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SFI WORKING PAPER: 1998-07-060

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J. Complex Systems (1998)

Random Walks, Fractals and the Origins of Rainforest Diversity

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(Received June 20 1998)

ABSTRACT. Rainforests are legendary because their extreme species richness. In the richest rain forests every second tree on a hectare is a different species. As a consequence, most species are rare. Using field data from studies in different parts of the world, we show that species-rich plots often display a distribution of number of species $N_s(I)$ represented by I individuals with a power-law shape $N_s(I) \propto I^{-\beta}$ with $\beta \approx 1.5$. Power laws are characteristic (but not exclusive) of systems poised close to critical points and this is supported by the analysis of the gap distribution over space in the Barro Colorado Island forest, which has been shown to be fractal. Here we propose a new model of rainforest dynamics which is able to account for a wide set of observations, strongly suggesting that indeed rainforests would be organized close to instability points, showing strongly path-dependent dynamics.
KEYWORDS: Diversity, Self-organized criticality, Rainforests.

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1. Introduction

Tropical rainforests are exceedingly rich ecosystems. Even a small area of these forests involves a huge number of species (for a recent review, see Gentry, 1990 and references therein). Interestingly, most of them are rare species. An example of the frequency distribution of tree species in a rainforest from Malaysia (Poore, 1968) is shown in figure (1). The distribution is based on a 1-ha plot study. The number of species with a single individual in the plot are roughly half of the total number of species.

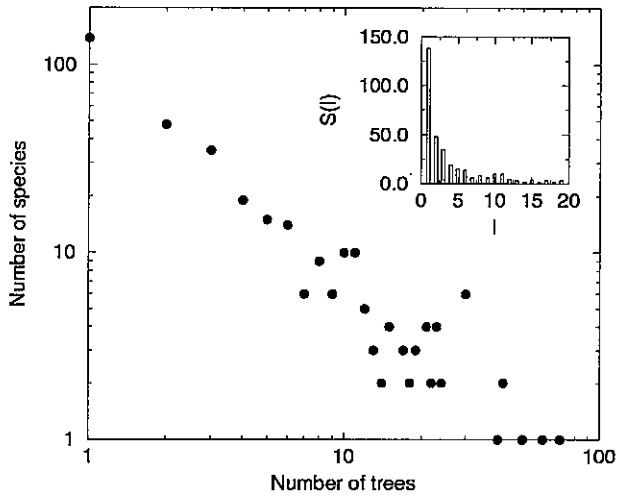

Figure 1. Frequency distribution of the number of species $N_s(I)$ formed by I trees for a Malasian rainforest in log-log scale (inset: standard plot)

This type of distribution is typical, and it is called a *power law*. Specifically, the number of species $N_s(I)$ represented by I individuals follows a distribution $N_s(I) \approx I^{-\beta}$. Most species are represented by one or a few specimens. In figure 1 we have also represented the previous distributions in log-log scale. If a well-defined power law is at work, a straight line should be observed. These data sets are well fitted by a power law, with $\beta = 3/2$. This power-law is also observed in the species-rich plots analysed at the Barro Colorado rainforest (data from Thorington et al, 1996).

Hence two important observations are involved: rainforests are very diverse and most species are rare. In rich rainforest plots species abundance follows a

power-law distribution and not a log-normal one, as it is usually assumed. These properties have been a matter of discussion for field ecologists over decades. In trying to explain diversity levels, many theories have been proposed. They involve climatic variations, variety of habitats available (edaphic properties), degree of isolation of the faunas and floras or even historical factors. Many authors considered such problem as the result of an incomprehensible web of causes.

Figure 2. A canopy gap at the Barro Colorado Island (see Leigh et al. 1996). This gap was formed because of the fall of a large tree and it has been colonized by seedlings. Here is shown in the early building phase. Sometimes, the gap is created through the fall of several trees. Such gaps can be very large and the overall distribution of gap sizes follows a power law $N(G) \propto G^{-2}$. The continuous state of flux linked with gap dynamics leads to a complex spatial pattern (drawing by Lynn Siri Kimsey), after Leigh et al., 1996.

Among competing theories, several imaginative proposals have been made. One of them is the Connell's intermediate disturbance hypothesis (Connell, 1976). It claims that high diversity is only sustained in an intermediate regime

of disturbances. This idea is well illustrated from the analysis of coral reefs. Extreme disturbances (such as storms) will simply damage most of the present species, being global diversity reduced. Null or very weak perturbations make possible competitive interactions to proceed further until exclusion takes place. But intermediate disturbances make competitive equilibrium unlikely to occur and so more species can coexist. Further analyses by Hastings supported this idea, although the relation does not need to be unimodal (Hastings, 1980). In this context we should cite the study by Nee and May, who explored the question of the effects of disturbances (habitat destruction) on a simple model of two-species competition (Nee and May, 1992). One of the conclusions of this work was that habitat loss can bring about changes in community composition in the remaining patches, even if such patches themselves undergo no intrinsic changes whatsoever.

Some authors have suggested that rarity (and so the origin of rare species) is a consequence of chaotic dynamics (Vandermeer, 1982). Strongly chaotic behavior (May, 1975) implies long periods of low population levels followed by population flushes. In this hypothesis internal causes and nonlinear interactions play the relevant role. Other phenomena which could play a relevant role are spatial chaos and supertransients (Solé et al., 1992; Bascompte and Solé, 1995): a set of locally interacting competitors on a given spatial domain can show very long transients before exclusion takes place. And recently, a remarkable analysis by Tilman on multispecies competition has shown how an adequate set of relationships between dispersal and extinction rates can lead to high diversity levels (Tilman, 1994). This study gave the explicit conditions for coexistence and stability of a complex community. Whithin Tilman's framework, there is no limit to the number of species that can coexist.

Some general comments are in order. First, space-explicit model ecosystems clearly show that space can make coexistence possible in situations where a space-free model predicts competitive exclusion (Solé et al., 1992; Bascompte and Solé, 1995, see also Condit, 1996). Second, many typical tropical rainforests are weakly altered by climate perturbations and so no *"intermediate regime" sensu* Connell applies, although high diversity is observed. In these systems, the source of perturbations is not exogenous but rather largely linked with *internal* causes: tree fall and gap formation (fig.2). In tropical rainforests, gaps in the canopy are the fingerprint of a strongly dynamical pattern. Recently, some authors (Solé and Manrubia, 1995a; 1995b) have shown that data available from a rainforest in Panamá (the Barro Colorado Rainforest, BCI) displays a fractal distribution of gaps over space. This fractal distribution cannot be trivially explained through simple statistical arguments. Fractal structures are typically the result of strong, self-organized large-scale correlations.

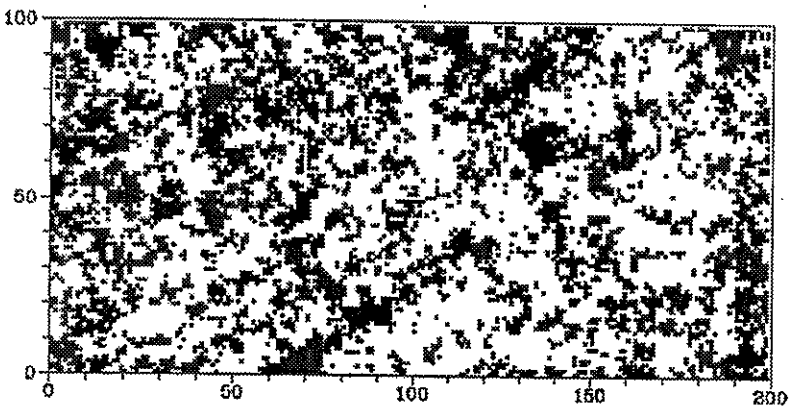

Figure 3. Gaps in the canopy. Here a picture of a canopy gap of Barro Colorado Island is shown. The area is divided in 5×5 m square. Black squares represent points where the height of the canopy was lower than 20 meters.

In figure 3 we can see the map of a 50-ha forest plot from BCI. Black squares indicate forest locations where the height of the canopy was less than 20 m (Wendel et al., 1991). Each point is in fact a 5×5 m square. These points give us an instantaneous picture of forest dynamics: they are linked with recent tree fall. Gap creation through falling trees is known to be a very important factor for rainforest diversity (Brokaw, 1985).

Barro Colorado is a fractal forest. We can see this in several ways. A first measure is the fractal dimension D_f of the previous map. Using the box-counting algorithm, we can calculate D_f. It is well known (Mandelbrot, 1982) that the number of boxes $N(\epsilon)$ of edge size ϵ necessary to cover the set is expected to scale as

$$N(\epsilon) \approx \epsilon^{-D_f} \tag{1}$$

in a recent study (Solé and Manrubia, 1995a, 1995b) It was shown that the BCI plot is in fact a fractal set with $D_f \approx 1.85$. These measurements were consistent with other quantities, such as the spatial autocorrelation and the multifractal spectrum. We can also appreciate the self-similar structure of these rainforests by means of the statistical structure of the tree size distribution (which follows

a power law) or the size distribution of gaps $N(G)$. Here we found $N(G) \approx G^{-2}$, a scaling law that seems to be rather common to different rainforests.

What we have, in short, is a complex dynamical system with long-range spatial correlations of self-similar type. Fractal structures are widespread in nature, and their origin has been a matter of discussion over the last decade. A novel approach to this problem was introduced by Bak, Tang and Wisenfeld in 1987: the so-called theory of self-organized critical processes (Bak et al, 1987). This remarkable paper suggested that fractal structures spontaneously emerge in nature as a consequence of the evolution towards a so-called critical state. Such critical points are well known from the physics of critical phenomena (Binney et al., 1993) and are characterized by the existence of fractal patterns, self-similar fluctuations and power laws. At criticality power laws spontaneously arise and the details of the system under consideration become irrelevant, except for a very small number of properties. A consequence of this fact is *universality*. By universality we mean that apparently very different complex systems behave in the same way close to critical points and that very simple models can exactly account for all the relevant macroscopic properties. This is a rather important result if we try to formulate a theory about the dynamics of an extraordinarily complex system such as the rainforest (Solé et al., 1998).

In the next section we discuss a theoretical simple model of species dynamics. We find anallitically the steady-state distribution of species abundance. In section 3 we introduce a spatially-extended model trying to mimic the dynamics of different species of trees in a rainforest plot. In both models we get a power-law distribution of species abudance $N(I) \propto I^{-\beta}$. The exponent β is 1.0 for the first model and 1.5 for the second one. In the last part of the section 3 we relate the exponent $\beta = 1.5$ to a critical branching process (Alstrom, 1988). Finally we discuss how these models can help us to understand the origins of diversity and the abundance of rare species in mature ecosystems.

2. Random Walks and the Polya Problem

The rainforest structure seems to suggest that a non-trivial self-organized pattern emerges from the interactions. On the other hand, the close observation of how species are scattered and how they fluctuate in their abundance have generated some interesting hypotheses. Hubbell and Foster (1989) have advanced the idea that the abundances of species in rainforests would be determined by random local mortality and colonization, leading to random drifts in abundances (see also Wilson, 1995). More specifically, they hypothesized that rainforest diversity may be maintained *" by a loose balance between speciation and the slow extinction of functionally identical species"*. Their study on the BCI plot sug-

gested that the presence of many of the rare species appeared to be the result of immigration from populations from outside the plot. These species in fact do not appear to have self-maintaining populations. In this section we explore this idea as the simplest null hypothesis.

We can assess the previous conjecture by using a simple model of species dynamics based on the so-called Polya Urn Problem (Brian Arthur, 1990; Johnson and Kotz, 1977). This simple, but highly nontrivial problem has been the source of a new theoretical approach to economics. Let us imagine an urn with infinite capacity to which balls of two possible colors (red, R, and white, W, say) are added. Starting with one red and one white ball in the urn, the evolution goes according to a simple rule: choose a ball in the urn at random. If it is red, add a red, and if white add a white. In 1931 George Polya proved that: (1) the proportion of red (or white) balls tends to a limit $X \in (0,1)$ with probability one and (2) X is a random variable with uniform distribution between 0 and 1. In complexity theory, this is called a path-dependent process.

We consider this simple urn model because it gives us a glimpse of how two growing populations with equal chances to reproduce can show path-dependent evolutions. Here if X_r and X_w are the population numbers of R and W respectively, the chances of reproduction under the previous rules are $p_r = X_r/(X_r + X_w)$ and $p_w = X_w/(X_r + X_w)$ respectively. As the experiment proceeds, these probabilities move towards a stationary value, as far as no limit to their population is considered.

Now let us follow this approach assuming that the urn is finite (but very large) and that a large number S of colors (species) and N balls (trees) is considered. At a given step, each color is represented by n_j balls. The finiteness of the urn is a crucial point. When a given ball is reproduced (with probability $P_j = n_j/(\sum n_i)$) another ball must be removed. This picture can be translated to a hypothetical ecosystem made by N individuals and S possible (different) species where the chances of reproduction (and hence of survival) are the same. It can be shown that, under this extreme situation, the distribution of species formed by I individuals is a power law $N_s(I) \approx I^{-1}$

To see this, let us consider a simple Polya process where a number of sites N can be occupied by a ball of a given color. Let us assume that S different colors are possible. Each time step, we take one of the balls at random and select another site also at random. Then we make a copy of the ball in the new site, replacing the color present at the second site. Additionally, we also introduce "mutation" in our rules. With a given probability μ (assumed small) the new ball will be of a different color than the ancestor. We can understand this change as an immigration event. In this rule we choose any of the other colors available. The mutation rule introduces new species into the ecosystem. This feeding term

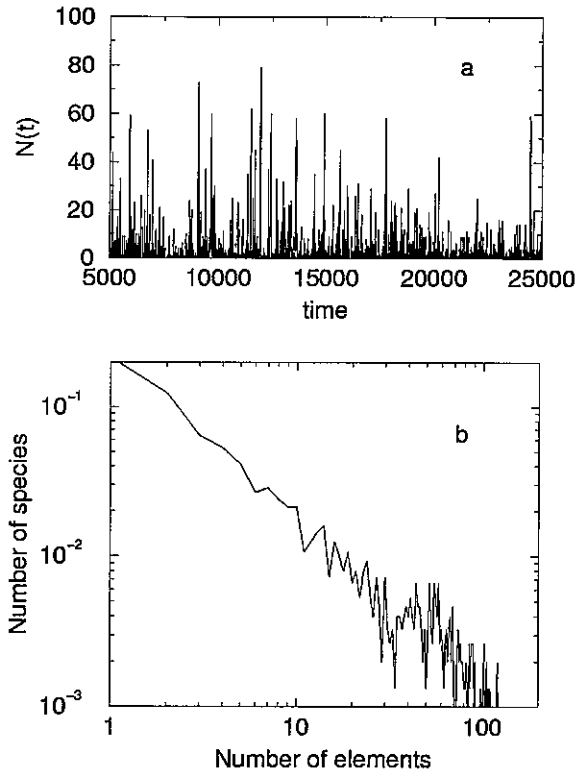

Figure 4. Temporal evolution of the Polya process (see text). Here $S = 100$, $N = 250$, $\mu = 0.005$. Only the population fluctuations of one of the species is shown. We can clearly appreciate a wide spectrum of population fluctuations. In (b) the statistical distribution $N_s(I)$ is shown. The power law scaling gives $N_s(I) \approx I^{-1}$ for small I.

is very important: if our community is closed to immigration/speciation, then a single-species stand will allways be observed at the end of a long-term simulation experiment (Hubbell, 1979).

Let $p(n,t)$ be the probability of getting exactly n balls of a given color. The time evolution of this probability will be given by the master equation (Nicolis and Prigogine, 1989; Haken, 1976):

$$\frac{\partial p(n,t)}{\partial t} = \sum_j p(j,t)\omega(n|j) + p(n,t)\sum_j \omega(j|n) \tag{2}$$

where $\omega(a|b)$ is the transition probability (per unit time) of jumping from b objects to a objects. If a time scale where only transitions involving a single individual are considered, we have:

$$\frac{\partial p(n,t)}{\partial t} = p(n-1,t)\omega(n|n-1) + p(n+1,t)\omega(n|n+1) -$$
$$-p(n,t)\Big[\omega(n-1|n) + \omega(n+1|n)\Big] \tag{3}$$

Let us further assume that the number of species S is very large, and consider the rest of the species as a single set. In our model the specific form of the master equation reads:

$$\frac{\partial p(n,t)}{\partial t} = (1-\mu)\Big(\frac{n-1}{N}\Big)\Big(1-\frac{n-2}{N-1}\Big)p(n-1,t)+$$
$$+\mu\frac{1}{S-1}\Big(1-\frac{n-1}{N}\Big)\Big(1-\frac{n-1}{N-1}\Big)p(n-1,t)+$$
$$+(1-\mu)\Big(1-\frac{n+1}{N}\Big)\Big(\frac{n+1}{N-1}\Big)p(n+1,t) + \mu\Big(\frac{n+1}{N}\Big)\Big(\frac{n}{N-1}\Big)p(n+1,t)-$$
$$-p(n,t)\Bigg\{(1-\mu)\Big(\frac{n}{N}\Big)\Big(1-\frac{n-1}{N-1}\Big) + \mu\frac{1}{S-1}\Big(1-\frac{n}{N}\Big)\Big(1-\frac{n}{N-1}\Big)+$$
$$+(1-\mu)\left(1-\frac{n}{N}\right)\left(\frac{n}{N-1}\right)+\mu\left(\frac{n}{N}\right)\left(\frac{n-1}{N-1}\right)\Bigg\} \tag{4}$$

In order to solve this equation, we can consider a simple case where $n \ll N$ and a large number of species. We will expand the master equation into a so-called Fokker-Planck equation, which is easily solvable at the steady state (Roughgarden, 1979; Van Kampen, 1990). Let us consider the following two transition rates:

$$\omega(n+1|n) = (1-\mu)\Big(\frac{n}{N}\Big)\Big(1-\frac{n-1}{N-1}\Big) + \frac{\mu}{S-1}\Big(1-\frac{n}{N}\Big)\Big(1-\frac{n}{N-1}\Big)$$
$$\omega(n-1|n) = (1-\mu)\Big(1-\frac{n}{N}\Big)\Big(\frac{n}{N-1}\Big) + \mu\Big(\frac{n}{N}\Big)\Big(\frac{n-1}{N-1}\Big)$$

Then the following moments are calculated:

$$M^+ \equiv \omega(n+1|n) + \omega(n-1|n)$$
$$M^- \equiv \omega(n+1|n) - \omega(n-1|n)$$

Using the previous approximations, and calling $x = n/N$, we can show that $M^-(x) \approx -2\mu x/S$ and $M^+(x) \approx 2(1-\mu)x$.

The Fokker-Planck equation for this process is given by (Van Kampen, 1990)

$$\frac{\partial P(x,t)}{\partial t} = -\frac{\partial}{\partial x} M^-(x)P(x,t) + \frac{1}{2}\frac{\partial^2}{\partial x^2} M^+(x)P(x,t) \tag{5}$$

$$= \frac{\partial}{\partial x}\frac{2\mu x}{S} P(x,t) + \frac{\partial^2}{\partial x^2}(1-\mu)xP(x,t) \tag{6}$$

The stationary solution $P_s(x)$ is obtained from $\partial_t P(x,t) = 0$ and is given by (Roughgarden, 1979):

$$P_s(x) = \frac{\mathcal{N}}{M^+(x)} \exp\left[+2\int^x \frac{M^-(x)}{M^+(x)} dx\right] \tag{7}$$

$$= \frac{\mathcal{N}}{2(1-\mu)x} \exp\left[-2\int^x \frac{\mu x}{S(1-\mu)x} dx\right] \tag{8}$$

which give a scaling law:

$$P_s(x) = \frac{\mathcal{N}}{2(1-\mu)} x^{-1} e^{-\omega x} \tag{9}$$

Here $\mathcal{N}$ is a normalization constant and $\omega \equiv 2\mu/(1-\mu)S$. The last term is a cut-off depending on the immigration rate and the number of species S in the pool.

So a simple Polya process where all colors (say species) are equally likely to reproduce, leads to a power law distribution with an exponent $\gamma = 1$. This can be tested through numerical simulations and a very good fit to the previous scaling is obtained. This is shown in figure 4(a-b). Here the previous set of rules is applied to an $N = 250$ system with $S = 100$ species and with $\mu = 0.005$. After $\tau = 10^3$ steps, we follow the dynamics over $T = 10^4$ time steps. An example of the time fluctuations of one of the species is shown in figure 4a and the statistical distribution of $N_s(I)$ is shown in figure 4b. Here we see that a widely fluctuating pattern of population size is generated and that a power law with an exponent $\gamma \approx 1$ is observed. So a simple density-dependent random process where species are fully equivalent and no complex interactions are allowed, leads to a power-law distribution that is not in completely agreement with the observations (see figure 1).

How are these observations linked with spatial fractals and power-law distributions of tree species? In the previous stochastic model no spatial distribution of trees is considered and in particular no differences among tree species (and so in

their interactions) are taken into account. In the following section we introduce a simple, spatially-explicit model of rainforest dynamics able to reproduce the main statistical properties observed in these ecosystems.

3. The Diversity Game: Spatial model of rainforest dynamics

In this section we present a simple model of rainforest dynamics where space is discretized as a $L \times L$ lattice of patches. This model takes into account species diversity. It is inspired on a previously studied model involving only a single-species population of trees (Solé and Manrubia, 1995a; 1995b) which was known as the Forest Game. The new model, which we call the Diversity Game (DV), involves rules which try to get a clear though oversimplified picture of rainforest dynamics. Of course, the real forest is much richer and subtle, but we should keep in mind that (a) only broad, large-scale statistical properties are searched for and (b) if generic mechanisms are at work (as it occurs close to instability points) then no need for specific details is required.

The system starts from a random initial condition where trees of several species are randomly scattered over space (the specific properties of this initial condition do not modify the final outcome of the simulations). For simplicity, we use a $L \times L$ lattice where "trees" are placed. Each tree is defined by a state (the size) $S_m(i,j;t)$ where (i,j) indicates the spatial position and m stands for the particular species under consideration. If no tree is present at (i,j), we say that we have a canopy gap point.

Tree diversity is defined in a simple way and a simple set of rules is considered. These rules are applied asynchronously. Each time step, each lattice point is updated, but this updating rule is applied in a random order. We use this procedure in order to avoid spurious correlations. The species properties and rules are defined as follows.

Tree diversity

As it is well known, the strategies of a tree species for growth, dispersal, colonization, and survival are extremely rich in complexity. A lot of subtle differences among them can be distinguished. How to introduce tree diversity in a simple model? It seems natural to introduce some kind of trade-off between growth and reproduction. If a large amount of energy is used in producing successful seeds, a lower amount of energy can be dedicated to effective growth. There are many possibilities of limiting the strategies used by a given species. Our model takes

into account these constraints in a very simple way:

$$R_m = 1 + [\frac{m}{K}] \quad ; \quad m = 1, 2, ..., S \tag{10}$$

$$R_m \in \{1, 2, ..., \frac{L}{2}\}$$

$$g_m = g_0\Big(1 - \frac{m}{S}\Big) \; m = 1, 2, ..., S \tag{11}$$

where g_0 and g_m stands for the maximum growth rate and the growth rate of the m-th species repectively and R_m for seed dispersal radius. $L/2$ is the total number of dispersal cathegories, S is the total number of species and $K = 2S/L$ is the number of species that have the same dispersal radius. Other models that introduce a trade-off between the capacity of growth and the likelihood of leaving offspring can be proposed. We have studied several of them and obtained very similar results. The balance between growth and reproduction allows many species to remain in the system. On the other hand, as we will show later, the species frecuency distribution is consistent with field data.

Birth

A given empty lattice point can always be externally colonized with probability P_e ($P_e = 0.01$) by a tree species which is chosen randomly among the species pool. Tree birth size is S_0 (here $S_0 = 0.1$). If a tree of a given species m at the lattice point (a, b) has a size higher than S_1 (here $S_1 = 1$), then it can produce seeds. We look at a random point in a circle of radius R_m around (a, b). If it is empty, a seed of species m germinates and a new tree of a size S_0 is stablished there.

Death

Each tree can die with a fixed probability P_d (in our simulations $P_d = 0.015$, in agreement with field data, Gentry, 1990)

Growth

The size of a tree is updated according to:

$$S_m(i, j; t+1) = S_m(i, j; t) + g_m \Theta\Big[\, 1 - \frac{\frac{1}{q}\sum_{<i,j>}^{q} S_n(l, k; t)}{S_m(i, j; t)} \,\Big] \tag{12}$$

Here $\Theta(z) = z$ if $z > 0$ and zero otherwise. q stands for the number of neighboring trees used ($q = 8$ in our study). g_m stands for the growth rate of the m-th species and the sum is performed over the eight nearest neighbors. As we can see, if the mean size of the neighbors is larger than tree size at the central point, then no

growth is allowed. On the other hand, no growth is allowed over a maximum size S_m ($S_m = 40$). We have tested slightly different similar rules and the final outcome does not seem to be affected by the specific function $\Theta(z)$ at work.

Gap formation

When a tree dies, it falls and leaves a gap in the canopy. This is simulated in a similar way as in previous models (Solé and Manrubia, 1995a; 1995b). However, in the present model a tree death can only have a direct effect on the set of the 8 nearest neighboring trees. Only the trees of this neighborhood which satisfy:

$$\sum_{<i,j>} S_n(r,s;t) \leq S_m(i,j;t) \tag{13}$$

are eliminated. Here $< i,j >$ stands for the $q = 8$ nearest neighbors of the (i,j) tree. Therefore a primary gap can only involve one to eight neighboring trees in the present model.

Gap Expansion

We introduce the field observation that those trees at the edge of a gap have an increased probability of dying (Welden et al, 1997). When a primary gap G_0 is formed, defined as

$$G_0 = \{\mathbf{r}_\mu \ : \ S(\mathbf{r}_\mu;t) = 0 \ , \ \mu = 1,...,n_0 \ , \ n_0 \leq 9\} \tag{14}$$

(here $\mathbf{r}_\mu \equiv (i,j)_\mu$ with $1 \leq i,j \leq L$), we next consider the boundary of the gap

$$A(G_0) = \{\mathbf{r}_\mu \ : \ d(\mathbf{r}_\mu, G_0) = 1 \ , \ \mu = 1,...,n\} \tag{15}$$

where

$$d(\mathbf{r}_\mu, G_0) = \min_{\mathbf{r}_\mu \notin G_0, \mathbf{r}_\nu \in G_0} \{d(\mathbf{r}_\mu, \mathbf{r}_\nu)\} \tag{16}$$

and $d(\mathbf{r}_\mu, \mathbf{r}_\nu)$ is the city distance. That tree belonging to $A_1(G_0)$ and presenting the sharpest relative change in its enviromental conditions –i.e. in the 8-neighbor-mean size– dies. We define the relative enviromental change of a point at the edge of a gap in this way:

$$\beta(\mathbf{r}_\mu) = \frac{\Omega_0(\mathbf{r}_\mu) - \Omega_1(\mathbf{r}_\mu)}{\Omega_0(\mathbf{r}_\mu)} \tag{17}$$

where $\Omega_0(\mathbf{r}_\mu)$ and $\Omega_1(\mathbf{r}_\mu)$ stand for the 8-neighbor-mean size before and after canopy gap formation. We compute the relative enviromental change of each point, $\beta(\mathbf{r}_\mu)$. The tree at $\mathbf{r}_\mu \in A(G_0)$, such that $\beta(\mathbf{r}_\mu)$ is maximum dies and the state of the point $\mathbf{r}_\mu$ is set to zero. A tree death at the boundary of a gap is (or not) able to generate a new primary gap. It depends on the size of the tree just

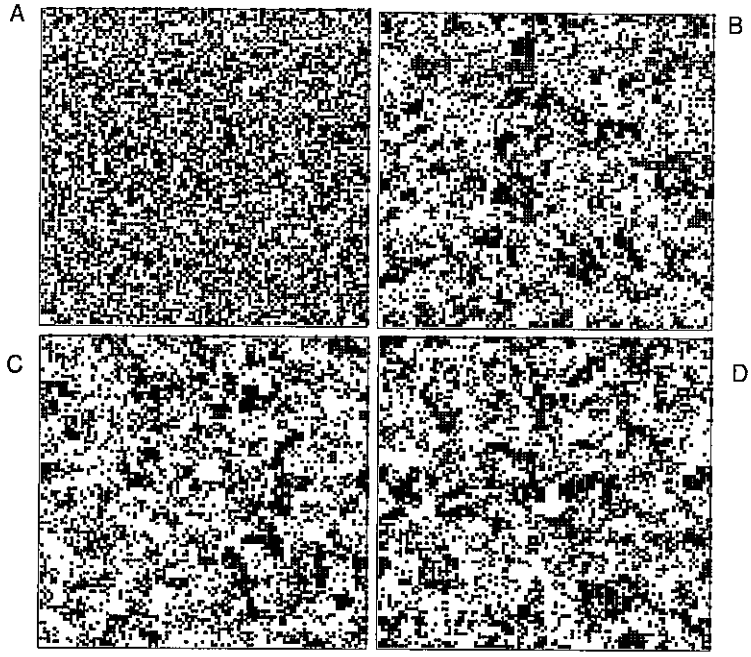

Figure 5. Four snapshots of a $L = 100$ cellular automata model of forest dynamics. A, B, C and D are images corresponding to initial time, 10, 20 and 100 time steps respectively. Black squares are gap points. After a transient period where growth dominates over gap creation, a steady state is reached with a gap size distribution following a power law.

died. We consider the border trees of the whole gap formed and then we repeat the same process to determine whether or not gap expansion continues. There is some kind of extremal dynamics (Bak and Paczusky, 1995): expansion goes further as a consequence of the death of the most perturbed tree at the edge of the expanding gap.

A first picture of the dynamics of our simulated forest is given in figure (5) where the spatial distribution of canopy gap points is shown at four different time steps. Here black squares indicate lattice points where the size is less than S_0. We start with a lattice conteining half of the points with a small tree of minimum size and each one belonging to one of the possible species (the choice is made at random). As trees grow, the canopy size grows and only small gaps are observed. But after a transient period, we can see that gaps of a wide range of

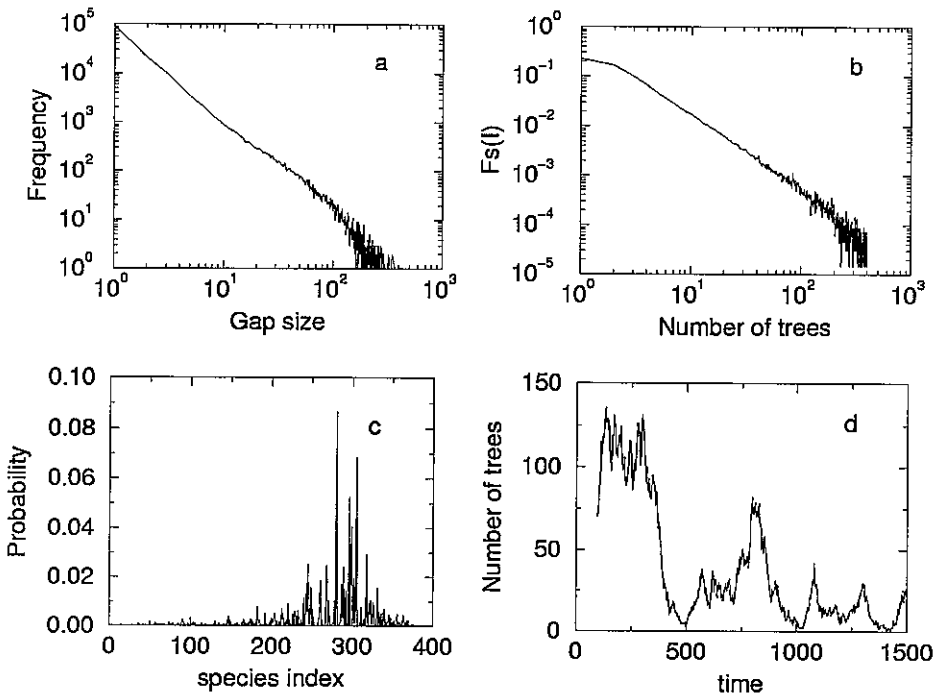

Figure 6. Some graphic results from the simulated model. Calculations have been made after a transient period of 800 time steps. (a) Gap size distribution following a power law $N(G) \approx G^{-2}$. We have accumulated the numbers during 201 time steps. (b) Distribution of relative frequency of species $F_s(I)$ represented by I individuals with a power-law shape $F_s(I) \propto I^{-\beta}$ with $\beta \approx 1.5$. (c) Relative composition of tree species in the final state $\tau = 2800$. (d) Temporal evolution of one species (index 214) followed during 1500 time steps.

sizes are formed and that the statistical distribution of gaps remains stationary in time independently upon the initial condition. Then a frequency-distribution of gaps of a given size G can be computed (as we did for the BCI data) and the power law $N(G) \approx G^{-2}$ is also found (figure 6a).

If we look at the time dynamics of this model, we see that complex fluctuations are observed (figure 6d). Here the temporal evolution of the number of trees of a given species is shown suggesting a random-walk behavior. However, the fluctuations display a rather complex behavior, with extinctions and reappearences. If we analyse the frequency distribution $N(I)$ we again find a power-law now

with an exponent $\beta \approx 1.5$, also consistent with field data (figure 6b, see also figure 1). In figure 6c we plot the distribution of the trees belonging to a given species index, as defined by (10-11). We can see that none of the extreme cases is likely to be observed, but a broad range of intermediate strategies is found. This distribution, however, is highly irregular and isolated peaks involving many individuals of a given species are easily found. There is no guarantee that such peaks remain even a few generations in time: the dynamics is extremely path-dependent and the species composition strongly unpredictable. So by means of a more realistic simulation model involving simple rules of interaction and gap formation, we get a self-organized system which exhibits the main observed statistical features of real rainforests. In previous studies, it was suggested that the BCI data are compatible with a complex system poised near a critical point (Solé and Manrubia, 1995a, 1995b). If true, then rainforest diversity should also be linked with criticality. Let us remind that, after a transient period, the forest reaches a stationary regime with fractal structures, power laws in gaps, tree sizes, and diversity. This occurs in a self-organized way and some specific scaling exponents are obtained. Which type of self-organized critical dynamics is taking place? The answer of this question would come from the theory of branching processes (BP) where the $\beta = 3/2$ exponent is rather well known (Harris, 1963). Roughly speaking, a BP is defined as a stochastic process where individuals can reproduce with some probability leaving a number of offspring or be extinct. Let us consider a simple BP by which in each generation an individual is replaced by zero, one or two descendants with probabilities P_0, P_1 and P_2 respectively. This process, starting from a given individual, generates a tree of descendants. The mean increase in the number of individuals from one generation to the next is

$$< N >= \sum_k kP_k = P_1 + 2P_2 \tag{18}$$

and criticality is defined by the condition $< N >= 1$ i. e. $P_0 = P_2 = (1 - P_1)/2$.

For a critical branching process (CBP) some general statistical properties can be derived (Harris, 1963, Alstrom, 1988). By using the generating function

$$G(z) = P_0 + P_1 z + P_2 z^2 \tag{19}$$

the probability $P(s)$ that a BP creates a tree with s "individuals" is, for large s:

$$P(s) = \left[\frac{G(\sqrt{P_0/P_2})}{4\pi P_2}\right]^{1/2} A^{-s} s^{-\tau} \tag{20}$$

where A is a given constant (obtained from P_0 and P_2) and, at criticality, $\tau = 3/2$. This exponent is precisely the β exponent observed in rainforests. Given the long

life span of trees (so we see both parents and descendants) perhaps the observed distribution is just a consequence of a CBP.

If the previous scenario is correct, then we should be able to say something about the expected number of tree species in a rainforest. Our conjecture is that the system evolves towards a self-organized state where the distribution of species follows a power law i. e.

$$N_s(I;\beta) \approx I^{-\beta} \tag{21}$$

and if M is the maximum number of individuals in the ecosystem (a given forest plot) we could derive some general relations concerning the number of species in a given rich-species forest plot as well as how this number is related to the number of rare species.

The total number of species $S(\beta)$ is easily obtained from the integral

$$S(\beta) = \int_1^M N_s(I;\beta)dI \tag{22}$$

which, for $\beta > 1$ leads to

$$S(\beta) = \frac{N_s(1;\beta)}{\beta - 1}\left[1 - M^{1-\beta}\right] \approx \frac{N_s(1;\beta)}{\beta - 1} \tag{23}$$

For the critical branching limit, i. e. $\beta = 3/2$ we get

$$S(\beta = \frac{3}{2}) = 2N_s(1) \tag{24}$$

So the total number of species is just twice the number of rare species or, in other words, in a given plot half of the species will be rare, only represented by a single tree. This result is consistent with the observation: for the Cocha Cashu rainforest, we have $S = 201$ and $N_s(1) = 109$, and for the Malayan forest we have $S = 328$ and $N_s(1) = 150$. For another two species-rich forests in Malaysia (Manokaran and Kochummen, 1987) we also get $S = 493$ and $N_s(1) = 244$ for Sungani Menyala and $S = 515$ and $N_s(1) = 264$ for Bukit Lagong. In all these areas, no strongly dominating species was present. In other cases, a few number of tree species have very large populations and this generates discrepancies from our result. Such abundant species make the power law $N_s(I) \propto I^{-3/2}$ deviate from actual data. If these species are not considered, the previous result is recovered.

4. Discussion

In this paper we tried to address several questions concerning rainforest diversity by means of a simple model and a few theoretical arguments. The main

problem under consideration was in fact the origins of diversity as well as an explanation for the abundance of rare species. Our proposal is that rich-species rainforest plots would be dynamically poised to a critical state. By means of a continuous "driving force" provided by constant immigration the system moves towards unstability. At this point, interactions keep the community balanced in an unstable state where changes in species composition can propagate throughout the system giving a complex pattern in abundance fluctuations. This is reflected in the power-law distribution and in rarity. The analysis of the tree species abundance distribution in different tropical rainforests shows that a power-law $N_s(I) \propto I^{-\beta}$ is obtained, with a characteristic exponent $\beta \approx 3/2$ which is compatible with a critical branching process. If a CBP is acting, the probability of a given tree to leave offspring equals the probability of no reproduction. This balance results in a complex fluctuation of species abundances and a highly path-dependent behavior. The specific characteristics of the time-fluctuations will be analysed elsewhere. Let us mention that they typically deviate from simple random walks and behave in terms of fractional Brownian motion (fBm).

If a large number of species is allowed to interact, the model ecosystem evolves towards a stationary state where the following properties have been detected: (1) a power-law distribution of low canopy gaps $N(G) \approx G^{-\alpha}$ with a characteristic exponent $\alpha = 2$; (2) a fractal distribution of gaps over space, with a fractal dimension $D = 1.8$, consistent with a previous analysis of the Barro Colorado plot; (3) a power-law distribution of tree sizes; (4) a diversity distribution where the number of species $N_s(I)$ formed by I trees shows a power law decay with a characteristic exponent $\beta \approx 3/2$. (5) fractional Brownian motion (fBm) behavior in time evolution of species abundances. As a consequence of fBm, from time to time a rare species can start to grow (just by chance events) and get a large population with strong fluctuations (figure 6d).

It is interesting to mention that not only in rainforests but also in other rich ecosystems the same exponent $\beta = 3/2$ has been observed. For instance, Frontier (1994) has pointed out that Zipf-Pareto model of species diversity $F_r = CTE(r+b)^{-\gamma}$, represented by a retroaccumulative curve of Rang Frecuency Diagram (RFD), fits well to ecological data in certain stages of ecosystem evolution and at a certain observation scales. He has analyzed several data sets from mature ecosystems and found a characteristic exponent $\gamma = 2$. It can be easily shown the equivalence between Zipf-Pareto model and a power-law distribution $N_s(I) \propto I^{-\beta}$, where $\beta = 1 + 1/\gamma$. Therefore this exponent $\beta = 1.5$ seems to be a very general property of rich, mature ecosystems.

A consistent scenario emerges from a self-organized dynamical state. Tree species evolve, disperse and diversify interacting in complex ways, not just among them but also with other biological groups. Any improvement leading to more

offspring will be sooner or later threatened by the evolution of other competitors. In this scenario, the only limits to diversity are determined by the critical state. As the system approaches a high diversity level, the balance between speciation/immigration and extinction leads to a CBP a consequence of which is rarity, precisely in the way observed in real rainforests. If true, then the way diversity is created and maintained should be reinterpreted in dynamical terms. Fractal patterns are the spatial counterpart of a dynamical, perhaps critical, behavior. Diversity and self-similarity appear to be connected in a subtle, nontrivial fashion. Self-similarity arises in ecosystems at multiple scales, from the ecological scales (Sugihara and May, 1990; Keitt and Stanley, 1998) to the evolutionary ones (Solé et al., 1997).

If the previous results can be generalized to other groups of organisms (at least at some spatial and temporal scales), we get an interesting picture of the ecosystem where the instability state is spontaneously reached as a consequence of (a) a driving force represented by constant immigration-speciation events taking place at a low rate, and (b) the presence of macroscopic, generic constraints to ecosystem stability which introduces the generation of ecological "avalanches". This scenario has been proposed by Keitt and Marquet in relation to the extinction of Hawaiian birds (Keitt and Marquet, 1996). At some scales, collective properties depending upon the universal features o f complex systems would be crucial to the final state of the ecosystem. Given the current destruction rate of wild life and natural habitats, specially rainforests, it is of great importance to understand how complex, many-species ecosystems are likely to react under external pertubations. If the intrinsic dynamics is both hightly non-linear and path-dependent, then very complex responses are likely to be observed, which would make any kind of prediction very difficult.

Acknowledgments

The authors would like to thank M. Cabeza, B. Luque, A. McKane, S. Manrubia, K. Sneppen, J. Pérez-Mercader, B. Goodwin, P. Bak, and S. Kauffman for useful discussions. RVS thanks Joe Wright for inviting him to visit the BCI rainforest, and also Rick Condit and Egbert Leigh for interesting discussions. DA would like to thank his friend J.M. Rey for discussions, encouragement, and help with computer facilities. This work has been supported by a grant DGYCIT PB94-1195 and a grant of Fundacion Caja de Madrid 1998 (DA) and by the Santa Fe Institute (RVS), where part of this work was done.

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