

Self-organization of plants in a dryland ecosystem: Symmetry breaking and critical cluster sizeAriel G. Meyra,¹ Guillermo J. Zarragoicoechea,^{1,2,3,*} and Victor A. Kuz¹¹*IFLYSIB (UNLP, CONICET), 59 No. 789, B1900BTE La Plata, Argentina*²*Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, Argentina*³*Diseño Industrial, Facultad de Bellas Artes, UNLP, La Plata, Argentina*

(Received 28 September 2014; revised manuscript received 1 April 2015; published 19 May 2015)

Periodical patterns of vegetation in an arid or semiarid ecosystem are described using statistical mechanics and Monte Carlo numerical simulation technique. Plants are characterized by the area that each individual occupies and a facilitation-competition pairwise interaction. Assuming that external resources (precipitation, solar radiation, nutrients, etc.) are available to the ecosystem, it is possible to obtain the persistent configurations of plants compatible with an equitable distribution of resources maximizing the Shannon entropy. Variation of vegetation patterns with density, critical cluster size, and facilitation distance are predicted. Morphological changes of clusters are shown to be a function of the external resources. As a final remark, it is proposed that an early warning of desertification could be detected from the coefficient of variation of the mean cluster size together with the distribution of cluster sizes.

DOI: [10.1103/PhysRevE.91.052810](https://doi.org/10.1103/PhysRevE.91.052810)

PACS number(s): 89.75.Fb, 87.23.Cc, 87.10.Rt

I. INTRODUCTION

Climatic change, overgrazing, soil erosion, etc., contribute locally to change biomass density over large regions and consequently to desertification, which is more an effect than a cause. In this century, one third of the land surface of the world could be in drought conditions via desertification. The livelihood of $\sim 25\%$ of the world population will be affected if desertification progresses according to the present detection and quantification [1]. Diagnosis of critical shift in ecosystems has been the subject of continuous research by many authors [2–11]. Criticality in ecology generally applies to a system that exhibits threshold behavior, with sudden shifts between states, due to the high sensitivity to the environmental parameters controlling its dynamics [12]. Besides the different causes that induce changes upon ecosystems, the proposed models are able to predict the morphologies of some of the observed patterns and indicate qualitative operative options to attenuate or remove some of the causes that promote desertification and their catastrophic effects.

In arid and semiarid regions of the Earth plant biomass self-organizes in periodic or quasiperiodic patterns. Different models try to explain how plants self-organize by using partial differential equations (PDEs) [2,8,13–19]. Most of these models hypothesized that movement of water, due to runoff, or diffusion or infiltration in the soil, causes the vegetation patterns. There is an interesting experimental paper, in which the infiltration rates and soil moisture in groved mulga is measured [20]. When the fundamental unit is not the patch, but the individual plant, it is assumed that a plant interact with others through its above- and below-ground organs, canopy, and root systems, respectively. Models that consider plant-plant interactions have been also studied with cellular automaton algorithms [1,9,21], by individual-based model methods [22], or a variational method with numerical simulation [10]. It is worth mentioning that, in dryland vegetation, patches are often formed by single plants, and each

individual is still capable of responding continuously to water stress by letting parts of its canopy die. This is because of the modular hydraulic systems dryland plants typically have, which consist of hydraulically independent multiple stems [23].

It has been previously suggested that positive interactions between neighbors are exerted by the aerial part of the plants, which are known to improve the water budget in the soil [24,25] as well as increase the water infiltration [20,26], whereas competitive effects result from lateral resource (water) absorption by the shallow root systems. Roots tend to grow superficially and larger than the canopy size to gain enough water from the individual's surrounding [16,27]. This interplay between competition and collaboration [2] has been modeled also by Gilad and co-workers [17,18], and recently reviewed by Meron [28]. Following these ideas, the present model [10] considers that spatial periodic vegetation patterns (PVPs) in semiarid ecosystems are caused by a collaboration-competition struggle process for the limited resource, specifically water, even though, in a recent work [29], different vegetation patterns were obtained with a PDE model where the authors state that the facilitative interaction was not included.

Individuals (plants) are objects that use an exclusive area and a facilitation-competition pair interaction. In that previous work we showed that shape and size of clusters, and biomass density are functions of the water activity in the environment. Presently, it is worth analyzing other important aspects of the desertification problem: the critical threshold transition, pattern variation (with density, critical cluster size, and facilitation strength), and the morphological change of clusters with the external resources. Furthermore it is shown how ecosystems, plants in a limited resource system, undergo a sequence of self-organized spatial two-dimensional patterns as they approach the critical threshold transition. Pattern organization is the answer for increasing aridity, and a regular pattern characterized by spots of vegetation signals the proximity of a threshold or symmetry breaking to catastrophic desertification [4,5,30,31]. Previously to discuss the clusterization of the elements (plants), we introduced a specific criterion to define the inter- and intracluster distance

*Corresponding author: vasco@iflysis.unlp.edu.ar

via the use of the coefficient of variation of the mean cluster size. The coefficient of variation is a powerful tool, because as it is a dimensionless quantity, it could be compared with other coefficients of variation (e.g., precipitation, temperature, net radiation, etc.) to build up some spatial experimental correlation. Cluster formation depends on the external resources and on the synergetic resources of the system associated to the facilitative-competitive contribution of the interacting plants. In this context we show how clusters of plants could be self-organized. A quantitative characterization of aridity is suggested for values of the synergetic resources below to those corresponding to the critical threshold. Also changes upon pattern morphologies due to the effects of grazing and human actions are considered by varying the canopy-root relationship or by examining the system at different values of the external resources.

II. DESERTIFICATION MODEL

In a previous work [10], the general foundations have been established by which it is possible to capture the general aspect of PVP in arid and semiarid ecosystems. The model was developed from statistical mechanics, thermodynamics, and information theory. Furthermore, it is proposed that plant interactions could be described via a pairwise potential with the following contributions: The aerial part of the plant contributes with a short-range facilitative interaction while the root system contributes via a long-range competitive interaction. The N individuals of the same species are distributed in an area A and their variation (grand canonical ensemble) is represented by the death and birth of individuals. Each individual occupies an element of area and consumes a certain amount of resources (water, solar radiation, nutrients such as nitrogen, phosphorus, etc.). It must be remarked that while facilitation reduces the evaporation rate from the soil, competition reallocates and increases the potential resources that could be absorbed by the individual from its area of influence. These kind of potentially generated resources are called r_i^{int} . Then the resource balance r_i managed by a generic individual is

$$r_i = r_i^c + r_i^{\text{int}}. \quad (1)$$

r_i^c are available resources that can be consumed by any individual without interaction and r_i^{int} are the potential resources available to the individual if and only if there are interactions among them, being $r_i^{\text{int}} = \frac{1}{2} \sum_{j=1}^N v(x_{ij})$, with $v(x_{ij})$ the plant-plant pairwise interaction, and $x_{ij} = (\vec{x}_i - \vec{x}_j)$ the interdistance between individuals i and j ($i \neq j$). The total resource balance [10] for a given configuration of N individuals is

$$R = \sum_{i=1}^N r_i = \sum_{i=1}^N r_i^c + \frac{1}{2} \sum_{i=1}^N \sum_{j=1}^N v(x_{ij}), \quad (2)$$

where $v(x_{ij})$ is composed of two parts:

$$v(x_{ij}) = v_h(x_{ij}) + v_{fc}(x_{ij}). \quad (3)$$

$v_h(x_{ij})$ represents the exclusive use of the space by each individual, and $v_{fc}(x_{ij})$ is the short-range facilitation and long-

range competition interaction (f/c), modeled by [32]

$$v_{fc}(x_{ij}) = -\varepsilon_f \left(\frac{L_a}{L_f} \right)^2 e^{(-x_{ij}/L_f)} + \varepsilon_c \left(\frac{L_a}{L_c} \right)^2 e^{(-x_{ij}/L_c)}. \quad (4)$$

ε_f and ε_c are the strengths of the interaction, L_a is the dimensionless average crown (set to unity), and L_f and L_c are quantities proportional to the canopy and root dimensions. $(L_a/L_f)^2$ and $(L_a/L_c)^2$ are two morphological quantities, which in fact are area ratios. Equation (2) is a fundamental equation that rules, via its minimization, the persistent or self-sustained ecosystem configurations. Why does the minimization of Eq. (2) determine the persistent plant configuration? Because minimum total resources (e.g., moisture in the soil) are equivalent to a maximum biomass on the top soil. The total mean resources $\langle R \rangle$, compatible with the observed configurations, are calculated by using the maximum entropy principle [10,33,34].

If R_α and N_α represent the total resources and the number of individuals for a particular vegetation distribution α with a probability p_α , then the total expected values $\langle R \rangle$ and $\langle N \rangle$ are obtained by the maximization of the entropy with the constraints $\sum_{\alpha=1}^n p_\alpha R_\alpha = \langle R \rangle$, $\sum_{\alpha=1}^n p_\alpha N_\alpha = \langle N \rangle$, and $\sum_{\alpha=1}^n p_\alpha = 1$. The maximization process gives, as the result the Boltzmann probability distribution for p_α ,

$$p_\alpha = \frac{e^{-\beta R_\alpha - \gamma N_\alpha}}{\Xi} \quad \text{with} \quad \Xi = \sum_{\alpha=1}^n e^{-\beta R_\alpha - \gamma N_\alpha}. \quad (5)$$

β and γ are the two Lagrange multipliers coming from the maximization, with

$$\langle R \rangle = - \left(\frac{\partial \ln \Xi}{\partial \beta} \right)_\gamma, \quad \langle N \rangle = - \left(\frac{\partial \ln \Xi}{\partial \gamma} \right)_\beta \quad (6)$$

Then the total mean resource $\langle R \rangle$ is

$$\langle R \rangle = \langle R^c \rangle + \langle R^{\text{int}} \rangle. \quad (7)$$

$\langle N \rangle / \beta = \langle R^c \rangle$ represents the average consumed resources without interaction and R^{int} are the redistributed or locally gained resources as a consequence of the f/c interaction between individuals under the effect of the input of resources from the environment (γ). Equation (7) in conjunction with the probability distribution p_α justify using numerical simulation for studying the properties of the proposed model. Then minimization of Eq. (7) via the grand canonical Monte Carlo (GCMC) technique allows us to find the persistent configurations for each simulated system. Standard GCMC simulations have been done in a two-dimensional box of area $A = 150L_a \times 150L_a$ with periodic boundary conditions [35,36]. A cutoff of $10L_a$ has been considered to capture the fact that roots spread an order of magnitude beyond the crown diameter L_a [8]. A total of 10^6 GCMC steps for equilibration and not less than 10^5 GCMC steps for production have been done. N individuals are initially randomly distributed in the simulation box. The election of the place to create a new individual (birth) and the election of the individual that will die are chosen at random (from a uniform probability distribution). Next, creation or deletion of individuals is accepted or rejected

based on the following rules [35,36]:

$$a(\text{creation}, N \rightarrow N + 1) = \frac{Az}{N + 1} e^{-\beta(R_{N+1}^{\text{int}} - R_N^{\text{int}})},$$

$$a(\text{deletion}, N \rightarrow N - 1) = \frac{N}{Az} e^{-\beta(R_{N-1}^{\text{int}} - R_N^{\text{int}})},$$

$z = e^{-\gamma}$ being the activity (soil water activity) of the system. Beneath these acceptance rules lies a Markov birth-death process (a stochastic process where the next configuration depends only on the present configuration). Markov chain models are widely used in ecology modeling (see Refs. [37–39], to quote only a few). The rules define an importance sampling of the phase space, in order to get the more relevant configurations from the Markovian process. The water activity z might be identified with the inverse of aridity or dryness index (\emptyset) [40], which is defined as the ratio of potential evapotranspiration E_0 to precipitation P . Then it is proposed that z is the ratio of precipitation to potential evapotranspiration, $z \approx 1/\emptyset$ (See Fig. 1).

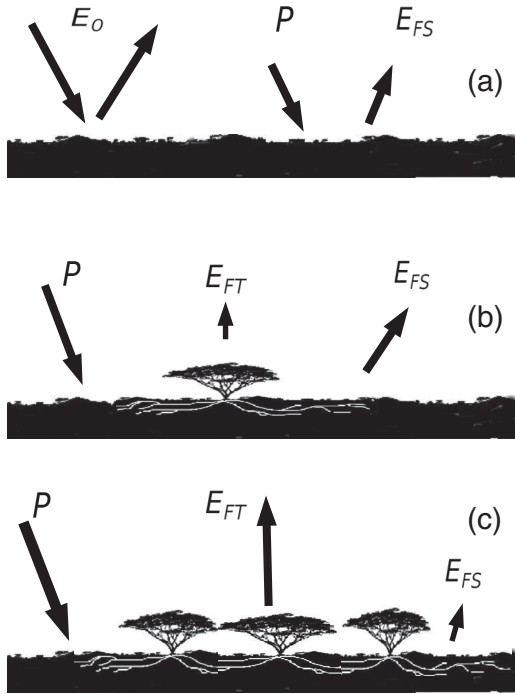


FIG. 1. Schematic of a local water balance in semiarid or arid ecosystems. This ideal system does not consider runoff. E_0 is the potential evapotranspiration that is proportional to net radiation; P is precipitation [38]; E_{FS} and E_{FT} are evapotranspiration from the top soil and the tree leaves, respectively. (a) Absence of plants and runoff, then $E_{FS} = P$. (b) For low biomass density, $E_{FS} \rightarrow P$, and the difference is E_{FT} , the quantity directly related with the resources that each individual consumes without interaction, r_i^c . (c) As $z = P/E_0$ increases, then plant density increases and the relationship is modified, now $E_{FT} \rightarrow P$. It should be remarked that the interaction among individuals is the cause of self-organization in the ecosystem, giving as a result an important increment in the amount of available resources r_i^{int} . Therefore, it is worth emphasizing that the most efficient ecosystem is the one that accomplishes the goal of $E_{FS} \rightarrow 0$.

To evaluate the influence of the interaction parameters in the vegetation patches, we study z in the range $0.05 \leq z \leq 10$, for mean consumed resource per individuals $\langle R^c/N \rangle = \langle r^c \rangle = 0.5$ and $\langle r^c \rangle = 0.6$. The interaction parameters were fixed to $(L_a/L_f)^2 = 1$ and $(L_a/L_c)^2 = 0.25$, and $\varepsilon_f = \varepsilon_c = 1$. Other systems with $\langle r^c \rangle = 0.6$, and $\varepsilon_f = 1$, $\varepsilon_f = 0.95$, or $\varepsilon_f = 0.90$ have also been simulated, in order to show how the persistence of the vegetation patterns are affected by a change of some of these quantities.

III. RESULTS

A. Density description of pattern behavior

To begin with, we present a quantitative description of the self-organization. Figure 2 shows GCMC results for population density $\rho = \langle N \rangle/A$ versus the soil water activity.

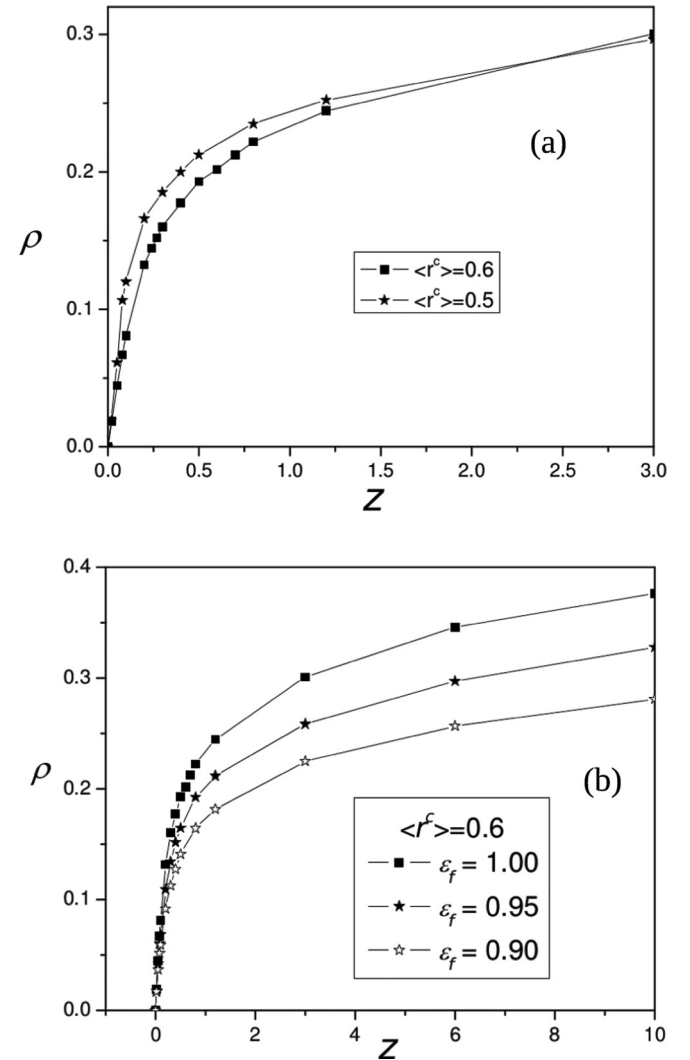


FIG. 2. (a) GCMC results for density versus the activity of the external resources (the resources uptake), for two different consumed resources. As can be seen less consuming plants are more abundant. (b) Examination of the variation of the crown's strength ε_f , for the same consumed resources. It characterizes the cooperation between plants and its variation could reflect pollution signals, overgrazing damages, etc. For the same activity of the external resources, $\rho(z)$ decreases when crown's strength decreases.

In Fig. 2(a), $\rho(z)$ is explored for two different mean consumed resources $\langle r^c \rangle = \beta^{-1}$ that mimic species with different morphologies and/or metabolic rate. It is clearly seen in this figure that, for the same water activity z , the less consuming species is more abundant. Also the foliage density effect ($\sim \varepsilon_f$) in the population density [Fig. 2(b)] is analyzed. If foliage density decreases then the cooperative strength ε_f becomes smaller. This variation of the crown's strength could represent anthropogenic effects, pollution signals, overgrazing damages, etc. It should be emphasized that ε_f is a measurement of the cooperation between plants. There is a direct correspondence between the crown's strength and biomass density. As cooperation intensity decreases, the interaction between individuals becomes more competitive. The result is a diminution in the number of individuals, per area, that can persist.

The average density $\rho(z)$ shows a nonlinear behavior (Fig. 2), and the GCMC data is well fitted to the following equation:

$$\rho \approx \frac{(1 - r^c)^{1+r^c} z^{r^c}}{r^c + (1 - r^c)z^{r^c}}. \quad (8)$$

This is a typical Langmuir-like shape equation [10]. This function shows two dissimilar regions (with significant changes in the slope) that can be well described with the concept of sensitivity (χ), the ratio between the changes of population density to the water activity in the ecosystems ($\Delta\rho/\Delta z$) [9]. This abrupt change in the sensitivity slope could be associated to the catastrophic threshold, and it seems to occur in the vicinity of $z \sim 0.5$ for the cases studied here. When water activity $z < 0.5$, slight fluctuations of z produce large changes in the biomass density, the ecosystem being very sensitive. A typical snapshot of the ecosystem in this region is shown in Fig. 3(a). The other region is observed when $z \gg 0.5$. The population density is not affected even by large changes in the external resources meaning that ecosystem sensitivity is null or very low. In Fig. 3(c) a snapshot for $z = 3.0$ shows the closed structure of the system that precludes significant changes in density for big changes in z . Around the threshold in the vicinity of $z \sim 0.5$ vegetation patterns are extremely symmetric, with spots of around 20 individuals arranged at the vertices of a quasiregular hexagonal grid [Fig. 3(b)]. The symmetry breaking of these quasihexagonal vegetation patterns characterizes desertification–green forest transition or simply a “drought-wet” transition or vice versa. The system could move back and forth or may shift permanently to an alternative state if the underlying changes persist, moving the system to only one stable state. This symmetric system, clusters hexagonally arranged, could be viewed as an early-warning signal of a critical threshold approaching.

B. Patterns and characterization of clusters

In Fig. 4 spatial distribution of individuals, for the three typical configurations mentioned above ($z = 0.1, 0.5, 3.0$), are analyzed with the help of a pair correlation function $g(r)$ [35,41]. This function gives the probability of finding an individual at a given distance from the center of another individual. For all cases studied the function shows high peaks at short distances (see inset in Fig. 4) and one or more smooth peaks at larger distances. Clearly the first peaks tell us about the cluster

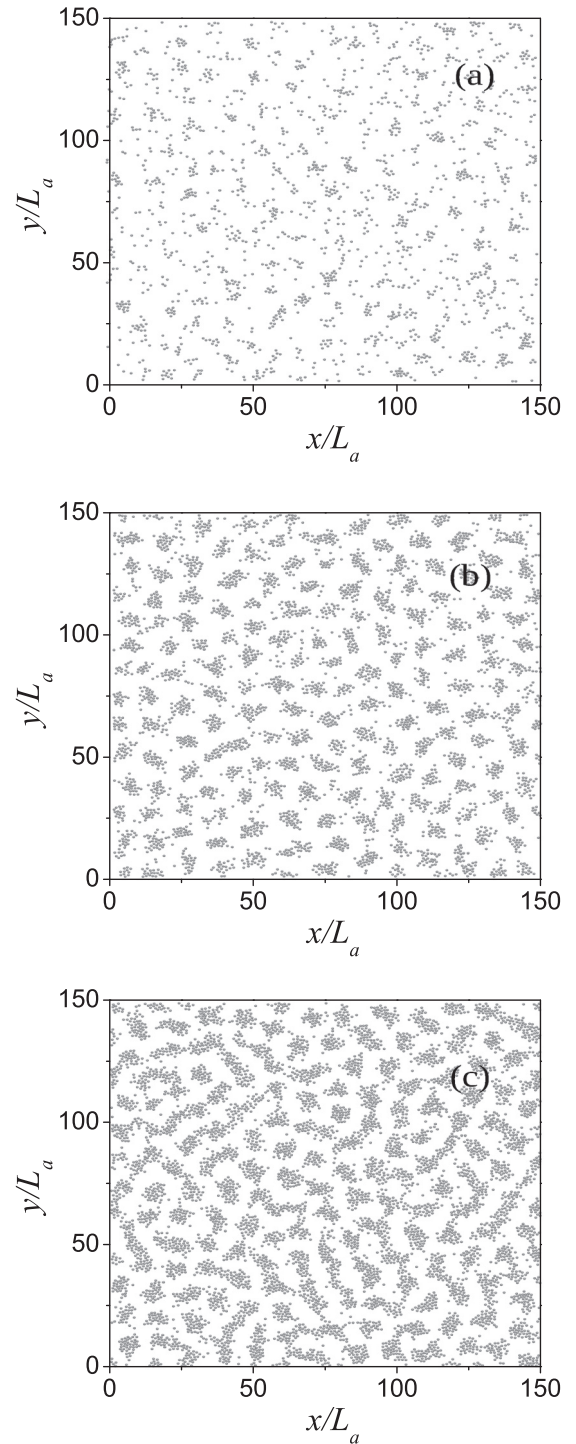


FIG. 3. (a) Snapshot of an irregular pattern, for $z = 0.1$. This configuration is typical of a very sensitive region. Similar patterns are observed in Argentina ($43^\circ 48' S, 65^\circ 41' W$). (b) Snapshot from the system with $z = 0.5$. Trees form nearly ordered clumps producing an almost arranged honeycomb structure. (c) Snapshot captured from a simulated system at $z = 3.0$. As z increases coalescence of drops (b) produces a labyrinthine pattern. These external resources produced an almost insensitive ecosystem ($\Delta\rho/\Delta z \approx \text{const.}$)

and cluster's size, while the peaks at larger distances give us information of cluster arrangement. It must be pointed out that when $z = 0.1$ there are not peaks at a larger distance, which

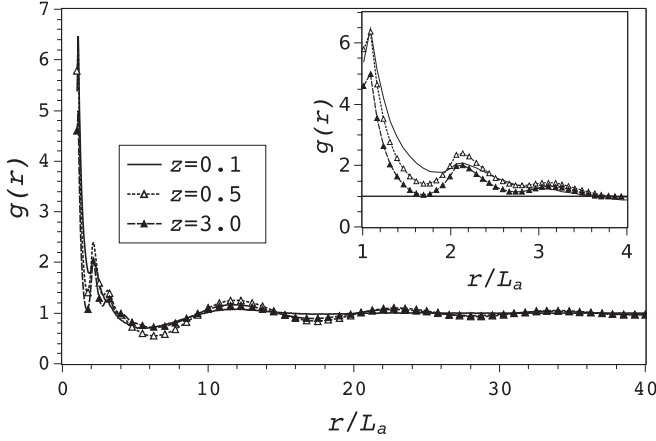


FIG. 4. Comparison of pair correlation functions for three different values of z . For $z > 0.5$ oscillations at long distances indicate certain long-range order of tree clumps.

means that ecosystems are formed by irregular clumps [see Fig. 3(a)]. For larger z the oscillations in $g(r)$ indicate order at long range as in Figs. 3(b) and 3(c). For $z = 0.5$, the symmetry of the system is manifested by peaks with greater amplitude.

Individuals self-organized in clusters—and at the same time clusters of different shapes and sizes—distribute on a given surface. Our technical problem is that there is not a unique criterion to identify a cluster (see [42] and references therein). It is established that two individuals belong to the same cluster if their interdistance is shorter than a facilitative or clustering distance d_f [42]. Then the main challenge of this section is to detect cluster size distributions, by estimating a value of d_f that allows each plant in that cluster to better manage the basic resources to survive in a given environment. But what is that facilitative distance? For each persistent plant community configuration, found via GCMC, different distances d are considered (with $L_a < d < 4L_a$) for setting up the cluster size frequencies $f_d(n)$ (number of clusters with n individuals belonging to the clump, $n = 1, N$, characterized by the particular d). Then the mean cluster size $\langle n \rangle_d = \sum_{n=1}^N f_d(n)n / \sum_{n=1}^N f_d(n)$, corresponding to the distance d , is estimated. With these data we compute the coefficient of variation (CV) of the mean cluster size, defined as the ratio of the sample standard deviation to the sample mean for a given set of data:

$$C_V(d) = \frac{\sqrt{\sum_{n=1}^N f_d(n)(n - \langle n \rangle_d)^2 / \sum_{n=1}^N f_d(n)}}{\langle n \rangle_d}. \quad (9)$$

The dimensionless function $C_V(d)$ characterizes the dispersion of the cluster sizes, the higher the CV the greater the cluster size dispersion. As it has been shown in microalgae stressed ecosystems [43], the variation of biomass increases with higher stress intensity, giving some support for the notion that selection effects become more important in more stressed ecosystems. Then high dispersion of cluster size could be necessary for the ecosystem to guarantee different sizes and variety of different structures, in order to provide itself with different self-organization options. Then it is proposed that the facilitative distance is the one that gives the maximum

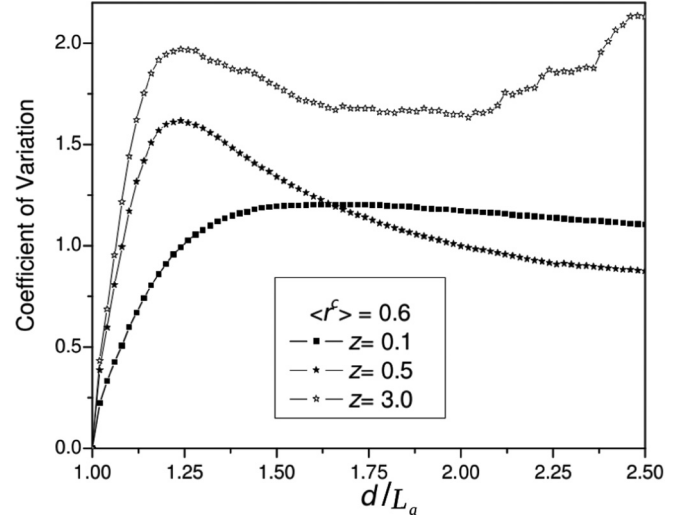


FIG. 5. Coefficient of variation of the clusters size versus the plant-plant interdistance, represented for a consumed resources per individual $\langle r^c \rangle = 0.6$ and different values of the activity of the external resources $0.1 \leq z \leq 3.0$. For low resources the area needed to survive is larger. For $z \sim 0.5$ (desertification threshold) the maximum $C_V(d)$ occurs at $d \sim 1.22L_a$.

CV. $C_V(d)$ is represented in Fig. 5 for consumed resources per individuals $\langle r^c \rangle = 0.6$ and different values of the activity of the external resources, $0.1 \leq z \leq 3.0$. For low values of the water activity of the external resources, e.g., $z = 0.1$, the biomass density is very low [Fig. 2(a)]. In this case maximum dispersion of the clusters' size occurs at $d \sim 1.7L_a$, implying that plant interdistance is too long to avoid evaporation from the soil (reduction of facilitative effect). For $z \sim 0.5$ the interdistance at which the maximum $C_V(d)$ occurs is $d \sim 1.22L_a$. The system is in the transition region [Figs. 2(a) and 3(b)]. For $z = 3.0$ the maximum CV occurs at d slightly larger than $1.22L_a$. Then the minimum interdistance at which the CV is maximum occurs at $z \sim 0.5$, so this distance is chosen as the optimum facilitative distance $d_f \sim 1.22L_a$. Figure 6 shows a zoomed snapshot for the $z = 0.5$ system [Fig. 3(b)]. It can be seen how the election of the clustering distance defines the cluster formation for the same clump of individuals. As was previously mentioned there is not a unique way to define a cluster [42,44], but the use of the CV could be an interesting approach in the determination of the facilitative distance if a cluster is defined by the individuals that belong to the same clump and collaborate each other.

Now with the previously defined distance d_f , we study how the cluster size distribution changes for $\langle r^c \rangle = 0.6$ with $0.1 \leq z \leq 3.0$ (see Fig. 7). For the lowest values of z [$z = 0.1$ in Fig. 7(a), for instance] the distribution of cluster size is Pareto-like, a truncated power law which is rather similar to that obtained by Kefi *et al.* for different conditions of grazing [1,37]. In our model this range of z is characterized by a high value of sensitivity (see Fig. 2). With z increasing, bimodal distributions of the intermingled clusters occur: a power law for small clusters and a Gaussian distribution for the other cluster sizes (Fig. 7). This change in the distributions characterizes a clear change in the obtained patterns, from polydisperse aggregates with no apparent order [Fig. 3(a)] to

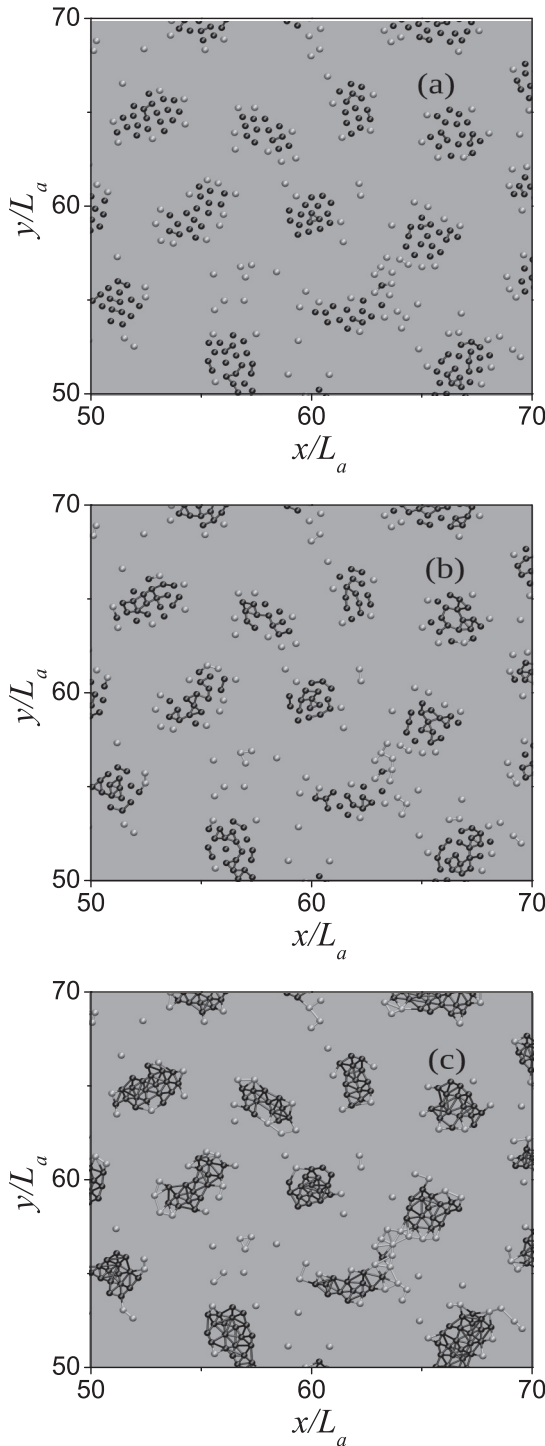


FIG. 6. Representative clumps have been zoomed from a snapshot for $z = 0.5$ [Fig. 3(b)]. Black and gray symbols indicate individuals that have r^{int} larger or smaller than $(r^c) = 0.6$, respectively. A bond is drawn between two individuals when their interdistance is less than or equal to d . (a) When considering a connectivity distance $d = 1.1L_a$, it is evident that all the relevant individuals in the patch are not included in the same cluster. (b) For $d_i = 1.22L_a$, black-colored individuals are clustered in nearly one cluster and there is a clear exclusion from the cluster of those individuals that do not have enough resources, the gray ones. (c) For $d = 2.0L_a$ it seems that individuals other than those in collaboration are also included in the cluster.

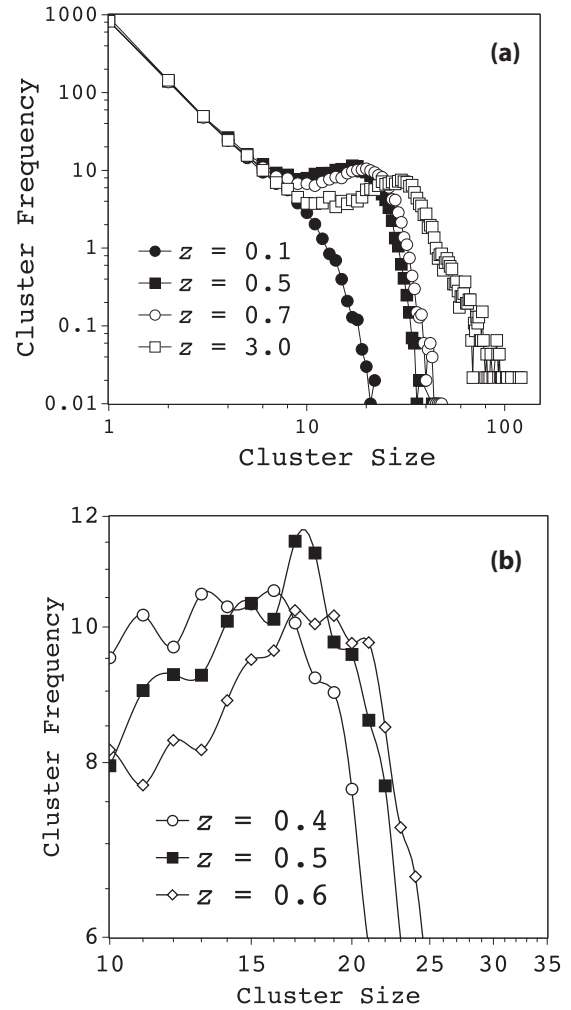


FIG. 7. (a) Changes of cluster size distribution with z , for $d_f = 1.22L_a$. For the lowest z values the distribution of cluster size is Pareto-like (truncated power law), but as z increases Pareto and Gaussian distributions are mixed up. (b) A close-up view of the distributions around $z = 0.5$. This result confirms that around this value of z the system has the smallest dispersion in the mean cluster size and a maximum in the cluster frequency. This finding when assessed jointly with the pair correlation function, Fig. 4, clearly shows that clusters of around 16–20 individuals are homogeneously distributed.

droplike clusters hexagonally arranged [Fig. 3(b)]. Another result that reinforces this self-organization is the change from a system with high sensitivity to one with low sensitivity [Figs. 2(a) and 3] which occurs at $z \sim 0.5$. The symmetry in the system is clearly seen when the clusters' size and their spatial distribution are observed (see Figs. 3, 4, and 7). Over $z = 0.5$ [Figs. 2(a) and 3(c)] clump size increases, the mix of cluster size distributions being less noteworthy. A study has been done to show that, for the chosen system parameters in this work, the cluster frequency gives a maximum for $z = 0.5$ [Fig. 7(b)]. From this analysis, the desertification threshold could be associated with the transition in the cluster size distributions (maximum symmetry in the spatial distribution of vegetation and an abrupt change in the sensitivity of the system [30,31]). The transition in the distribution of cluster sizes that happens at $z \sim 0.5$, from a Gaussian distribution with

a power law tail to a truncated power law and vice versa, might indicate the presence of extreme events. The system may go to a desertification due to a self-thinning process or increase its density via a self-organization around this region (small causes \leftrightarrow big changes). As it has been previously shown [30,31], critical transition to a barren state is characterized by regular patterns because of a symmetry-breaking stability. It is worth mentioning that for higher values of z , the system experiences different self-organized patterns, from clumps to a percolated system with voids hexagonally arranged [10,45]. It is worth emphasizing that in the description of an arid or semiarid ecosystem, the facilitative distance d_f together with the spatial distribution of clusters and distribution of cluster size might indicate how far the system from the desertification threshold is. When the system is close to this point, individuals that belong to the clumps should be separated by a distance smaller than $1.22L_a$, the facilitation distance, and the individual mean density of the system should be close to but less than 0.2.

It is interesting to mention at this point that a more exhaustive analysis of the kind of interaction studied here has been done by Archer and Wilding [46]. They state that the effect of repulsion generates an inhomogeneous region, between the gas and liquid phases, limited by two first-order transition lines, in substitution of the liquid-vapor critical point and a portion of the associated liquid-vapor transition line. This inhomogeneous region corresponds to the structured system, from a fluid of spherical liquidlike clusters to a fluid of spherical voids.

IV. DISCUSSION

Maximization of Shannon entropy is the first step to find the resource probability distribution function of the ecosystem. Then the minimization of resources [Eq. (2)] via the Monte Carlo technique allows us to predict different biomass densities and persistent vegetation patterns, when plants interact via a facilitation-competition pairwise interaction. These competing interactions when introduced in the description of real ecological processes between individuals are, within the framework of statistical mechanics, a powerful tool that provides an alternative probabilistic interpretation of the behavior of complex systems of dissimilar nature [10].

In this reductionist view of complexity, vegetation patterns are determined by a balance between facilitation and competition for the scarce resources, mainly water. Each individual obtains resources from a common zone of influence. The area occupied by a plant at the critical threshold is πd_f^2 . The facilitative distance d_f depends on the plant's characteristics and its environment. Evidence of the threshold transition is shown when the quasi-hexagonal symmetry of clusters [Fig. 3(b)] is broken by decreasing or increasing density [Figs. 3(a) or 3(c), respectively]. The dimensionless function $C_V(d)$ together with the cluster size distribution could be useful tools to identify how far a system is from the critical threshold.

In agreement with the experimental predictions, the model shows that facilitation in extreme environments (see [19] and references therein) is more important than competition. In fact, simulations with $\langle r^c \rangle = 0.6$ and $0 < z < 4.0$ and $\varepsilon_f = 0$ have been done. Contrary to the work of Martinez *et al.* [29],

neither clusters nor patterns were observed in the simulated ecosystems without collaboration.

Collaboration and competition for resources only reveals a basic mechanism of surviving in a hostile environment. Organization of complexity (evolutionary transitions) may result from the facilitative-competitive interaction among the individuals [47].

The present model reproduces results and vegetation patterns as that predicted by the work of Gilad *et al.* [17,18]. In that theoretical work, for drylands with a precipitation less than 500 mm/yr (in our representation, $z < 0.5$), densities are of the order of or less than 0.3 [see Figs. 2(a) and 2(b)]. The patterns obtained in the present simulations (Fig. 3) are similar to those obtained by Gilad and co-workers. Predicted densities are in qualitative agreement with experimental values for shrubs in water limited ecosystems [48].

The model introduces a tool for studying the self-organized ecosystems in order to describe the system at individual scale. As a consequence, it would be possible to compare the model parameters with those from real ecosystems. Quantities that describe individuals (structural ratio between crown and root lengths, foliage density or facilitative strength, root length and the geometry or strength of competition, etc.) can be included in the model and simulated. The facilitative interdistance d_f is an important parameter as it could be measured in arid or semiarid ecosystems. It is worth remarking that in cellular automata this distance is taken constant and equal to unity (the distance between two adjacent cells in a grid) [1,9]. Other quantities, representing the external environment or the inhomogeneities of the surface, like soil-water distribution inside and outside the cluster, the slope of the surface and runoff, etc., are feasible to introduce in the model.

In the present version, the model cannot capture time evolution of the system, which can be very desirable when studying how desertification evolves. Anyway, there are some implementations in statistical mechanics in which it is possible to do some equivalence of a Monte Carlo step with a time step [49–51], an interesting improvement that could be implemented in future works. Including time in the simulation process might be a powerful tool in order to study the reaction of the system when small variations in the external water activity are considered, whether this variation produces hysteresis, and the effects on the spatial distribution of the clusters due to the addition of new individuals or the deletion of those that die. Even more, in an individual-based growth model, from a particular initial configuration, different lineages can be tracked over time following an interesting birth-death process [51].

The model outlined here could be easily extended to include two or more species coexisting in the ecosystem, in order to study or give some insight, for instance, in invasion biology or in colonization processes [52].

ACKNOWLEDGMENTS

Financial support from Comisión de Investigaciones Científicas de la Provincia de Buenos Aires CICPBA, Consejo de Investigaciones Científicas y Técnicas (CONICET), Argentina, and Universidad Nacional de La Plata (UNLP), Argentina are acknowledged.

- [1] S. Kéfi, M. Rietkerk, C. L. Alados, Y. Pueyo, V. P. Papanastasis, A. ElAich, and P. C. de Ruiter, *Nature* **449**, 213 (2007).
- [2] R. Lefever and O. Lejeune, *Bull. Math. Biol.* **59**, 263 (1997).
- [3] R. HilleRisLambers, M. Rietkerk, F. van den Bosch, H. H. T. Prins, and H. de Kroon, *Ecology* **82**, 50 (2001).
- [4] J. von Hardenberg, E. Meron, M. Shachak, and Y. Zarmi, *Phys. Rev. Lett.* **87**, 198101 (2001).
- [5] M. Rietkerk, S. C. Dekker, P. C. de Ruiter, and J. van de Koppel, *Science* **305**, 1926 (2004).
- [6] T. M. Scanlon, K. K. Caylor, S. A. Levin, and I. Rodriguez-Iturbe, *Nature* **449**, 209 (2007).
- [7] M. Rietkerk and J. van de Koppel, *Trends Ecol. Evol.* **23**, 169 (2008).
- [8] R. Lefever, N. Barbier, P. Couteron, and O. Lejeune, *J. Theor. Biol.* **261**, 194 (2009).
- [9] R. M. Bailey, *Proc. R. Soc. B* **278**, 1064 (2011).
- [10] A. G. Meyra, G. J. Zarragoicochea, and V. A. Kuz, *Mol. Phys.* **110**, 173 (2012).
- [11] G. Bel, A. Hagberg, and E. Meron, *Theor. Ecol.* **5**, 591 (2012).
- [12] M. Pascual and F. Guichard, *Trends Ecol. Evol.* **20**, 88 (2005).
- [13] C. A. Klausmeier, *Science* **284**, 1826 (1999).
- [14] M. Rietkerk, M. C. Boerlijst, F. van Langevelde, R. HilleRisLambers, J. van de Koppel, L. Kumar, H. H. T. Prins, and A. M. de Roos, *Am. Nat.* **160**, 524 (2002).
- [15] J. A. Sherratt, *Nonlinearity* **23**, 2657 (2010).
- [16] M. C. Molles, *Ecology: Concepts and Applications*, 2nd ed. (McGraw-Hill, Boston, 2002).
- [17] E. Gilad, J. von Hardenberg, A. Provenzale, M. Shachak, and E. Meron, *Phys. Rev. Lett.* **93**, 098105 (2004).
- [18] E. Gilad, J. Von Hardenberg, A. Provenzale, M. Shachak, and E. Meron, *J. Theor. Biol.* **244**, 680 (2007).
- [19] R. W. Brooker *et al.*, *J. Ecol.* **96**, 18 (2008).
- [20] D. L. Dunkerley, *J. Arid Environ.* **51**, 199 (2002).
- [21] H. Da-Yin and W. Lie-Yan, *Chin. Phys. Lett.* **24**, 3586 (2007).
- [22] V. Grimm and S. F. Railsback, *Individual-based Modeling and Ecology* (Princeton University Press, Princeton, 2005).
- [23] H. J. Schenk, S. Espino, C. M. Goedhart, M. Nordenstahl, H. I. M. Cabrera, and C. S. Jones, *Proc. Natl. Acad. Sci. USA* **105**, 11248 (2008).
- [24] N. Barbier, P. Couteron, R. Lefever, V. Deblauwe, and O. Lejeune, *Ecology* **89**, 1521 (2008).
- [25] F. Borgogno, P. D'Odorico, F. Laio, and L. Ridolfi, *Rev. Geophys.* **47**, 1 (2009).
- [26] R. Foti and J. A. Ramirez, *Hydrol. Earth Syst. Sci.* **17**, 63 (2013).
- [27] H. J. Schenk and R. B. Jackson, *J. Ecol.* **90**, 480 (2002).
- [28] E. Meron, *Ecol. Modell.* **234**, 70 (2012).
- [29] R. Martínez-García, J. M. Calabrese, E. Hernández-García, and C. López, *Geophys. Res. Lett.* **40**, 6143 (2013).
- [30] M. Scheffer and S. R. Carpenter, *Trends Ecol. Evol.* **18**, 648 (2003).
- [31] M. Scheffer, J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, E. H. van Nes, M. Rietkerk, and G. Sugihara, *Nature* **461**, 53 (2009).
- [32] A. Imperio and L. Reatto, *J. Phys.: Condens. Matter* **16**, S3769 (2004).
- [33] C. E. Shannon, *Bell Syst. Tech. J.* **27**, 379 (1948); **27**, 623 (1948).
- [34] R. C. Dewar, *Entropy* **11**, 931 (2009).
- [35] M. P. Allen and D. J. Tildesley, *Computer Simulation of Liquids* (Clarendon Press, Oxford, 1987).
- [36] D. Frenkel and B. Smit, *Understanding Molecular Simulation. From Algorithms to Applications* (Academic Press, San Diego, 1996).
- [37] A. Manor and N. M. Shnerb, *Phys. Rev. Lett.* **101**, 268104 (2008).
- [38] J. T. Wootton, *Ecology* **82**, 580 (2001).
- [39] H. Balzter, *Ecol. Modell.* **126**, 139 (2000).
- [40] V. K. Arora, *J. Hydrol.* **265**, 164 (2002).
- [41] R. Law, J. Illian, D. F. R. P. Burslem, G. Gratzler, C. V. S. Gunatilleke, and I. A. U. N. Gunatilleke, *J. Ecol.* **97**, 616 (2009).
- [42] J. B. Plotkin, J. Chave, and P. S. Ashton, *Am. Nat.* **160**, 629 (2002).
- [43] B. Steudel, A. H. T. Friedl, C. Lofke, M. Lorenz, M. Wesche, and M. Kessler, *Ecol. Lett.* **15**, 1397 (2012).
- [44] R. O. Duda, P. E. Hart, and D. G. Stork, *Pattern Classification*, 2nd ed. (Wiley, New York, 2012).
- [45] G. J. Zarragoicochea, A. G. Meyra, and V. A. Kuz, *Mol. Phys.* **107**, 549 (2009).
- [46] A. J. Archer and N. B. Wilding, *Phys. Rev. E* **76**, 031501 (2007).
- [47] Z. Kikvidze and R. M. Callaway, *BioScience* **59**, 399 (2009).
- [48] M. Sternberg and M. Shoshany, *Ecol. Res.* **16**, 335 (2001).
- [49] U. Nowak, R. W. Chantrell, and E. C. Kennedy, *Phys. Rev. Lett.* **84**, 163 (2000).
- [50] O. Chubykalo, U. Nowak, R. Smirnov-Rueda, M. A. Wongsam, R. W. Chantrell, and J. M. Gonzalez, *Phys. Rev. B* **67**, 064422 (2003).
- [51] W. R. Young, A. J. Roberts, and G. Stuhne, *Nature* **412**, 328 (2001).
- [52] P. Caplat, P.-O. Cheptou, J. Diez, G. Guisan, B. M. H. Larson, A. S. Macdougall, D. A. Peltzer, D. M. Richardson, K. Shea, M. van Kleunen, R. Zhang, and Y. M. Buckley, *Oikos* **122**, 1265 (2013).