

From companies to colonies: The origin of Pareto-like distributions in ecosystems

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Abstract

Recent studies of cluster distribution in various ecosystems revealed Pareto statistics for the size of spatial colonies. These results were supported by cellular automata simulations that yield robust criticality for endogenous pattern formation based on positive feedback. We show that this self-organized criticality is a manifestation of the law of proportionate effect, first discovered in the context of business firm size. Mapping the stochastic model to a Markov birth-death process, the transition rates are shown to scale linearly with cluster size. This mapping provides a connection between patch statistics and the dynamics of the ecosystem; the "first passage time" for different colonies emerges as a powerful tool that discriminates between endogenous and exogenous clustering mechanisms. Imminent catastrophic shifts (like desertification) manifest themselves in a drastic change of the stability properties of spatial colonies, as the chance of a cluster to disappear depends logarithmically, rather than linearly, on its size.

In spatially extended ecosystems the observed patchiness supplies a lot of information on a given system's parameters and may signal that the system is approaching a transition [1]. Of particular interest are ordered [2, 3, 4, 5] and disordered [6] vegetation patterns in the semi-arid climatic zone, where climate changes and overgrazing lead to an accelerated process of desertification [7]. Recently, two groups of researchers simultaneously published new results about patch-size statistics. Using high-resolution remote sensing techniques, these groups found power-law distributions of vegetation patch size (the probability of finding a vegetation patch of size n falls like $n^{-\beta}$ where β is greater than unity and can vary between different regions) along the Kalahary Transect [8], and in three Mediterranean ecosystems [9]. Another new study [10] has shown that the spatial distribution of ant colonies in a tropical agroecosystem is also Pareto-like. Power-law statistics indicate the absence of an intrinsic scale in the system, and in many cases its appearance signals that a stochastic system is "at criticality", i.e., experiencing a continuous phase transition [11]. It is surprising to find scale-free distributions along a wide range of environmental conditions; in most systems it appears only at the transition point [12]. The challenging problem, thus, is to identify the mechanism that yields robust critical behavior for different ecosystems under a wide scale of environmental conditions.

To support and explain their findings, all three groups suggested (slightly different) cellular automata models that support self organized criticality. Effectively, there are only two parameters in these models: the global constraint on the overall fractional tree cover, f^* , and the local strength of positive-feedback between plants (for the sake of concreteness we use hereon the spatial vegetation terminology; our results, however, are generic). Facilitation implies that the chance of an occupied cell to become empty decreases, and the chance of an empty cell to become occupied increases, if its neighboring cells are occupied. It turns out that these two constituents are sufficient to ensure self-organization and power-law distribution of patch sizes, while the details of the model (like the definition of neighborhood, kernel function, etc.) affect only the slope β . These results increase the need to identify the underlying feature that makes criticality a robust property of models with global capacity constraints and positive-feedback.

In order to elucidate the dynamical law that governs self-organized criticality, we have mapped the cellular automata used by Scanlon et. al. into a Markov chain. The cellular automaton introduced by [8] was used here with only slight modifications. Every cell is either

empty (0) or covered by tree canopy (1), and local facilitation determines the transition probabilities between these two states. The actual overall fraction of occupied cells, f , affects the dynamics if it deviates from the fractional tree cover allowed by the environmental conditions (the carrying capacity) f^* . The transition rates in the (i, j) cell are,

$$\begin{aligned} P_{i,j}(0 \rightarrow 1) &= \rho_{i,j} + \frac{f^* - f}{1 - f} \\ P_{i,j}(1 \rightarrow 0) &= \rho_{i,j} + \frac{f - f^*}{f}, \end{aligned} \quad (1)$$

where $\rho_{i,j}$ reveals the effect of facilitation by other biomass units in the local neighborhood,

$$\rho_{i,j} = \frac{1}{S} \sum_{k,l \in S} \sigma_{k,l}, \quad \sigma_{k,l} = \begin{cases} 1 & \text{if site } (k, l) \text{ is populated} \\ 0 & \text{if site } (k, l) \text{ is empty} \end{cases} \quad (2)$$

where S is the area of a region of diameter r centered at the (i, j) cell. Grazing was added to the model by letting a fraction G of the "death" events occur at a constant rate, independent of the local density $\rho_{i,j}$.

During the simulation, clusters were tracked and their sizes were monitored. The birth and death rates for size n clusters were determined by dividing the number of transitions $n \rightarrow n + 1$ and $n \rightarrow n - 1$, respectively, by the average number of size n patches. The parameters γ , α and Δ_0 were extracted from b_n and d_n using linear regression.

Switching to patch size oriented dynamics, the events where a patch of size n is grown or decreased were monitored to yield the corresponding transition rates. It turns out that a stochastic birth-death process (where only ± 1 transitions are allowed) is a remarkably good approximation for the real dynamics. If b_n is the birth rate (the chance of a patch of n cells to grow by one cell, or one vegetation unit, to $n + 1$) and d_n is the corresponding death rate, the time evolution of the patch size distribution $P_n(t)$ is described by the master equation:

$$\frac{d}{dt} P_n(t) = -(b_n + d_n) P_n(t) + d_{n+1} P_{n+1}(t) + b_{n-1} P_{n-1}(t), \quad (3)$$

and its steady state π_n should satisfy the local balance equation $\pi_n b_n = \pi_{n+1} d_{n+1}$. This allows for a recursive solution for the steady state [13], once the birth-death transition probabilities are given.

Figure 1 shows the dependence of b_n and d_n on n . Apparently, both b_n and d_n grow linearly with n . However, the death rate is larger by a constant Δ , i.e.,

$$b_n = \gamma n \quad d_n = \gamma n + \Delta. \quad (4)$$

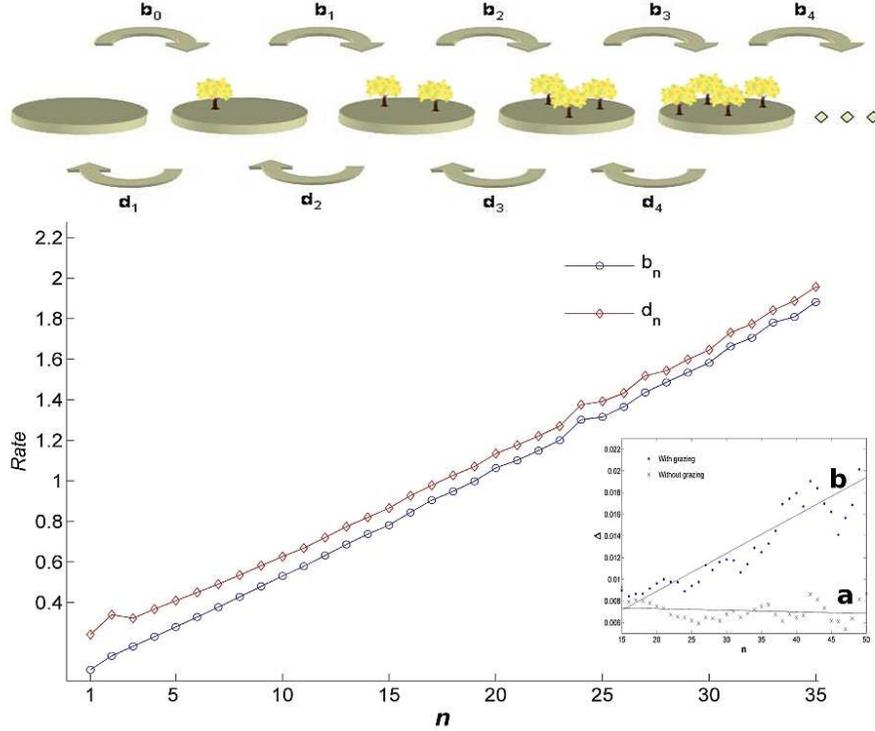


FIG. 1: Tracing the stochastic simulation along time, the rates in which clusters of size n grow by one biomass unit, b_n , or decay by one unit, d_n , were monitored (see methods, here the parameters are $f^* = 0.1$, $r = 3$). Neglecting merging and splitting of colonies, where size is changed by more than one unit, one gets the Markov birth-death process illustrated in the upper panel. In the lower panel the birth-death rates (in arbitrary units) are shown in the absence of grazing pressure; the rate of both processes grows linearly with the colony's size, where the death rate is always larger by a constant Δ . In the inset, the difference $\Delta(n) \equiv d_n - b_n$ is presented without (a) and with (b) grazing pressure together with a linear fit. While $\Delta(n)$ is approximately constant without grazing, it shows, on average, linear growth where grazing is present. This gives the ground for the approximation $\Delta(n) = \alpha n + \Delta_0$, where α increases with grazing pressure.

Using the local balance equation the steady state may be obtained analytically:

$$\pi_n = \frac{b_0 \pi_0}{d_n} \prod_{m=1}^{n-1} \frac{b_m}{d_m} = \frac{b_0 \pi_0}{\gamma n + \Delta} \prod_{m=1}^{n-1} \frac{\gamma m}{\gamma m + \Delta}, \quad (5)$$

where π_0 is determined by the normalization condition. The product (5) may be calculated exactly, and then approximated for $n > 1 + \frac{\Delta}{\gamma}$ to yield,

$$\pi_n = \frac{b_0 \pi_0}{\gamma} \frac{\Gamma(n) \Gamma(1 + \frac{\Delta}{\gamma})}{\Gamma(n + 1 + \frac{\Delta}{\gamma})} \approx A n^{-(1 + \frac{\Delta}{\gamma})}, \quad (6)$$

where A is a normalization constant. Comparison between the distributions obtained from the cellular automata simulations and the power-law (6) using the calculated values of γ

and Δ shows excellent agreement (Figure 2, upper panel). This supports the approximation made by replacing the general Markov chain with a birth-death process.

The monotonic increase of event rates with cluster size emerges, thus, as the dynamical law that generates criticality. This, in fact, is the law of proportionate effect [14], introduced many years ago in order to explain the Pareto distributions in economic systems [15, 16, 17]. Similar mechanisms were shown to underly surname statistics [18], relative species abundance [20], urban population size [19] and many other observations. Although here the geometric random walk is biased towards extinction, the multiplicative nature of the process guarantees power-law distributions, where the slope is determined by the bias Δ . The results presented here are for facilitation radius $r = 3$; testing the model under different conditions, the slope β was found to increase with r . Approximating the real Markov chain as a birth-death process turns out to be exceptionally good; for all cases tested by us ($r = 2, 3, 4$) the slope obtained from Δ and γ differs only by 5 – 10% from the slope measured directly on the cellular automata.

As indicated by the field data analyzed by Kéfi et. al., patch distribution deviates from power-law in the presence of grazing pressure. A truncated power-law has been suggested in that case, where the strength of the grazing determines the typical patch size above which the distribution crosses over to exponential decay. Introducing grazing into our model through a density independent mortality rate (see methods), the same truncated power-law has been obtained. Mapping to a birth-death Markov chain, the only qualitative difference is that, under grazing, the leftward bias Δ grows linearly with the patch size, i.e., $\Delta = \Delta_0 + \alpha n$ (See inset of Figure 1). Substituting in (5) one attains,

$$\pi_n = \frac{b_0 \gamma \pi_0}{(\gamma + \alpha)^2} \frac{\Gamma(n) \Gamma(1 + \frac{\Delta_0}{\gamma + \alpha})}{\Gamma(1 + n + \frac{\Delta_0}{\gamma + \alpha})} \left(\frac{\gamma}{\alpha + \gamma} \right)^n. \quad (7)$$

In the limit of $n \gg 1$ this expression becomes the truncated power-law,

$$\pi_n = A n^{-(1 + \frac{\Delta_0}{\alpha + \gamma})} e^{-n/n_0}, \quad (8)$$

where $n_0 \equiv \left[\ln\left(\frac{\alpha + \gamma}{\gamma}\right) \right]^{-1}$ is the patch size above which π_n decreases faster than a power law. The equilibrium distributions (6) and (8) fit perfectly the power law and truncated power law obtained from direct numerics, as seen in fig. 2.

The main characteristic that distinguishes endogenous from exogenous cluster formation mechanisms is the dynamic of the system. If spatial heterogeneity plays a major role and

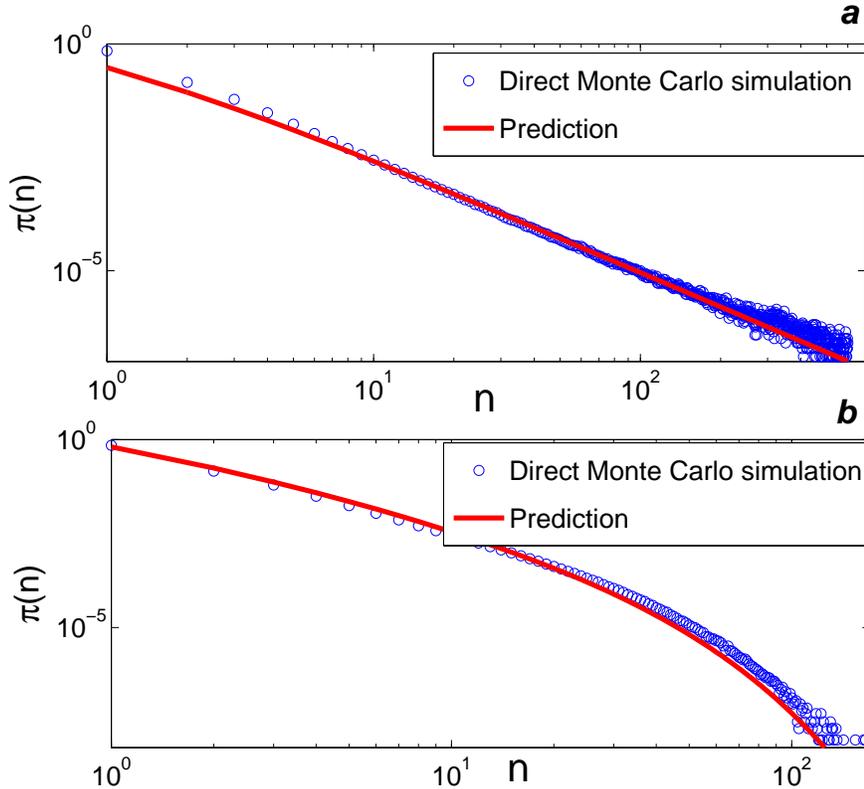


FIG. 2: The equilibrium probability π_n is presented vs. n on a log-log scale, showing power-law behavior in the absence of grazing [upper panel, (a)]. The circles are results attained from the stochastic cellular automata, where the full line corresponds to the analytic expression (6) for the solution of the birth-death process. The lower panel (b) shows the same in the presence of grazing ($G = 0.6$, see methods), where the truncated power law attained from the simulations is compared with (8). The relevant parameters α , γ and Δ_0 are those extracted by linear regression from Figure 1.

determines the location and the size of large colonies, the chance of such a colony to disappear due to demographic stochasticity is exponentially small [21], so in practice, on experimental time scales, large colonies never disappear. This feature was used by Vandermeer et. al. [10], who utilized the appearance/disappearance of large ant colonies as a manifestation of endogenous population dynamics. Our mapping of the system into a Markov chain allows us to quantify these characteristics and to establish a connection between the steady-state distribution and the dynamics of a single cluster.

We define τ_n^m as the mean first passage time [22] from some initial cluster size n to some smaller size m . Since the mean time for a cluster of size n to undergo a birth/death step is

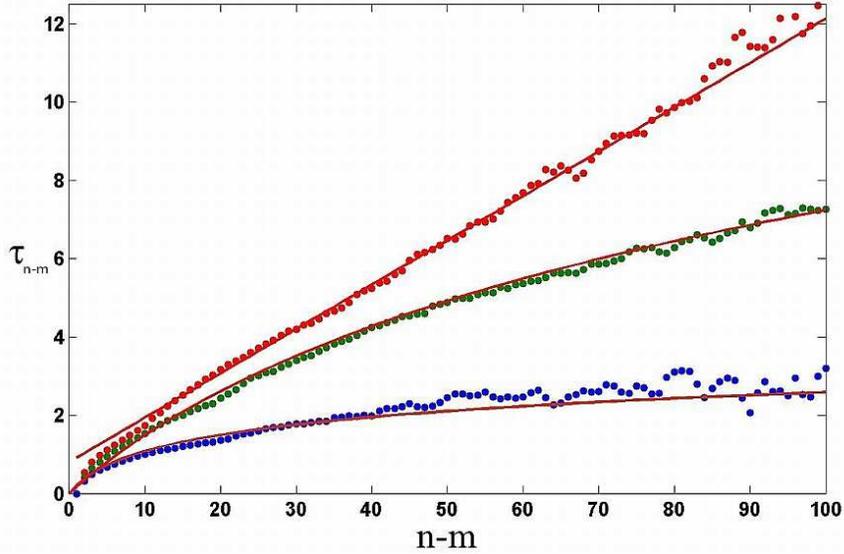


FIG. 3: τ_{n-m} , The average time elapsed until a colony of size n reaches a smaller size m at the first time is plotted against $n - m$ for different environmental conditions. In the absence of grazing ($G = 0$, red circles) the stability of a colony grows linearly with its size. Under grazing pressure ($G = 0.4$, green and $G = 0.6$, blue) the time to extinction grows only logarithmically with the patch size. Datasets were taken directly from the simulation of the cellular automata with $r = 3$ and $f^* = 0.1$, and are fitted (full lines) to the predictions (10) using nonlinear curve fitting.

$1/(b_n + d_n)$, the mean first passage times should satisfy:

$$\tau_n^m = \frac{1}{b_n + d_n} + \frac{b_n}{b_n + d_n} \tau_{n+1}^m + \frac{d_n}{b_n + d_n} \tau_{n-1}^m. \quad (9)$$

Substituting $b_n = \gamma n$ and $d_n = \gamma n + \alpha_n + \Delta_0$, we get, for $n \gg 1$:

$$\tau_n^m = \frac{1}{\alpha} \ln \left(\frac{\alpha(n - m) + \Delta_0}{\Delta_0} \right). \quad (10)$$

In that limit, the first passage time depends only on the difference $n - m$. In the absence of grazing ($\alpha \rightarrow 0$), we get $\tau_{n-m} = (n - m)/\Delta_0$.

Evidently, under grazing pressure, the dependence of τ_{n-m} on $n - m$ is logarithmic, while in the absence of grazing, the dependence is linear, as demonstrated in Figure 3. Tracking the temporal variations of colonies of different sizes (e.g., using satellite images taken yearly or seasonally) is thus an effective tool for detecting desertification. If large patches remain large, and their chance to reach a fixed, small size within some time frame decays exponentially with their size, it is plausible that the spatial structure reflects spatial heterogeneity, effects of local topography and so on. If the rate of disappearance for large clusters depends linearly

on size, it indicates that positive feedback plays a major role in the clustering process. Grazing, and other processes that lead to desertification, are characterized by logarithmic dependence on size differences. These three characteristic dynamics - exponential, linear, and logarithmic - differ strongly from each other, and thus temporal tracking provides a very reliable indication of the state of the system.

It is interesting to note that, as firm size is governed by the same dynamical law, similar techniques are used for financial risk assessment. A Firm defaults when the value of its liabilities exceeds its assets. Merton [23] estimated the distance to default (DD) by modeling a firm assets as a geometric random walk, where the "step size" is proportional to the volatility. The expected default frequency [24] (EDF), which is the critical parameter that determines credit risk, is in fact an estimation of the typical time window needed for the geometric random walker to reach the default point; this quantity is just the inverse of the first passage time considered here.

The models of [8, 9, 10] all use a fixed fraction of occupied cells f^* , i.e., a fixed total population. The differences in colony statistics quantify, in fact, the relative importance of the density-dependent growth factors (local facilitation, Allee effect, schooling) versus density-independent resources, like annual precipitation or the availability of food. If the patch distribution is Pareto-like with a relatively small slope β , the system admits larger patches; this implies that the effect of positive feedback is strong enough to oppose stochasticity (purely stochastic dynamics lead to Poisson-like statistics). A truncated power-law, on the other hand, shows that density-independent factors control the overall carrying capacity. Given two systems with the same tree coverage f^* but with different cluster statistics, the scale-free one is more robust against environmental changes (e.g., decreased annual rainfall) than the system characterized by a truncated power law. On the other hand, a strong Allee effect may result in irreversible transitions if the density falls below some critical level. The dynamical law presented here allows one to identify the transition between these states when the total population is still fixed; qualitative changes in the stability of large patches - from linear to logarithmic - may thus serve as an important precursor of catastrophic shifts [25] like desertification in arid ecosystems.

Acknowledgments

This work was supported by the EU 6th framework CO3 pathfinder. A.M. acknowledge the financial support of the Israeli Center for Complexity Science.

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