Plant Spread Dynamics and Spatial Patterns in Forest Ecology

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1 INTRODUCTION: THE BIOLOGICAL INVASION PROBLEM

Species in an ecosystem can be classified as *natives* and *exotics*. Native species are those that have coevolved together in the ecosystem while exotic ones have not. The introduction of exotic species into an ecosystem is usually associated to human influences and it can be intentional or accidental. Some exotic species do not survive, at least without an artificial assistance. But some others do quite well on their own in a new environment. Exotic species may have no natural predators in the new environment or they can make a better use of the natural resources than the natives, so they spread in the new territory, competing with some of the natives and eventually leading to their extinction. Exotic species that successfully establish and spread in an ecosystem are called *invaders*. The process by which an invader arrives and spreads into the new territory is called *biological invasion*. It is worth mention that, although invaders are usually exotic species,

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sometimes native species may also behave as invaders. That is, if an ecosystem suffers a strong disturbance, like fire or heavy grazing, some native species whose population were originally stable, may start to grow outcompeting other native species.

There are many examples of introduced species that became invaders, ranging from bacteria to cattle. Human accidental or intentional introductions are responsible for most of the present biological invasions, threatening the structure and functioning of many ecosystems.

There are many effects associated with biological invasions, perhaps the most important one being the possible loss of biodiversity in the long term. But also biological invasions may introduce changes in different environmental traits, like climate, hydrology (invaders may consume more water than natives), soil composition (for instance, some plants take up salt from soil and deposit it on the surface, making it unsuitable to some native species), etc. All these changes have a strong economical impact, considering their influences in agriculture, forestry and public health [9]. Hence, it is of interest to understand this phenomenon in order to predict the potential invasiveness of a species before the introduction in an ecosystem, and to develop strategies of control of invasive species already introduced.

Although the biological invasion has been recognized as potentially damaging for ecosystems functioning more than 40 years ago [5], there are still many important open questions about it. Perhaps the most important one is: What makes a successful invader? That is, why a given species behaves as an invader and a similar one does not? Why the same species behaves as an invader in a given ecosystem while it does not invade another different one? At the present specialists agree that this is an extremely complex problem and that the answer to this question depends on several factors. Among the most important factors for plants we can mention:

- Life history traits, that is, reproductive and growth properties of individual trees, like seed dispersal mechanisms, germination properties, age of reproductive maturity, etc. One point that is of particular interest is the posssible existence of long range seed dispersal distributions (in a statistical sense). Trees disperse seeds through several mechanisms, which generate different types of spatial seed dispersal distributions. There is evidence that some mechanisms may generate fat-tailed (that is, long ranged) distributions. This is a very important factor in the description of plant migration process, invasive or not, since this type of distribution may change the rates of spread of a species in orders of magnitude. We will discuss this topic with more detail later.
- Demographic traits, like the mortality rates at the different stages of growth
 of a tree,
- Environmental conditions, including disturbance regimes.
- Interspecific interactions, for instance, competition between the alien and native species, but also interactions of positive sign (like symbiosis or facilitation).

However, it is not clear the relative importance of all these factors and experimental results are frequently ambiguous and, sometimes, even contradictory. Hence, it is of interest to have accurate theoretical models to check all these hypotesis. In section 2 we present a recently proposed cellular automaton model [3] that describes the population dynamics of several interacting woody species (trees and shrubs) at an individual based level. The model includes most of the features that are believed to be important describing invasion processes, where the parametrization is made on the base of measurable quantities. In section 3 we show a comparison between field data estimations and predictions of the model, both for invasion and non invasion systems.

Another important point is how can we characterize the invasion process. That is, how do we *measure* the invasiveness of a species or the invasibility of the habitat? Usually the invasion process is characterized by means of the different rates of spread of the invasive species, that is, the velocities at which it spreads in the new environment. Although these are good measures, sometimes its calculation involves a series of problems. Experimentally, the rates of spread can be estimated, for example, from aerial photographs, by measuring the areas covered by the species at different times. However, this involves the usage of high resolution photographs taken during large periods of time (typically several decades). Hence, the available data are scarce and not very accurate and it is important to find alternative ways of characterizing the invasion process.

Sections 4 and 5 are devoted to the study of different scale-invariant (i.e., fractal) spatial patterns that may appear during invasion processes. The results presented in those sections suggest the fractal dimension of the particular fractal patterns as good (and measurable) quantities to characterize invasion processes.

A general discussion is presented in section 6.

2 THE MODEL

We first present a cellular automaton for the description of a single, non-interacting species. This model will be generalized later to the case of several interacting species.

2.1 SINGLE SPECIES CELLULAR AUTOMATON

The model [3] is defined on a square lattice of $N = L_x \times L_y$ sites or cells with open boundary conditions. Each cell can be occupied by at most one single adult individual. This rule fixes the spatial scale, in the sense that the area of a unit cell of the lattice will correspond to the average area covered by the canopy of the trees under consideration. For instance, in the case of the species considered in section 3 the average area is $25m^2$ [10], that is, the lattice unit corresponds to 5m.

To each cell we associate an integer variable $a_i(t)$ that represents the age of the individual located at it at time t, where the time unit is chosen to be one year. This time scale appears naturally since we consider annual rates of reproduction and mortality. We use a parallel dynamics. Reproductive traits are described by the following parameters:

- Every mature individual produces n seeds in a seed crop. We assume a self-breeding species, that is, every individual produces seeds.
- The dispersal of those seeds is described by a density function f(r), defined as the fraction of seeds dipersed by one individual to a distance r per unit area. This density is normalized in the plane.
- Every seed geminates with a probability f_q .
- Reproductive or mature individuals are those whose age is greater than t_m .
- Individuals produce seed crops every t_s years.
- An important factor for invasion is the existence of *juvenile banks*. Saplings of some species can survive under the shade of the parental, but they grow until certain high and then stop growing. They do not become reproductive while living under the shade of the parental. When the parental dies they can resume their growth and one of them replaces the parental and can become reproductive. The colection of saplings below the shade of the parental is called a juvenile bank. For species with juvenile banks we include another parameter, the average age t_J of the saplings.

Mortality in trees is much more higher at the first stages of growth (usually during the first and second years of life) than for older trees. Hence, we consider two probabilities of survival:

- q is the annual adult survival probability.
- P_s is the juvenile (< 2 years) survival probability.

The dynamics of the model is as follows. Let's first consider an occupied cell i at time t, that is, a cell for which $a_i(t) \neq 0$. If the species does not have juvenile bank, then the individual can survive and grow with probability q, and therefore $a_i(t+1) = a_i(t) + 1$, or it dies with probability 1 - q, leaving the cell empty $a_i = 0$. If the species has juvenile bank, the rule is very similar, except that when it dies instead of leaving the cell empty it is replaced by another individual with age t_J .

Let's now consider an empty cell i at time t, that is $a_i(t) = 0$. This cell can be colonized at time t + 1 with probability $p_i(t)$, that depends on the seeds received from other cells; $p_i(t)$ is the probability that at least one of the seeds received at time t germinates and that the corresponding juvenile survives until the adult stage. Assuming these two events as independent, p_i is given by

$$p_i(t) = 1 - (1 - P_s f_g)^{s_i(t)} \tag{1}$$

where $s_i(t)$ is the total number of seeds received by the cell at time t. How do we calculate s_i ? Suppose that the species produces crops every year. Then, the number of seeds received by the cell i, coming from a mature tree located at a cell j is $nf(r_{ij})$, where r_{ij} is the distance between cells. Hence, $s_i(t)$ is obtained by summing this quantity over all cells containing a mature tree. If the interval between seed crops t_s is greater than one, then cells containing mature trees only contibute to these sums every t_s years.

Now, what is the appropriate choice for the seed dispersal function f(r)? For many tree species seed dispersal has a limited range, that is, seeds are dispersed in the neighborhood of the tree. In this case f(r) will be short-ranged, that is, without long tails and the global spread properties are not expected to depend on the specific form of f(r). However, as we mentioned before, one open question about plant spread dynamics is the possible existence of long range seed dispersal mechanisms. This question was first addressed when people tried to explain the postglacial migration of different species of trees, like oaks. After the glaciers retreated they left an open area that the woods recolonized at a velocity of about 1 Km/year [4]. Applications of short range dispersal models to this problem, like the reaction-diffusion model, with realistic parametrizations predicted velocities ranging between 1 and 50 m/year [12]. This difference of about two orders of magnitude suggests the presence of long range seed dispersal distributions [8]. But then the question is, which type of mechanisms can lead to the occurrence of rare events of seeds dispersed very long distances? Trees use one or more different mechanisms of seed dispersal as a result of evolutionary adaptations. The most simple one is just gravity, that is, seeds just fall down near the canopy. This is clearly a short range mechanism.

Some plant species use mutualistic relationships with animals, like birds or mammals, as dipersal strategies. They produce fruits that have attractive colors and flavours. Then the animals eat the fruits together with the enclosed seeds, which pass unharmed through the digestive tract. So, the animals move and defecate the seeds in another place. Whether or not this type of mechanism could lead to long ranged dispersal effects depends on several factors, like the effective mobility and the habits of the animals. Experimental evidence is not conclusive at all.

Finally, the best candidates are wind dispersal mechanisms. Some seeds have a wing with the form of an helix (gyroscopic seeds). In the presence of strong winds these seeds leave the canopy, rotate and fly, so they can be driven by the wind over long distances. However, the experimental evidence is not conclusive in this case either. Unfortunately, it is very difficult to measure seed dispersal distribution functions. Field measurements of seeds distributions have large error bars and limited ranges. Therefore, attempts of fitting data with short and long range distributions cannot give a definite answer. Hence, it is interesting to look for other ways of detecting long range seed dispersal distributions.

To analyze this problem we used two different types of models for the seed dispersal function. For simulating short range dispersal mechanisms we proposed an exponential function:

$$f(r) = \frac{2}{\pi d^2} e^{-2r/d} \tag{2}$$

where d is the mean dispersal distance. For simulating long range dispersal mechanisms we proposed a power law:

$$f(r) = \begin{cases} \frac{A}{r^{\alpha}} & if & r \ge 1/2\\ 0 & if & 0 < r < 1/2 \end{cases}$$
 (3)

where A is a normalization constant and $\alpha > 2$ (otherwise the density function f cannot be normalized). We expect three different behaviours, according to the values of α . For $\alpha > 4$ this function has finite first and second moment. Therefore, the central limit theorem holds and short range behaviour is expected. When $3 < \alpha \le 4$ the first moment remains finite but the second moment becomes infinite. The mean dispersal distance is given by $d \equiv \langle r \rangle = (\alpha - 2)/2(\alpha - 3)$. Finally, when $2 < \alpha \le 3$ both first and second moment are infinite.

2.2 INTERACTIVE MULTIPLE CELLULAR AUTOMATA MODEL

Let's now consider the case of several interacting species. In this case we associated to each species one single cellular automaton of the type described in the previous subsection, all of them defined over the same lattice. In this way each cell of the lattice has associated several dynamical variables. Interactions are introduced by coupling them through new dynamical rules. We called this an Interactive Multiple Cellular Automaton model, or IMCA [3]. The type of interaction we are interested in is competition, which in an ample sense is competition by space, and involves competition by resources. This means that only one of the different dynamical variables associated to a given cell can be different from zero at the same time.

Concerning the colonization of an empty cell, in this case we count the seeds received by the cell from each one of the different species. Then we calculate the different colonization probabilities and compare them with independent random numbers. If only one species succeeds in the colonization, the cell follows the dynamics of a single species. If more than one species succeed we sort the winner with some probability that may depend on environmental conditions. If the different species use resources in a similar way the winner is sorted with equal probability among the different species present in the cell. If different species use resources in a different way the probability depends on the environmental conditions, which are described by a new set of variables. Those environmental variables may be dynamical or fixed. In the last case we can consider them as external conditions. An example of colonization rules that depend on environmental variables will be presented in the next section.

3 SIMULATIONS VS. FIELD DATA VALUES

To compare the predictions of our model with real situations we considered four different tree species from the mountain forest in Córdoba, Argentina, two of them exotics (Gleditsia triacanthos and Ligustrum lucidum) and two natives (Lithraea ternifolia and Fagara coco). L. ternifolia was once the dominant tree species in this region. The native woodlands are being invaded by several exotic species. F. coco coexists in some parts of the mountains with the dominant L. ternifolia. Seed dispersal in all these cases is short ranged; another remarkable fact is that both invaders have juvenile bank while the natives have not [10].

We started our simulations by considering an initial dense forest of the dominant native (L. ternifolia) with random ages, located in a rectangular area L_x sites of width. At the bottom of the area y=0 we put a row of individulas of one of the two exotic species, with random ages between zero and the age of first reproduction t_m . This configuration simulates a very typical situation, since these plants usually spread into the forests from roads or river sides.

In figure 1 we see the typical pattern of invasion at two different times, where gray points represent the natives, black ones are the invaders ($L.\ lucidum$ in this case) and white points are empty sites. We see that the invaders form a wide spread band that moves in the y direction, leaving a dense invaded forest behind it. The presence of juvenile banks turn the invasion inevitable and at large enough times the invaders cover the whole area.

To characterize the invasion process we defined the *invasion front* h(x) as the coordinate y of the farthest occupied site corresponding the x position along the bottom line (see figure 1). We then calculated the mean front position

$$\overline{h} = \frac{1}{L_x} \sum_{x=1}^{L_x} h(x) \tag{4}$$

as a function of time, and we averaged this quantity over different initial conditions and over different sets of random numbers.

In the case of invasion by G. triacanthos it is necessary to introduce environmental variables. L. ternifolia has a special ability to establish in shallow soils and rock crevices. G. triacanthos does not present this ability, that is, it grows much more slowly on shallow soils than in deep soils. In this case we introduced a set of soil parameters $\{c_i\}$ that can take two values: $c_i = 0$ represents a shallow soil cell while $c_i = 1$ represents a deep soil. These parameters are sorted with some distribution at the beginning of the simulation and kept fixed through it. The colonization rule of empty cells is the following: if $c_i = 0$ the native species always win with probability 1; if $c_i = 1$ the winner is sorted with equal probability.

In figure 2 we see the behaviour of the mean front position in this system, for the cases of homogeneous deep and rocky soil. We see that the effect of the soil type is just to slow down the process; both curves show the same qualitative

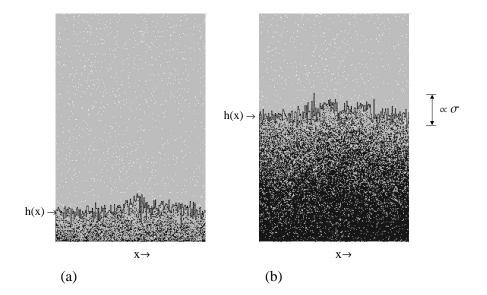


FIGURE 1 L. lucidum invasion (black cells) in a dense L. ternifolia forest (gray cells), for a simulation area of 80×160 cells; white cells correspond to empty cells. (a) $t = 50 \ years$; (b) $t = 150 \ years$.

invader	field estimation [m/y]	model prediction [m/y]
$G.\ triac anthos$	2.5 - 4	1.9 - 4.4
L. lucidum	11 - 12.5	13.6

TABLE 1

behaviour, that is, after some transient period, the front increases linearly with time, showing a well defined velocity V. We also performed several simulations with random mixtures of deep and rocky sites in different proportions. The behaviour is the same, with velocities between these two values. Hence, we can consider these values as *upper and lower bounds for the velocity prediction* of the model in this particular case.

We also performed similar simulations, but considering the other invader $L.\ lucidum$. In this case we did not introduce soil varibles, because this invader grows well in any type of soil, as well as the native. The results are qualitatively the same as in the previous case.

In table 3 we show a comparison between the predictions of the IMCA model with field data estimations made by using aerial photographs of the region [11].

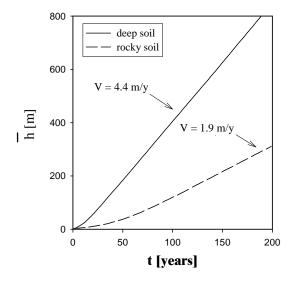


FIGURE 2 Mean front position as a function of time for G. triacanthos invasion in a dense forest of L. ternifolia.

In order to perform another comparison with field data values, we simulated the dynamics of both native species L. ternifolia and F. coco. In this case, as long as F. coco spreads into the area, cells behind the spreading front can be re-occupied by L. ternifolia. This lead, after some time, to a stationary situation of a mixed forest with a distribution of patches of both species. The stationary values of the population densities of both species are independent of the initial conditions, showing a proportion of 2.3 between both densities, that is consistent with the observed value 2 ± 1 [3].

4 FRACTAL GROWTH OF INVASION FRONTS

As it was mentioned in the introduction, it is interesting to look for alternative ways of characterizing the invasion process, not only using the rate of spread. If we look at the invasion front we see that it has some structure (see figure 1). To analize this structure we studied the behaviour of the average width of the front, which is proportional to the standard deviation:

$$\sigma(t) = \sqrt{\frac{1}{L_x} \sum_{x=1}^{L_x} \left(h(x, t) - \overline{h}(t) \right)^2}$$
 (5)

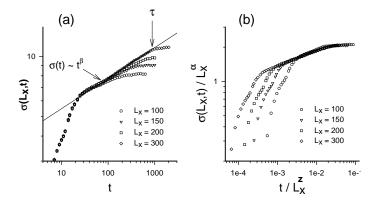


FIGURE 3 (a) Standard deviation of the invasion front as a function of t and the system width L_x . (b) Data collapse of the curves shown in (a) for $\alpha = 0.294$ and z = 1.93.

We calculated σ as a function of t and averaged this quantity over different initial conditions and different sequences of the random noise. In figure 3a we show the temporal behaviour of σ for different widths of the simulation area in a log-log plot. We see that, for any value of L_x , σ present three distinct regimes: a transient period that is independent of L_x , a power law regime and a saturation regime, where it becomes constant. For large values of L_x the power law regime also becomes independent of L_x , and it is characterized by a single exponent β . Both the crossover time τ from the power law to the saturation regimes and the saturation value depend on L_x . Moreover, it can be seen that for large values of L_x they present a power law dependency, characterized by two exponents α and z. All this phenomenology is characteristic of what is known as a roughening process. Roughening refers to some non-equilibrium phenomena associated with the growth of certain type of interfaces between two different media. Growing interfaces appear in a variety of phenomena in nature, like the fluid motion in a porous media. If you put a drop of ink in a sheet of paper you see that the patch grows with a well defined interface between the wet and dry parts. Also if you burn one edge of the paper you see a propagating interface between the burned and the unburned parts. If you look at anyone of these intefaces under a microscope you see that it is not smooth, but rather irregular. Moreover, as the interface propagates, the size of the irregularities increase. It is said that the interface roughens [1].

There is not a complete theory based on first principles that explains the dynamic roughening. However, most the basic properties of these type of processes are well described by a general *phenomenological scaling approach*, which can be summarized in the following scaling relation [1]:

$$\sigma(L_x, t) \sim L_x^{\alpha} F\left(\frac{t}{L_x^z}\right)$$
 (6)

where the scaling function F is such that

$$F(x) \sim \begin{cases} x^{\beta} & if \quad x \ll 1\\ constant & if \quad x \gg 1 \end{cases}$$
 (7)

and $z = \alpha/\beta$. This relation implies a crossover time $\tau \sim L_x^z$ such that, $\sigma(L_x, t) \sim t^\beta$ for $t \ll \tau$ and $\sigma(L_x, t) \sim L_x^\alpha$ for $t \gg \tau$. In the last regime the interface develops a self-affine structure, i.e. for a fixed time the profile h(x) satisfies (in an statistical sense) the property $h(x) \sim b^{-\alpha}h(bx)$, for arbitrary values of the scale factor b [1]. From this property follows that the local fractal or box dimension D of the profile is $D = 2 - \alpha$ for short length scales (for long length scales D always equals one [14]. The data collapse displayed for long times in figure 3b shows that the scaling assumption Eq.(6) holds for the invasion fronts with non trivial values of the exponents α , β and $z = \alpha/\beta$.

We then analyzed how variations in the life history parameters influence the roughening process of the invasion front. It can be shown that the invasion velocity is mainly determined by two parameters: the mean dispersal distance dand the age of first reproduction t_m [3]. So we calculated the two independent exponents of the roughening process α and z for different combinations of values of d and t_m . We found that α is sensitive to variations in d and t_m , while z is almost constant with a value near two for all the combinations of d and t_m we checked. In figure 4 we show a parametric plot of the local fractal dimension $D = 2 - \alpha vs$ the invasion velocity V; every point in this graph corresponds to the calculated values of (α, V) for a particular pair of values of (d, t_m) . We see that all points appear to fall into a single curve that saturates at a constant value around $D \approx 1.8$ for large values of V, showing that large invasion velocities can be expected for very rough fronts. This result also suggests that the local fractal dimension of the invasion front is a single valued, monotonic increasing function of the velocity. But the local fractal dimension is something that, in principle, we could *measure* from a high resolution aerial photograph. Hence, this result suggests that we would not need photographs taken at different times to estimate the invasion velocity; we could do that just with one photograph. In other words, we could make predictions about the long time dynamical behaviour from pure geometrical properties of a spatial pattern at a fixed time, at least in the case of an invader with short range dispersal and in the presence of a strong native competitor.

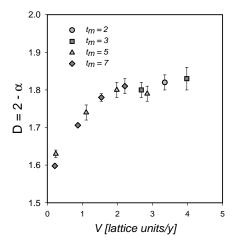


FIGURE 4 Parametric plot of the local fractal dimension vs the invasion velocity.

5 LONG RANGE SEED DISPERSAL AND SPATIAL PATTERN FORMATION

To analize the influence of long range seed dispersal we simulated the spread of a species with long range dispersal from a single focus, that is, we started the simulations with a single mature individual located at the center of a square area. To discriminate between the interaction and seed dispersal effects we neglected competition, that is, we considered the spread of a single species in a clean area. We chose a reasonable set of life history parameters, that is, a set of values inside the ranges of values for the different species considered, and we varied the exponent of the power law seed dispersal function.

In figure 5 we can see the difference between the typical spatial patterns generated by short and long range seed dispersal distributions, where the parameters values are the same in both cases (figures 5a and 5b). The short range case is characterized by a single compact cluster with an almost circular shape, surrounded by a few isolated trees.

The long range case presents a much more complex pattern. In the first years there is again a unique large cluster, which is more irregular and is surrounded by a few small clusters and a broad distribution of isolated trees. After some characteristic time, that dependes mainly on t_m , we observe the sudden appearance of a distribution of cluster of several sizes, including some large ones. This occurs because some of the trees located far away from the initial focus started to reproduce and formed new secondary focuses. As time goes on, the main cluster continues growing and absorbes neighbouring cluster. This effect gener-

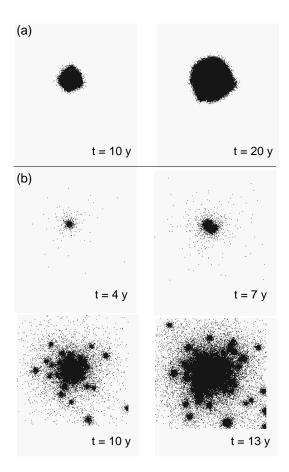


FIGURE 5 Comparison between spatial patterns generated by short and long range seeds dispersal strategies, in a simulation area of 200×200 cells and parameters values of $G.\ triacanthos.$ (a) Exponential distribution function Eq.(2). (a) Power law distribution function Eq.(3).

ates a very complex border structure that becomes self-similar (i.e., fractal) at large times, while new clusters of different sizes are being created continuously. The predicted pattern agrees qualitatively with those observed in *Criptostegia grandiflora* (a shrub with seed dispersal by wind) in northeast Australia [7].

We calculated the fractal dimension D of the main cluster border using a box-counting procedure. In figure 6 we see D as a function of time for different values of the exponent α , half of them corresponding to distributions with infinite first moment and the other half with finite first moment. We see in all the cases

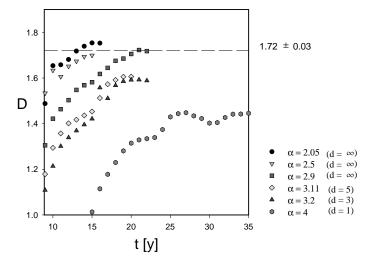


FIGURE 6 Fractal dimension of the main cluster border for different values of α and and $L_x = 1024$.

that, after some transient period, D saturates into a constant value, which seems be independent of α with a value around $D=1.72\pm0.03$ for distributions with infinite first moment. The fact that physical properties of the system become independent of α , when α is such that the first moment diverges, is characteristic of systems with interactions that decay as $1/r^{\alpha}$ [2, 6].

Finally, in figure 7a we can see the typical time evolution of the normalized frecuency P(s) of clusters with area s, for a particular value of α . We see that also this quantity reaches a stationary state at long times. An approximation of the stationary distribution is diplayed in figure 7b. We see that the long range quality of the basic interactions generates a complex distribution with crossovers between different power law regimes, which are expected to contain also information about the invasion process. This point deserves further investigation and some related work is in progress.

6 CONCLUSIONS

We have shown that the study of spatial pattern formation is indeed a valuable tool for the analysis and detection of several features associated with biological invasion processes. That is, we saw how stationary fractal patterns may be developed during different invasion processes and that the corresponding fractal

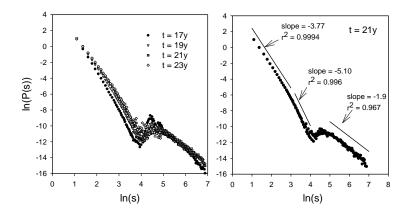


FIGURE 7 Normalized frequency of clusters with area s for $\alpha = 2.05$ and $L_x = 512$.

dimensions contain information about them. In particular, we showed that the competition between alien and native species lead to the appearence of a self-affine invasion front (as a result of a roughening process), whose local fractal dimension is proportional to the invasion velocity. This result suggests a possible technique for estimating invasion velocities through the analysis of spatial patterns in aerial photographs. But also the suggestion of a constant value of the dynamical exponent z opens the possibility of estimating the long time behaviour (i.e., the asymptotic velocity through the local fractal dimension D) by monitoring the short time behaviour of the growth exponent β of the standard deviation. Works along these lines are in progress.

Concerning the effect of long range seed dispersal, we showed that it generates a very particular stationary pattern that may serve as an indirect way of detecting its presence. In this case the fractal dimension D of the main cluster border increases as $\alpha \to 3^+$ and it seems to be independent of α when $2 < \alpha \le 3$. Of course, as α decreases, the different rates of spread (population growth is non linear in this case) increase. Hence, we see again what could be a general rule, that is, large fractal dimensions appear to be associated with fast invasion processes.

Finally, the presence of several power law regimes (and the corresponding crossovers between them) in the stationary cluster size distribution of a species with long range seed dispersal suggests a non extensive statistical formalism

([13], see also Montemurro in this book) as the appropriated framework for the analysis of this problem. Work along this line is also in progress.

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