



Facilitation, competition, and vegetation patchiness: From scale free distribution to patterns

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ABSTRACT

A new technique for the modeling of perennial vegetation patchiness in the arid/semiarid climatic zone is suggested. Incorporating the stochasticity that affects life history of seedlings and the deterministic dynamics of soil moisture and biomass, this model is flexible enough to yield qualitatively different forms of spatial organization. In the facilitation-dominated regime, scale free distribution of patch sizes is observed, in correspondence with recent field studies. In the competition controlled case, on the other hand, power-law statistics is valid up to a cutoff, and an intrinsic length scale appears.

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1. Introduction

The tension between competition and facilitation is known to be a major factor in determining inter- and intra-specific dynamic and life history characteristics for many species (Lambin et al., 2001; Berkowitz et al., 1995). In spatially segregated populations, these two effects contradict each other; while kin competition for a common resource favors high dispersal rates as an evolutionary stable strategy (Hamilton and May, 1977), kin facilitation tends to lead to spatial clustering (Jason et al., 2000).

In the semiarid climatic zone, shrubs, trees and annuals compete for water, which is considered the only growth-limiting resource. On the other hand, there is a positive feedback associated with the biomass, as its existence may reduce inorganic losses (decreasing evaporation and increasing infiltration). The interference between plants may thus yield either positive (facilitation) or negative (competition) effects (Holzapfel and Mahall, 1999). This paper deals with the interplay between intraspecific facilitation and competition for perennial flora in the semiarid climatic zone.

Two main approaches are employed in order to model the balance between these opposing tendencies. The first approach is based on deterministic, time-continuous partial differential equations, where both water density (soil moisture) and biomass density are considered as real, continuous variables (Wilson and

Agnew, 1992; Lefever and Lejeune, 1997; Klausmeier, 1999; von Hardenberg et al., 2001; Solé and Bascompte, 2006). Such models may support either homogenous or patchy solutions, where the resulting vegetation patterns are either regular (if Turing-like bifurcation takes place) or irregular (technically, this may happen when the bifurcation is subcritical). These models, however, fail to capture certain important features, such as the distribution of patch sizes; the typical size of a patch is dictated by either the model parameters (in the Turing case) or the initial conditions (for subcritical bifurcation, where two metastable solutions may exist simultaneously in the system, and the domains structure depends on system's history). For a recent review of this approach see Rietkerk and van de Koppel (2008).

Recently, two groups of researchers published compelling analyses of satellite image data (Scanlon et al., 2007; Kéfi et al., 2007), suggesting that patch sizes in the semiarid zone obey, at least in some parameter regions studied, power-law distributions. In order to account for that phenomenon, both groups suggested a new type of modeling for vegetation patterns. The new models are stochastic and individual based, resembling Kawasaki spin exchange models (Kawasaki, 1972). On a lattice, each vertex is either occupied or unoccupied, the number of occupied patches is conserved (this is the manifestation of the competition for a limited resource), and the chance of an old shrub to die, or of a new shrub to sprout, is proportional to the population in its vicinity, such that positive feedback is taken into account. The resulting cluster dynamics resemble very much the “rich get richer” dynamics underlying the appearance of a scale free network (Barabási et al., 1999); the chance of a large cluster to

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grow is larger than that of a small cluster. The distribution of cluster sizes becomes wide, and may obey a power-law in some cases.

Clearly, a disadvantage of the new type of stochastic models is that they neglect the water dynamic, and hence do not support a realistic, local competition term. Competition enters into the model only as a global constraint on the biomass density, as if all the biomass units “share” the same water resource.

In the following section, we suggest a hybrid model that incorporates the deterministic equations of both water and biomass with some stochastic elements. It turns out that our model may produce both ordered and disordered patterns and admits a parameter region where the cluster statistics obey power-law. Our model, thus, may produce all the observed patterns, both regular and irregular, from a simple, first principle simulation technique.

2. The model

We begin with the simplest set of partial differential equations that describe the deterministic dynamics of plants competing for water. The two basic ingredients are the biomass density b and the water density w . On a two-dimensional grid, the rate equations take the nondimensionalized form:

$$\frac{d}{dt} b_{ij} = b_{ij}(w_{ij} - \mu), \tag{1}$$

$$\frac{d}{dt} w_{ij} = R - w_{ij} - w_{ij}b_{ij} - D_w \left(w_{ij} - \sum_{\delta=\pm 1} [w_{ij+\delta} + w_{i+\delta j}] \right), \tag{2}$$

where i, j is the site index. The first and the second equations stand for the deterministic dynamics of the biomass density b , and the soil water density w , correspondingly. The difference $(w - \mu)$ is the local growth rate of the biomass, reflecting the dependence of growth on the consumption of water. The term $-w$ stands for abiotic losses of water (evaporation, percolation) while the $-wb$ term reflects losses due to plant usage. D_w is the “diffusion” term for the water, corresponding to the lateral water flow. Note that if a preferred direction exists, like in the case of a downhill flow, a bias term should be added to the model. Here, however, our main focus is on the comparison with the models used by Scanlon et al. (2007) and Kéfi et al. (2007), where this effect was not taken into account.

For any initial conditions, if the water deposition rate R is fixed, the dynamics induced by Eq. (2) lead to an $\{i, j\}$ independent, homogenous solution, where $b_{ij} = \bar{b} = (R/\mu) - 1$ and $w_{ij} = \bar{w} = \mu$. In order to observe patterns, we follow Shnerb et al. (2003) and consider a two-season scenario, where a wet season (for which $R = R_0$) is followed by a dry season (for which $R = 0$). The duration of each season is τ . As perennial shrubs always have a threshold size, small shrubs are eliminated from the lattice at the end of the dry season (see, e.g., Padilla and Pugnaire, 2007). Note that the only effect of seasonality is to introduce a threshold on the size of a biomass unit; without that the continuum description holds, as one may expect for annual flora. This process is stochastic and the elimination happens with probability P_{d1} :

$$P_{d1}(b) = \begin{cases} 1 & b < b_0, \\ \exp\left(-\frac{b - b_0}{b_0}\right) & b > b_0. \end{cases} \tag{3}$$

What (3) accounts for is the elimination of new seedlings that did not grow enough and fail to survive the dry season. The model should include a process of that type in order to explain the robustness of the emerging patterns; without that threshold, disordered patterns are unstable (Shnerb et al., 2003).

In order to incorporate a positive feedback mechanism into the model, we have introduced another stochastic, biomass independent mortality term. Each shrub, independent on its biomass, is removed with probability P_{d2} , which is a monotonically decreasing function of the surrounding biomass. For the simulations we have used

$$P_{d2} = \kappa(1 - \rho), \quad \rho = A \sum_{|\mathbf{r}-\mathbf{r}'| < r_0} \frac{b(\mathbf{r}')}{|\mathbf{r}-\mathbf{r}'|}, \tag{4}$$

where A is a normalization constant, $\mathbf{r} = \{i, j\}$ and r_0 the maximal facilitation range. The more populated is the immediate vicinity of a biomass unit, the bigger are its chances to survive.

Whenever a plant is removed, it may be replaced by a seed of random small size with a probability that depends, again, on its neighboring biomass, $P_s = \rho^\eta$, $1 < \eta < 2$. This models the fact that the chance of a successful germination rises in the vicinity of other shrubs.

Biomass units with good starting values manage to survive through their first summer. These plants grow, and consume water from within their vicinity. After a few cycles, water level in bare zones is no longer sufficient for new plants to survive the dry season. The process forms a mosaic of water-consuming areas, which are populated by vegetation, and bare water-contributing areas, which cannot support a new growth.

3. Patch size distribution, patterns and correlations

Recent reports (Scanlon et al., 2007; Kéfi et al., 2007) have demonstrated power-law statistics of the patch size for vegetation ecosystems in the arid and semi-arid climatic zone across a wide range along the annual rainfall gradient. As pointed out in Scanlon et al. (2007) and Kéfi et al. (2007), this phenomenon is actually puzzling.

Typically, the distribution of sizes in nature (the height of different individuals within a single species is a classical example) tends to be Gaussian; its average is dictated by physical and biological constraints (e.g., the ability of the muscles to support the body) and the deviations from the average are attributed to many “small” random effects, like the genetic mixture of an individual and resource availability during its development. The central limit theorem assures that, in such a case, the results are normally distributed around their mean, and large fluctuations (in units of the standard deviation) are exponentially rare. Power-law, or otherwise fat-tailed distributions, are an exception of this scenario, and when such a distribution appears one should look for a mechanism that invalidates that simple logic.

Indeed some natural systems, both at equilibrium and out of equilibrium, show power-law statistics of domains. This usually occurs close to a second order phase transition, when the correlation length ξ diverges and the system lacks an internal length scale. Slightly off criticality, the system still imitates its critical behavior up to the correlation length ξ that diverges at the transition; this implies that for any finite length scale one may find a range of parameters within which the system is almost critical. power-law statistics for a wide range of parameters, on the other hand, may occur when the system shows self-organized criticality (Bak et al., 1987); the Gutenberg-Richter law for earthquake statistics is believed to be an example of this phenomenon.

Another mechanism that yields power-laws and other fat-tailed distributions is multiplicative noise. This situation occurs when the random fluctuations that affect the system are proportional in magnitude to the size of the system itself. An example is the neutral theory of species abundance (Hubbell, 2001); if the chances of any individual to produce an offspring and

to die are the same, the abundance fluctuates along generations and the size of the fluctuation is proportional to the population. This “law of proportion effect” was first discovered in the context of business firm’s size (Gibrat, 1930; Simon and Bonini, 1958; Levy and Solomon, 1996) and is also relevant to the effect of small fluctuations in growing populations, like surname abundance (Manrubia et al., 2003) and degree distribution in scale free networks (Barabási et al., 1999).

We do not intend to solve the power-law mystery here; instead, let us show that our hybrid model may actually support the same behavior. Fig. 1 shows the spatial biomass distribution attained from our model (using forward Euler integration of the reaction–diffusion equations superimposed on the stochastic dynamics) for three different regimes of annual precipitation.

Note that while the stochastic models presented by Scanlon et al. (2007) and Kéfi et al. (2007) imposed a global constraint on the spatial coverage (related to either annual rainfall or grazing stress), here this parameter emerges as a result of different values of annual rainfall. The left panels of Fig. 1 show the cumulative distribution function for the cluster sizes, $P(S \geq a)$, defined as the probability for a vegetation patch to have an area equal to or greater than a . For all precipitation values, a power-law $P(S \geq a) = Ca^{-\beta}$ seems to fit the results.

Our model allows one to examine various regimes of growth parameters, and in particular to trace the crossover from facilitation-dominated to competition-dominated dynamics. The control parameter is the rate of water diffusion, D_w . When D_w approaches either zero or infinity, there is no length scale

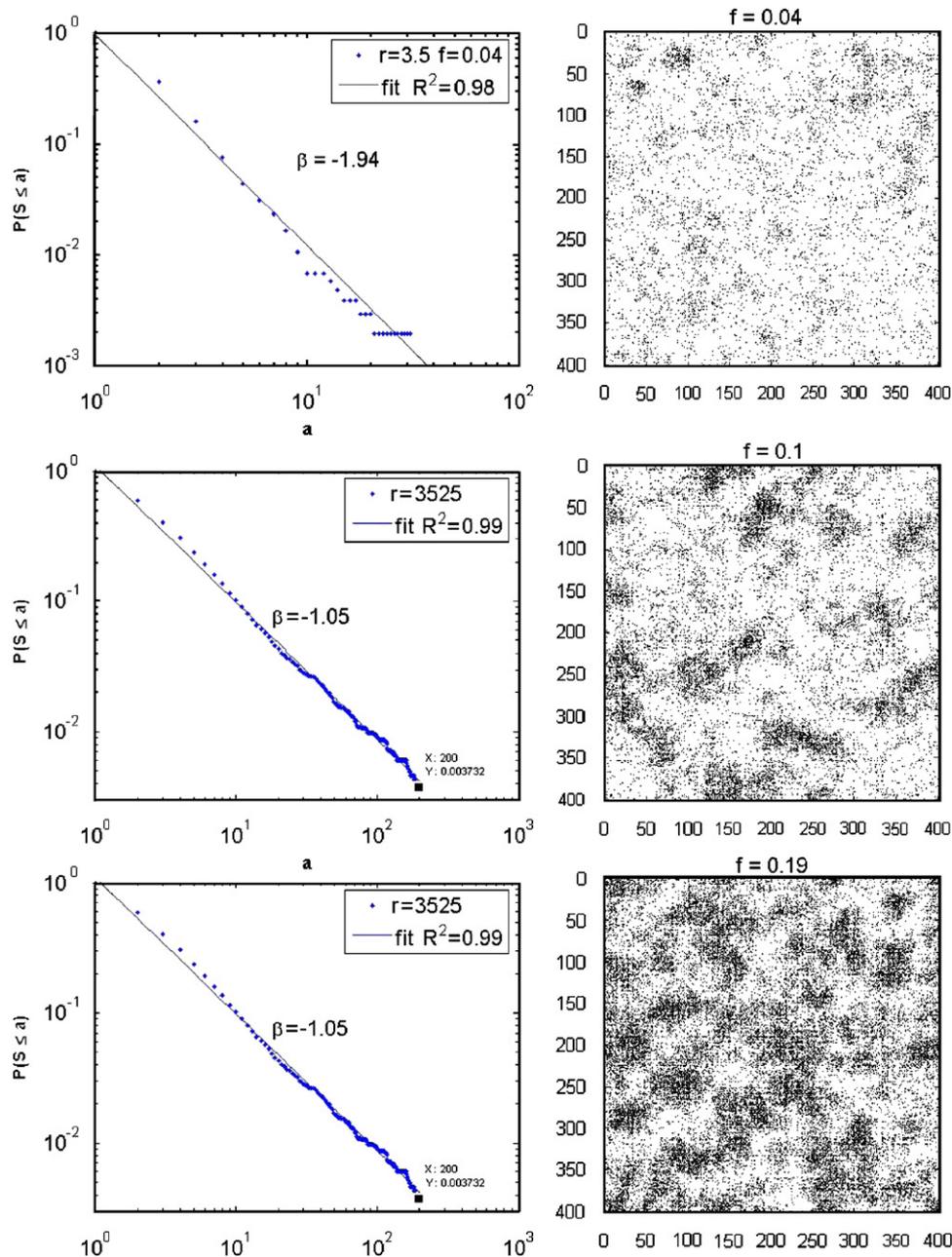


Fig. 1. Spatial coverage emerges from the model described above for different values of precipitation (three right panes) and the corresponding cumulative distributions of cluster area (left). The simulations used a 400×400 lattice, for 200 wet-dry (“yearly”) cycles. The initial condition for all simulations is a 30% coverage of random small seeds. The only difference between panels is the value of R in the simulation, taken as $R = 3.5$ (up), $R = 3.515$ (middle), and $R = 3.525$ (down). The fractional biomass coverage is $f = 0.04$ in the “arid” (or overgrazed) zone, $f = 0.1$ for the “semi arid” region and $f = 0.19$ in the last panel. Common parameters used for both simulations are $D_w = 10$; $b_0 = 0.1$; $r_0 = 10$; $\eta = 1.5$; $\mu = 0.2$ and $\kappa = 0.07$.

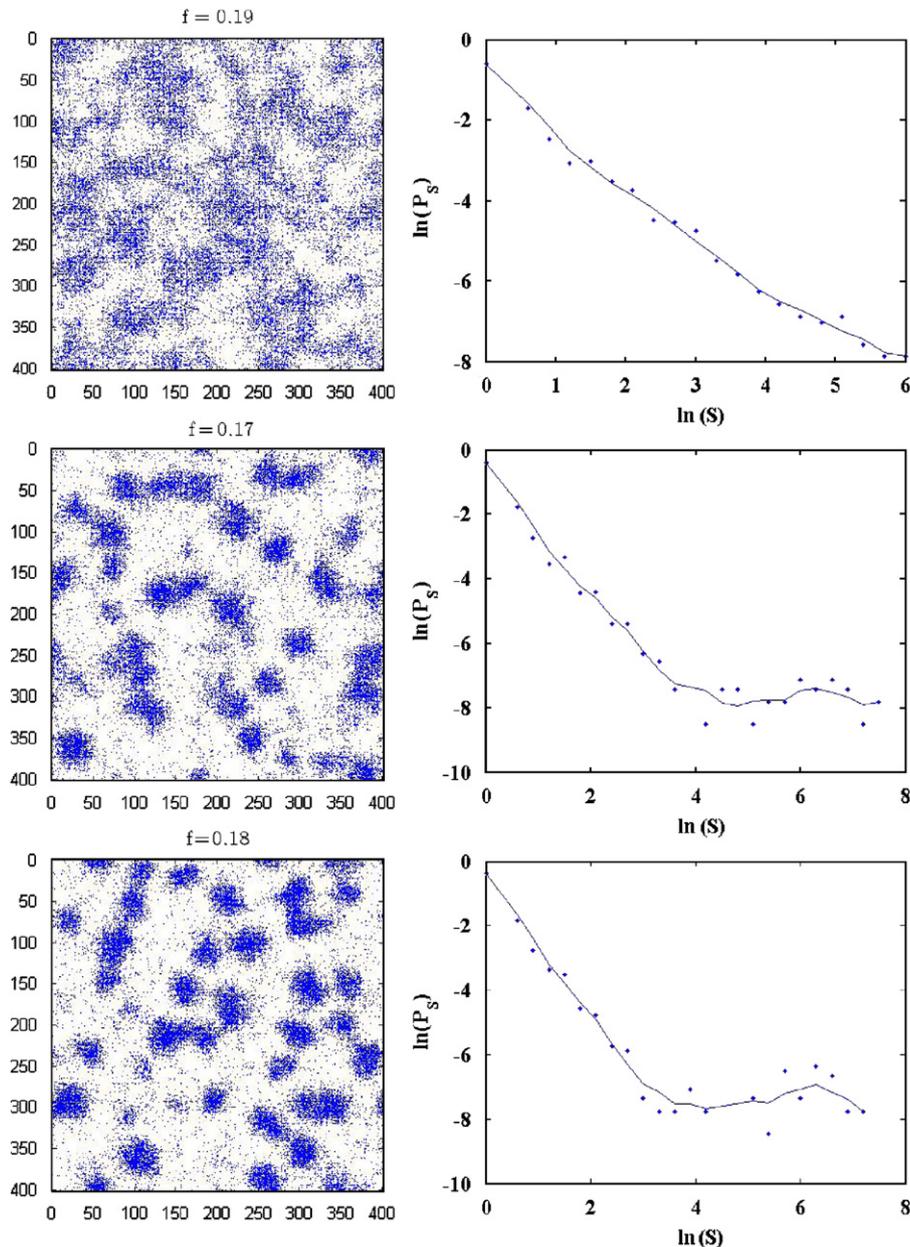


Fig. 2. Spatial patterns (left) and the corresponding patch size distribution (right) for three different runs of the simulation, identical except for the value taken for water diffusivity. The upper panel ($D_w = 10$) shows the scale free spatial pattern (right), manifested by the power-law statistics of patch sizes (left). In the middle and lower panels ($D_w = 50$ and 100 correspondingly), the formation of an intrinsic length scale—the competition length—is manifested. As D_w increases, the cluster size probability distribution function, P_s , reveals a power-law regime for small patch sizes, and a characteristic length scale (the right peak) for large cluster sizes. Simulations were conducted with $R = 3.523$ for 300 yearly cycles. Other parameters and initial conditions are identical with Fig. 1.

associated with the competition for water. In this parameter regime the dominant clustering process is the positive feedback; clearly, mutual facilitation leads to a “rich get richer” dynamic that results in scale free spatial distributions (Barabási et al., 1999). On the other hand, for intermediate values of water diffusivities the competition length determines a length scale for the system. This transition is demonstrated in Fig. 2, where the same model that yields the spatial patterns shown in Fig. 1 produces, with larger water diffusivities, qualitatively different patterns. Here one can easily track the emergence of a new length scale associated with the competition for water, and the formation of ordered, Turing like, structures that resemble Niger’s “tiger bush” (Wilson and Agnew, 1992; Lefever and Lejeune, 1997; Klausmeier, 1999; von Hardenberg et al., 2001; Solé and Bascompte, 2006). The system is now characterized by a power

law distribution of small cluster sizes up to some cutoff size, while the large clusters admit an intrinsic length scale.

The transition from facilitation-dominated to competition-dominated dynamics is best identified by the correlation function, as seen in Fig. 3. While a facilitation-dominated regime is characterized by positive, short range correlations, the competition dynamics lead to long range, negative correlations. As the competition range D_w increases, short range correlations start to form.

4. Discussion

Ecological processes are generally complex, and their modeling is a difficult task. Many of the models (and perhaps the most

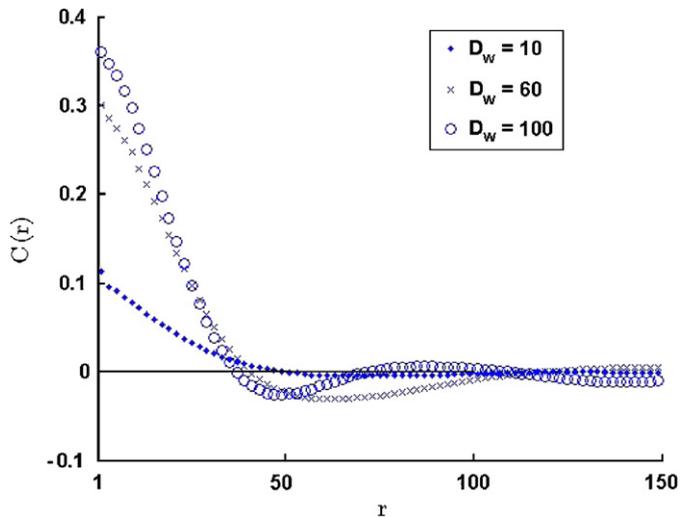


Fig. 3. The spatial autocorrelation (biomass–biomass) function for the three patterns of Fig. 2. The occupation of each site, $x(\mathbf{r}) \equiv x_{ij}$ is either zero (if the biomass is below threshold) or one. For any fixed distance r_0 the correlation function is defined as $\text{Cov}[x(\mathbf{r}), x(\mathbf{r} + \mathbf{r}_0)]$ normalized by the standard deviation and averaged over all pairs of sites of mutual distance $|r_0|$. The transition from facilitation-dominated to competition-dominated regime manifests itself in the appearance of negative correlations for large D_w . This implies that the plot is segregated into water contributing and water accepting areas. The short range autocorrelation is positive for all values of D_w , as a result of mutual facilitation. Clearly, the overall correlations grow stronger as D_w is increased. Clearly, the water–biomass correlations (not shown) are negative, with water-rich area in the gaps between shrubs.

useful of them) are greatly oversimplified, neglecting the realistic complexities in order to clarify a simple effect. Other models attempt to imitate reality using many parameters; their applicability depends on the availability of good estimates for the actual values of these parameters.

The model presented here lays roughly between these two extremes. It utilizes many parameters to describe the water dynamics, shrub growth, facilitation and so on; we are not familiar with a realistic estimate for many of these parameters. Yet, the model yields patterns that are extremely similar to those observed in nature. Moreover, it leads to a very intuitive understanding of the basic processes underlying vegetation dynamics. The observed patterns are attributed to the interplay between two opposing tendencies: facilitation supports scale free clustering and “rich get richer” dynamics, while competition supports ordered patterns characterized by a single scale. Solving Eq. (2) for the spatial water profile between two different boundaries, one finds that the competition length scales like $\sqrt{D_w}$. The crossover between the two behaviors, as demonstrated in Fig. 2, occurs when the facilitation range is of order of the competition length. This observation may be used in order to classify the reasons for deviations from the power-law behavior for the sizes

of vegetation patches. One may use, for example, the spatio-temporal correlations in order to study the role of spatial heterogeneity (microtopography), or to identify allelopathic negative interactions by the appearance of a new length scale.

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