But, as we can see, even in this situation a wide spectrum of generalized dimensions is obtained, showing a structured system. It is important to mention that if only D_0 were available, our conclusion would be a "random pattern". The multifractal approach allows us to observe the system at a deeper resolution (see Appendix).

4. Discussion

Far from equilibrium, even abiotic systems can produce macroscopic, ordered patterns in space evolving from microscopic chaos. This situation is specially evident when dealing with biotic communities evolving in a terrestrial or aquatic ecosystem, where similar patterns appears replicated at different scales (Margalef, 1978; Solé, 1991). The gap distribution in the BCI strongly suggests a connection between complex patterns and complex dynamical processes.

We have shown that a very simple CA model can account for some relevant part of the observed complexity of a rainforest when gap dynamics is present. Our intention was not the analysis of a detailed model of tree growth and interaction (see, for example,

Shugart, 1984). Instead, we have studied a simple, spatially extended model of forest succession involving the creation of low-canopy gaps. Starting from an arbitrary set of trees, the system self-organizes itself into a kind of critical state characterized by the existence of self-similar spatial patterns together with a self-similar time evolution characterizable through the $f^{-\beta}$ Fourier spectrum, with $\beta \approx 1$. As this state is reached, a "fractal succession" takes place where pattern and process are similarly defined at many length scales. The extent to which our results are robust will need a more detailed study, but the observed regularities seem to be in agreement with a typical situation. The extension of our study to a n-species ecosystem will be reported in a future work.

On the other hand, gap self-similarity is not the only possible situation in which this type of fractals can emerge in forests. Neotropical forests are exceedingly complex mosaics resulting from spatiotemporal segregation of co-evolved food webs. Species diversity depends, as mentioned above, on the existing spatial heterogeneity. The underlying conjecture would be that, in this sense, fractal structures must be present at other levels of this class of biological organization. Our simulation model shows that not only gap distribution, but also biomass, shows fractal properties. If these results can be translated to real forests, biomass (and may be productivity) would also show such type of self-similar behaviour. Conversely, the observed spatial patterns can give several clues for our understanding of the underlying dynamical process. Theoretical and computer models will be extremely useful here to reproduce and explain the observed patterns as well as to provide a quantitative measure for the effect of external energy or human actions.

Our study shows that generic dynamical properties can emerge from simple rules of forest growth. Our approach is then in the methodology of complex systems (Parisi, 1993; Ruthen, 1993). Of course a more detailed model can be proposed, but if a critical phenomenon is involved, then universal behaviour can be expected (Binney *et al.*, 1992). As a consequence of critical behaviour, the *details* of interactions are unimportant.

The present results can be very useful as a framework for our understanding of how species diversity is generated under non-equilibrium conditions (Connell, 1978; Solé, 1991). It is our belief that, in a constant environment where external perturbations are very weak, the way in which the system evolves to a *complex* state is linked with a critical phenomenon. At the critical state, *all* spatial and temporal scales are involved. Biologically, it means that *all* the opportunities are present, and so the highest diversity is generated.

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APPENDIX

The generalized dimensions can easily be calculated from real data. In order to obtain such a spectrum of dimensions, we first need to cover the set with a grid of boxes of equal size. The total covered surface should be normalized to size 1. Therefore, if $N(\epsilon)$ is the total number of boxes, $\epsilon = (N(\epsilon))^{-1/2}$ is their characteristic length.

Because of the discrete nature of our object, for a given ϵ_k we have an integer number of low canopy points inside each box. Let $n(i)$ and $N(j)$ be the number of low canopy points in the i-th box and the number of boxes containing j gap points, respectively. Then the sum in eqn (3) in the main text will be:

$$X_q(\epsilon) = \sum_{i=1}^{N(\epsilon)} p_i^q$$

$$= \sum_{i=1}^{N(\epsilon)} \left(\frac{n(i)}{N_P} \right)^q$$

$$= \sum_{j=1}^{j_{max}} N(j) \left(\frac{j}{N_P} \right)^q,$$

where N_P is the total number of low canopy points in the rain forest. Calculations become very simple with the use of the distribution function $N(j)$: the sum over boxes ($\approx 10^3$) transforms into a sum over occupation numbers (≈ 10). For the calculation of the multifractal spectrum, we need one of these ϵ_k values small enough, but large enough, to include a representative distribution of $N(j)$ (for a discussion see Falconer, 1990, and references therein). The standard procedure is to cover the set with several sets of boxes of different sizes and then calculate the slope of $\log[X_q(\epsilon)]$ vs $\log(\epsilon)$ (for a detailed study and applications, see Meisel *et al.,* 1992).

For the Barro Colorado Island we used $\epsilon = (1250)^{-1/2} \approx 1/35$ ($j_{max} = 16$) and $\epsilon = 1/20$ for the forest game ($j_{max} = 16$, also). After the choice of an adequate ϵ_k, D_q is estimated as:

$$D_q(\epsilon_k) = \frac{1}{(q-1)} \cdot \frac{\log[X_q(\epsilon_k)]}{\log(\epsilon_k)}.$$