Cellular Automaton Modeling of Pattern Formation

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Book review

Andreas Deutsch, Sabine Dormann, Cellular Automaton Modeling of Biological Pattern Formation, Characterization, Applications and Analysis, Birkhäuser, 2005, ISBN 0-8176-4281-1, 331pp.

The above book is one of the latest additions to the 'Modeling and Simulation in Science, Engineering and Technology' series, edited by Nicola Bellomo. The book focuses on application of so-called lattice-gas cellular automaton models to the field of biological pattern formation. Cellular automaton models are a spatial modeling formalism. They consist of a regular spatial grid in which each grid point (or site) can have a finite, and typically small number of discrete states (for a basic introduction see [1]). In the simplest models there are just two possible states; 0 for a site being empty, and 1 for a site containing a single individual. The next-state of a site depends on the states in the neighboring sites and a next-state function, which can be deterministic or stochastic. In traditional cellular automaton models implementing movement of individuals is not straightforward, as one site in the lattice can typically only contain one individual, and consequently movement of individuals can cause collisions when two individuals want to move into the same empty site (see Fig. 1(A)). In a lattice-gas model this problem is avoided by having separate channels for each direction of movement (see Fig. 1(B)). The movement steps are alternated with interaction steps, in which processes affecting, e.g., birth and death can be implemented. The lattice-gas method allows for a clear separation of effects of movement and interaction, especially if interactions are only allowed to occur within the site between the separate channels. In the examples given in the book, in most cases the interactions also depend on neighboring sites, and therefore the distinction between interaction and movement effects is less clear.

Lattice-gas methods are mostly known from physics, where they have been successful in, e.g., describing macroscopic gas and fluid dynamics, by implementing simple or even simplistic local interactions. Notwithstanding the caricatural nature of the local rules, for instance in the restriction of possible movement directions, often the overall macroscopic behavior of the system can very well be approximated if averages over larger spatial scales are considered [1].

In the book, the authors describe an interesting number of applications of the method in the field of biological pattern formation. The examples include tumor development, population growth, swarming behavior, and cell sorting. In some cases the models are aimed at specifying local rules that can generate a desired macroscopic behavior, and sometimes the models are more strategic in the sense that they explore possible behaviors for a certain type of microscopic interactions. My personal opinion is that the latter application of the method might proof most valuable. A problem with the first approach is that often many local rules can generate the same or very similar macroscopic behavior. We have recently shown that for instance Turing-like patterns

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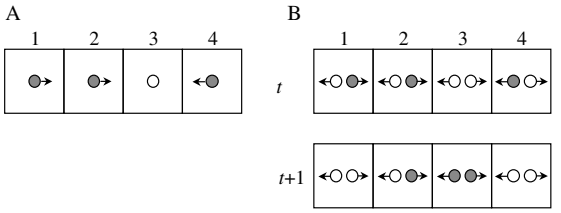

Fig. 1. Movement in (A) a simple one-dimensional cellular automaton model, and (B) in a corresponding lattice-gas implementation. Filled circles indicate occupied sites or channels, while empty circles denote empty sites or channels. In the cellular automaton two individuals, from position 2 and 4, want to move to position 3, causing a 'collision', as a single site can only contain one individual. As a result, also the intended movement of the individual in position 1 can be affected. In the lattice-gas simulation each movement direction has a separate channel, and thus collisions are avoided. The result of the movement step ($t + 1$) will be that both channels in position 3 will be occupied.

can be generated without the necessity of an underlying Turing instability in the local interactions [2]. The field of (biological) pattern formation actually urgently needs tools to distinguish between different potential underlying mechanisms that might be responsible for a macroscopic behavior. However, the lattice-gas method does not seem particularly appropriate for this kind of research, as the local dynamics are very much a caricature, and consequently the method does not seem suitable to pinpoint and verify the exact local mechanisms that cause a certain pattern. For instance, when modeling cell–cell interactions the lattice-gas method cannot incorporate any detail below the level of the complete cells. Interestingly, there is a cellular automaton-like approach that does incorporate this detail. In this approach a biological cell is encoded by an ensemble of cellular automaton sites, and the microscopic rules are describing expansion or retraction of the cell [3]. The total cell volume is monitored, and cellular expansion and retraction depend on deviations from a target volume. A nice example of the success of the method is a simulation of morphogenesis in the slime mold *Dictyostelium discoideum* [4].

The lattice-gas method does seem potentially valuable for a *bottom–up* approach, in particular to study new dynamical possibilities if individuals are allowed to move in a spatial domain with local interactions. However, I strongly feel that the methodology should include a thorough study of the effect of the spatial patterns, which in my opinion is largely lacking from the book. I will first give a verbal argument of how such a methodology should work, and than I will demonstrate it with an example. In the book, much emphasis is put on how to derive a so-called *mean field* approximation for a cellular automaton model. In a mean field approximation, by definition, all spatial correlations are removed from the system. A straightforward way to simulate mean field is to randomize the automaton after each time step, although this method is not exact as it does not destroy spatial correlations within a time step. But the critical question is: what insight can you gain from the mean field approach? The authors state that often the mean field approach yields a picture of the CA dynamics that is qualitatively correct. I think they are missing a crucial point here, which is that studying the mean field dynamics of a model gives a possibility to pinpoint the effects of spatial pattern formation. In fact, it is cases where the mean field approximation deviates from the spatial dynamics that should be of most interest for people studying spatial models. Then, the next step in the methodology should be to describe and/or quantify the spatial pattern, and to understand how and why the dynamics of the system are changed.

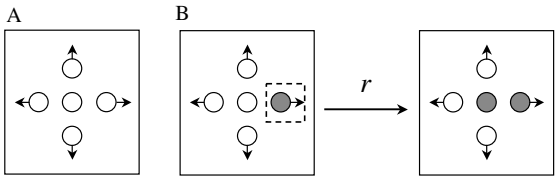

Fig. 2. Specification of a two-dimensional lattice-gas cellular automaton describing population growth. (A) Each site contains five channels consisting of four movement directions and one channel for stationary individuals. Each channel can contain one individual (filled circles) or be empty. (B) In the interaction step each empty channel randomly chooses one of the other channels within the site, and if this channel contains an individual with probability r the empty channel will become occupied as well. The growth process is drawn for the stationary channel in the middle of the site, which has randomly chosen the channel to the right (indicated by the dashed box).

Let me move to my example, which is akin to the population growth models that are discussed in Chapter 6 of the book. The model has five channels, consisting of four movement directions and one channel for stationary individuals (Fig. 2(A)). In the interaction step all empty channels randomly choose one of the other channels within the site, and if this channel contains an individual the empty channel will be occupied with probability r (Fig. 2(B)).

Before each movement step all channels within a site are randomized, so that movement is essentially random. Movement and interaction (growth) steps are alternated, and the growth probability parameter r and the number of movement steps between interaction steps can be varied. Let us first consider the mean field behavior of the model. For this we introduce the variable X_t, which is the total number of individuals at time t, and the constant K, which is the maximum number of individuals (i.e. $K =$ number of sites $\times$ number of channels per site). Now the expected change in the number of individuals within an interaction step is given by the product of the probability factor r, the total number of empty channels, which is $(K - X_t)$, and the chance that a randomly chosen channel is occupied, which is simply given by the frequency of occupied channels X_t/K. Therefore, the mean field equation for the expected number of individuals in the next time step is specified in Eq. (1):

$$X_{t+1} = X_t + r(K - X_t)\frac{X_t}{K}. \tag{1}$$

Simple rewriting gives Eq. (2), which is the logistic growth equation, which forms one of the cornerstones of theoretical biology.

$$X_{t+1} - X_t = rX_t\left(1 - \frac{X_t}{K}\right). \tag{2}$$

This result is very nice, as it allows us to link the spatial model to existing ecological theory. My 'trick', to avoid higher order terms in the mean field equation, is to only use information from one of the neighboring channels (or alternatively use the local density), instead of e.g. requiring for growth a threshold in the number of occupied neighboring channels, as is often done in the book. In a similar way spatial versions of, e.g., Lotka–Volterra competition and predation can be constructed. As typically the lessons that can be learned from the spatial pattern formation do not depend on microscopic modeling details, I strongly advocate using interaction rules that give simple mean field models.

Now consider the spatial behavior of the model. In Fig. 3(A) a snapshots of the pattern is depicted, which was initialized from a single individual in the middle of the field. In Fig. 3(B) the macroscopic behavior of the per capita growth rate γ as a function of the population density d is plotted. The per capita growth rate is the average growth rate per individual, specified by $(X_{t+1} - X_t)/X_t$. In the mean field equation (2), that is the logistic growth model, the individual

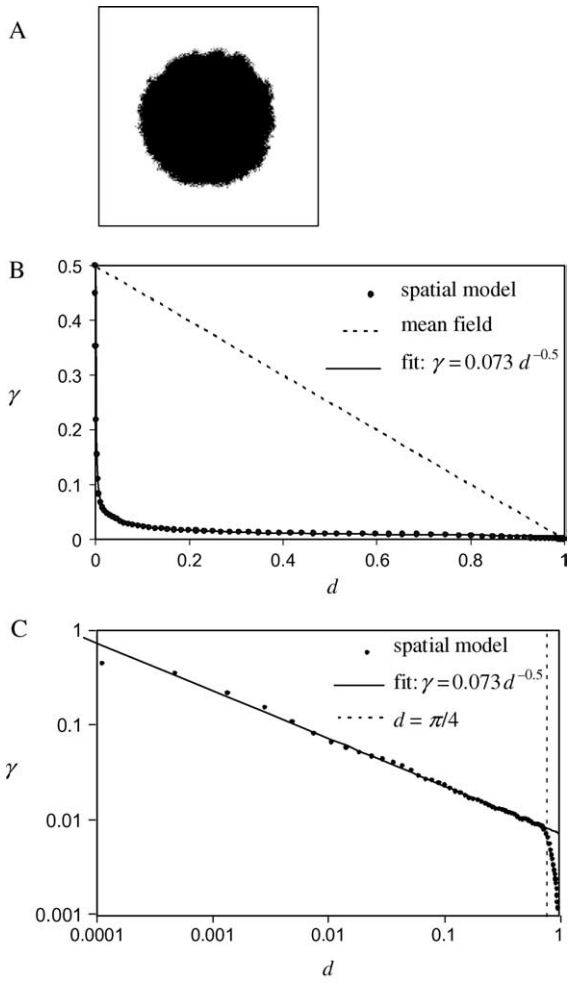

Fig. 3. Population growth in a lattice-gas model. The lattice has 150×150 sites, and local densities are indicated in gray shades (white being empty). The simulation is started from a single individual in the middle of the field. (A) Pattern after $t = 125$ interaction steps, growth rate $r = 0.5$, and one movement step after each interaction step. (B) Per capita growth rate γ as a function of density d. In the mean field model (dashed line) individual growth rate is a linearly decreasing function of population density. In the spatial model, individual growth rate decreases sharply for increasing density, already at very low densities. (C) same as B, but now in a log–log plot. The fitted circular growth function $\gamma = 0.073d^{-0.5}$ (solid line) accurately fits the observed values for the spatial model, except for very low and high densities, where, respectively, the circular growth pattern is not fully developed or it hits the boundary of the field. The circular growth pattern hits the boundary at approximately $d = \pi R^2/(2R)^2 = \pi/4$ (dashed line).

growth rate is decreasing linearly with increasing density, starting at maximal growth rate r and ending at growth rate 0, for $X_t = K$ (see Eq. (3)).

$$\gamma = \frac{X_{t+1} - X_t}{X_t} = r - \frac{r}{K} X_t. \tag{3}$$

In the spatial model (see Fig. 3(B)) this relation is dramatically different. The growth rate still starts near maximum $r = 0.5$, but steeply decreases already for very low densities. Now we should try to qualitatively or, even better, quantitatively understand these spatial dynamics from effects of the spatial pattern formation. The key observation here is that essentially the growing pattern in Fig. 3(A) expands as a circle. This is also the case for all the growing patterns that are described in Chapter 6 of the book. In a circle, growth effectively only takes place at or near the boundary, as the inside of the circle is already in steady state and the outside is still empty. The number of individuals in the circle is proportional to its surface, i.e., $X_t \sim \pi R^2$, whereas the boundary of the circle is proportional to its circumference, i.e., $(X_{t+1} - X_t) \sim 2\pi R$ (note the use of capital R for the circle radius to distinguish from the growth rate r). Using these relations, Eq. (4) gives the scaling relation between the population growth and the population size.

$$(X_{t+1} - X_t) \sim \sqrt{X_t}. \tag{4}$$

Consequently, the per capita growth rate scales with the density as Eq. (5):

$$\frac{X_{t+1} - X_t}{X_t} \sim \frac{1}{\sqrt{X_t}}. \tag{5}$$

Indeed, we can very accurately fit the points in Fig. 3(B) and (C) (log–log plot) with a function $(X_{t+1} - X_t)/X_t = aX_t^{-0.5}$, where a is a fitting parameter. The fit is less accurate at very low and very high densities, as here, respectively, the circle pattern is not yet fully developed or it interacts with the boundaries of the field. It would be interesting to derive the exact growth curve for the spatial pattern formation, and for instance its dependence on the movement of individuals, but this is beyond the scope of this review.

Here, I wanted to demonstrate the importance of qualifying the type of spatial pattern that occurs in the local population growth models, and to study its impact on the population dynamics. A similar methodology of describing and quantifying dynamics of spatial patterns has for instance been used in describing emergent host patch dynamics in a spatial parasite–host system [5], and explaining competition for outbreak frequency in a spatial epidemiology model [6].

As stated before, I think the major strength of the lattice-gas method lies in unraveling the potential effects of movement of individuals. These effects can be very complex, as, e.g., has been demonstrated in a model on evolution of 'clever' parasitoid movement towards patches with high host density [7]. In this model various spatial patterns can emerge, including spiral waves and turbulence. The direction of selection of parasitoid aggregation behavior depends on the spatial pattern, and even on the location within the pattern. The complexity here arises from a feedback loop between the patterns and the movement, that is, the spatial patterns affect which movement strategies will be selected, but also the movement strategies of individuals affects the spatial patterns. In principle, this feedback loop can for instance lead to evolutionary cycling or bistability, where the evolutionary attractor depends on the initial spatial pattern. The topic of effects of spatial pattern formation on evolutionary dynamics is still largely unexplored [8].

The book is a good starting point for scientist and students that would like to move into the field of studying effects of spatial pattern formation in biology. The introductory chapters are fun reading, although they are a bit of a 'taschenatlas' (the famous Wiley pocket guide series), with half a paragraph devoted to every great thinker or concept. The introduction to the lattice-gas method is thorough and sound, and the array of applications of the method to systems of biological pattern formation is impressive and inspiring. The book also describes some of the pitfalls of spurious modeling results, such as effects of the underlying grid topology, which might lead to anisotropy in the spatial patterns. I particularly like the format of suggesting potential further projects at the end of each chapter, which shows that the field is only starting and many research questions still have to be explored. To my taste, there should be more emphasis on studying the spatial patterns that develop and their potential impact on dynamics. The research question should shift from 'can we make the pattern', to 'can we understand the pattern, its origin, and its consequences?' The lattice-gas method is a valuable tool in this research area, and the book gives a good starting point to learn the method and its potential applications.

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