

The need for biological realism in the updating of cellular automata models

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Abstract

Spatially explicit models like cellular automata are widely used in ecology. The spatio-temporal order of events is a new feature of these models that does not have to be considered in equivalent non-spatial models. We considered simple stochastic cellular automata to test sensitivity of model response under different spatial and temporal sequences of events. The results indicate that very important differences in model output can be found as spatio-temporal ordering is changed, even in a very simple model. A careful choice of the way events are evaluated has to be made: the spatio-temporal ordering must be selected to match the biological characteristics of the target ecological system to be modelled. Further, a complete description of the details of this ordering should be specified in order to let others reproduce published simulation experiments. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

The great development of spatially explicit models in ecology over recent years raises issues of improved model reliability and carefully made model specifications (Conroy et al., 1995), but

some implicit assumptions are often made in the development of this type of model that have not been considered. Only a few studies address the necessity of a careful choice of the spatio-temporal sequence of events. The consequences of the spatio-temporal ordering or synchronization of the different local processes were analyzed by McCauley et al. (1993), who found qualitative and quantitative effects of this on the dynamics of their predator–prey model. Related results were obtained by Huberman and Glance (1993) and

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Ruxton (1996). Most of these spatial models developed in ecology can be framed into the cellular automaton (CA) or stochastic cellular automaton class of spatial models (Hogewed, 1988), although the complexity of some (e.g. Wiegand et al., 1995; Ellison and Bedford, 1995) greatly exceeds the limits of the original definition (Wolfram, 1984). CA models have been principally used in understanding spatial processes in plant and animal populations (e.g. Inghe, 1989; Green, 1989; Hassell et al., 1991; Colasanti and Grime, 1993; Liu, 1993), but also have been used to answer more applied and critical conservation issues (Pulliam et al., 1992; Walters et al., 1992; Dunning et al., 1995). All these models consider the spatial area under investigation to be partitioned into a fixed number of sites. Each site can have a number of variable characteristics associated with it, e.g. the presence or absence of a given species or the abundance of that species. Time also is discretized in the model. At each time step, the characteristics of each site are updated according to a set of rules which consider the current state, both of that site and potentially of other sites in the system. These updating rules can be stochastic or deterministic. Whilst publications generally provide explicit definitions for the updating rules, they often do not specify the order in which sites are considered or in which rules they are applied. Here we investigate, using a very simple CA model, whether the details of the spatial and temporal ordering of events have an effect on the global behavior of the model.

2. Methods: model description

A simple, but general, stochastic cellular automata was considered. Space was subdivided into a regular $L \times L$ square lattice, with periodic boundaries, i.e. points on opposite edges are considered neighbors. Each of the L^2 sites is uniquely specified by two coordinates (x, y) , and must be either empty or occupied. The sites can be interpreted as either an individual or as a population, in the last case the size of the occupying population is implicitly ignored. Only two possible events can occur: colonization and extinction. An

extinction event (E_{ev}) changes an occupied position to an empty position (with probability P_e , conditional on the site being occupied). A colonization event (C_{ev}) is only possible when the focal site is occupied, then one of its eight nearest neighbors is chosen randomly and if this site is empty it becomes occupied with probability P_c .

Time is discretized into uniform intervals and one time step is completed when the two events are evaluated for all the sites. Thus, for each time step we perform $2 \times L^2$ event evaluations, different combinations of spatial and temporal ordering of events are considered

2.1. Spatial sequences of events

Sequential (S): the events are evaluated in sequential order of their site's coordinates, i.e. (1, 1), (1, 2), (1, 3).....(L, L).

Random (R): the spatial coordinates of the sites are selected randomly without replacement.

2.2. Temporal sequences of events

Fixed (F): all the $L^2 E_{ev}$ are evaluated first and then all the C_{ev} .

Conditional (C): for each position, an E_{ev} is evaluated first and, if the site does not become empty, a C_{ev} is evaluated before moving on to the next site.

Random (R): in each site the temporal order of the events is selected randomly without replacement.

We arbitrarily choose to implement only four of six possible {spatial, temporal} combinations: SF, SC, RF and RR.

The case of RR is a spatial and temporal ordering at the same time, because at some sites C_{ev} may occur before E_{ev} . Further, both events may occur at one site before either has occurred at another. In all cases, if a site becomes empty due to a E_{ev} occurring at that site earlier in the time step, then the C_{ev} at the site will be unsuccessful.

Generally, the CA models have a time delay of one step, although this is not always stated explicitly in model descriptions. The computer implementation of that type of CA model has to

maintain two arrays of positions, one holding the actual state of the system and another containing the state that the system will be in at the beginning of the next time step. At the start of each time step, both of these are identical. We consider that E_{ev} events act instantaneously, and so changes due to these are recorded on both matrices. C_{ev} events, however, are assumed to act only after a delay, hence changes due to these are marked on the next step matrix but not on the actual state one. When all cells have been evaluated, the next matrix is copied into the current matrix and a new cycle begins. We say that such a system has a time type 2. Another way to implement a CA is using only one array of states, so all changes in the states of the sites are immediately registered (time type 1). The four selected combinations were run considering both time types.

3. Results: comparison between model implementations

3.1. Extinction

As we consider stochastic cellular automata, given an infinite amount of time, they will eventually become a population of empty sites (Durrett and Levin, 1994). In this case, we say that the population becomes extinct. However, the extinction time varies with the extinction and colonization probabilities (P_e and P_c) in a highly non-linear way. Consider the case where we hold P_c constant (at unity) and vary P_e . If P_e is very high, then the rate of extinctions greatly exceeds the rate of new colonizations and this system very rapidly falls to extinction. As P_e is reduced, the decline in the number of colonized patches over time is slower, and so extinctions happen less quickly. However, if P_e is below a critical value, then the average number of colonized patches does not decline over time but fluctuates around an equilibrium value. The system will still go extinct, but only when the random processes drive the fluctuations in colonized patches down to zero. This can take a very long time, even for modest lattice sizes. As P_e is decreased even fur-

ther, the equilibrium occupancy value moves further and further away from zero, hence extinction requires an even more extreme combination of chance events, and extinction takes even longer to achieve.

In this section we present the critical value of P_e for each model implementation (with $P_c = 1$). These were calculated using the method of Buttell et al. (1993). We also present the median time until extinction when P_e exceeds this value; for comparison purposes, the same value was used for each implementation ($P_e = 0.6$) (Table 1).

The critical extinction probabilities (CP_e) are in close relationship with the extinction median (EM) (Table 1). The RR implementations have the highest CP_e and EM with very similar values. Although the EMs are significantly different from each other (Mann–Whitney test on the medians of the two distributions, $P < 0.01$), as one would expect given that they differ in whether colonizations act immediately (time type 1) or only after a delay (time type 2). Immediate acting colonizations generally promote persistence and so lead to a higher median extinction time and critical value of P_e , except in the SC implementations where the time type 1 have a shorter extinction time than

Table 1

Critical extinction probabilities (CP_e) and median time until extinction (in time steps) for the eight model implementations considered^a

	Critical Probability	Extinction Median ^b
Model		
RR1	0.56	210
RR2	0.56	197
SF1	0.52	53
RF1	0.52	63
SF2	0.41	28
RF2	0.41	28
SC1	0.41	18
SC2	0.41	22

^a The CP_e were computed using the method of Buttell et al. (1993), the equilibrium densities were determined using the last 1000 values of simulation runs of 2000 steps, the extinction probabilities (P_e) ranging from 0.4 to 0.15 and at least 3 runs were simulated for each P_e .

^b Extinction medians were calculated from a distribution generated from 10 000 simulations, each starting off with a random 10% of sites occupied.

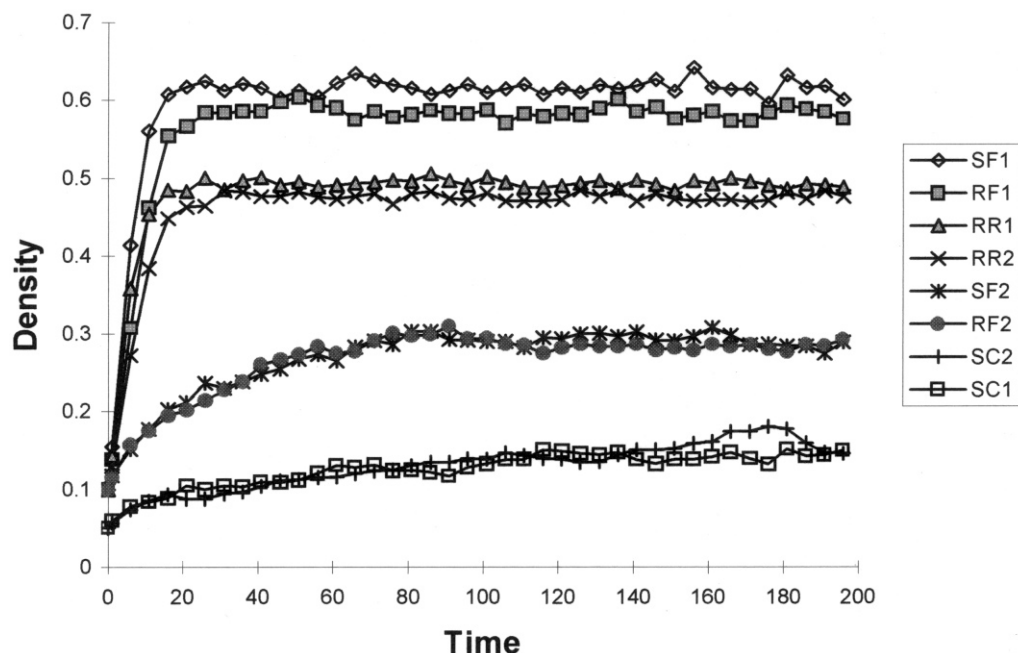


Fig. 1. Density (fraction of sites occupied) vs. time for all the models using a constant extinction probability (0.40).

the time type 2. We also expect that the temporal ordering of events, denoted R , should enhance system persistence as this is the only temporal sequence which allows sites which become extinct in a given time step to attempt a colonization before the actual time step ends.

Next in this table, the SF and RF implementations with time type 1 are grouped (group F1), and the same happens for time type 2 (group F2). The F1 EMs are significantly different (Mann–Whitney test, $P < 0.05$) but the F2 ones are equal. These results also highlight a very significant finding. When spatial (colonization) processes act instantly, then one site can be affected within a time step by the action of another. Hence, in this case, the spatial order in which sites are evaluated matters. However, if these spatial processes only cause changes in other sites after all sites have been evaluated, then the order in which evaluation occurred does not matter. For these two groups, the time type is more important than the spatial order of evaluation. Finally the SC implementations have the lowest CP_e and there is no difference between time types 1 and 2 (the differ-

ence between the two median extinction times is not significant; Mann–Whitney test, $P > 0.1$). We can make a hierarchical classification using the temporal ordering as a first separating variable, then the time type and finally the spatial ordering.

3.2. Descriptions of persistent systems

If the P_e is below the critical value, then the system will not head towards a quick extinction, instead it will persist for a long time with site occupancy varying around a mean value (Fig. 1 shows an example of such trajectories). In this section we consider measures of the state of persistent systems and investigate whether these are sensitive to the spatio-temporal ordering of evaluations defining the model implementations. The most obvious measure to use is the mean occupancy: i.e. the long-term temporal average of the number of sites occupied at a given time. This system has a point attractor called equilibrium density (ED). This is presented for each of our eight model implementations in Table 2. For each one we show the average fraction of sites occupied

in a model with $L = 100$ and $P_e = 0.4$. The results are insensitive to the size of L providing L is large and insensitive to initial conditions (Durrett and Levin, 1994).

Our CA is not well mixed, in that interactions only take place locally between nearest neighbors. Under such circumstances, one would expect that short range correlations should become apparent, in some cases leading to distinct pattern formation. A useful measure for characterizing such spatial correlations is Moran's I spatial autocorrelation index (MI) (Henebry, 1995). Table 2 also presents a measure of this for each of our eight model implementations. In repeated stochastic realizations, we found that the calculated ED for a given implementation never deviated from the quoted table value by more than 0.02. Hence as a general guide, we consider implementations whose density values differ by < 0.04 to be 'similar'.

The F1 implementations have the highest ED for $P_e = 0.4$, but there is a considerable difference between SF1 and RF1. The RR implementations follow and the difference between them is less. The implementations SC have the lowest ED values and are relatively close to the F2 implementations. If the RR implementations are excluded then the EDs have the same pattern as CP_e and EM (i.e. event order, then time type, then spatial order).

The results of the MI are also similar to the CP_e and EM, in the sense that the same groups can be formed, but the implementations RR have extremely low autocorrelation values for their

Table 3

Moran's I spatial autocorrelation index for all the models maintaining the equilibrium density (ED) at constant values

ED	Moran's I	
	0.6	0.3
Model		
RR2	0.054	0.112
RR1	0.060	0.139
SC2	0.088	0.186
SC1	0.096	0.190
SF2	0.119	0.247
SF1	0.121	0.238
RF1	0.128	0.225
RF2	0.135	0.218

density. It is well known that the MI is correlated with the ED (Oden, 1995), with higher values of density, lower values of the MI are obtained.

To control the density effect, the estimation of the MI on simulations of the model implementations maintaining the ED constant were carried out. To see if there exists a differential behavior of the autocorrelation ED values, we performed simulations at a relatively high and low ED, 0.6 and 0.3, respectively (Table 3).

For the constant density simulations, the RR implementations have the lowest MI values, as in the previous results. The SC implementations have the second lowest values, which is very different from the results obtained with the P_e constant. Further, there is a much reduced spread of index values, so we did not attempt to order the implementations into a classification scheme.

3.3. Spatial indices

We compute some additional spatial indices to characterize spatial patterns, the fractal dimension (FD), the number of patches (NP) and the largest patch index (LPI) (McGarigal and Marks, 1995). We choose the FD because it is believed to be independent of some characteristics of the images (Vedyushkin, 1994) and it is a characteristic measure of some CA models (Hastings and Sugihara, 1993). A description and some ecological applications of the FD can be found in Sugihara and May (1990). The LPI is the proportion of the

Table 2

Moran's I spatial autocorrelation index for all the models maintaining the probability of extinction (P_e) at 0.4

	Moran's I	Density
Model		
RR1	0.085	0.4860
RR2	0.072	0.4681
SF1	0.128	0.6780
RF1	0.137	0.5848
SF2	0.227	0.2639
RF2	0.238	0.2816
SC1	0.253	0.1537
SC2	0.252	0.1477

Table 4

Largest patch index (LPI), number of patches (NP) and fractal dimension (FD) for all the models

Pe	0.4			ED	0.6			0.3		
	LPI	NP	FD		LPI	NP	FD	LPI	NP	FD
Model										
SF1	99.5	11.4	1.997		99.5	9.6	1.997	14.2	148.6	1.905
RF1	99.2	13.9	1.995		99.5	10.0	1.997	12.0	149.7	1.905
RR2	93.5	63.4	1.994		99.5	12.2	1.999	7.9	306.0	1.955
RR1	95.8	51.5	1.993		99.5	11.7	1.999	7.2	269.9	1.947
RF2	7.4	191.8	1.895		99.3	11.2	1.997	10.1	175.4	1.915
SF2	6.7	191.2	1.881		99.2	11.8	1.998	12.1	174.9	1.915
SC1	4.7	198.7	1.888		99.6	9.5	1.998	12.0	183.6	1.927
SC2	4.4	201.1	1.856		99.6	11.0	1.999	11.3	186.3	1.928

In the first three columns the probability of extinction (P_e) was constant across the models and in the rest of the table the equilibrium densities (ED) were constant. LPI and NP were determined by averaging over ten simulations after 2000 time steps using the FRAGSTATS program; FD was estimated in the same way using a box-counting algorithm.

total number of sites ($L \times L$) occupied by the largest patch. For the NP and LPI, a patch was measured as a continuous region of occupied sites assuming as contiguous the eight closest sites.

These three indices depend on density (Gustafson and Parker, 1992), so additionally to the simulations at constant P_e , we again performed simulations keeping the density constant (by adjusting P_e until the ED equalled a selected fixed value) and calculated the indices (Table 4). At high densities (ED = 0.6), all model implementations have very similar indices, at low densities we can see that the differences become apparent. The NP and FD indices seem to follow the same pattern, the groups formed are the same as before: F1, RR, F2 and SC. Very different groups are formed looking at the LPI index; the implementation SF1 is alone with the highest LPI value, a group formed by SF2, SC1 and RF1 follows then the RF2 and SC2 implementations and finally the RR group.

4. Discussion

Simple models like the one used in this paper are not intended to give a detailed and precise description of ecological systems, but only to capture the conceptual dynamics. Hence some might argue that the differences in measures between

different model implementations reported here may not be of critical importance. However, they could be important in more applied models, where quantitative predictions are required. Further, the accumulation of these differences is likely to lead to very profound differences in behavior between versions of more complex models.

When we change both the spatial and temporal ordering of events, we appear to have found a synergistic effect in the model dynamics, the group RR is always differentiated from the rest, and breaks some clear relationships between descriptors of the other models. This group has several striking characteristics: only it can produce a C_{ev} before the corresponding E_{ev} , it produces a large quantity of small patches (the lowest LPI and the highest NP), and in consequence always has the lowest MI. These features increase the number of successful C_{ev} s because an occupied site has a lower probability of having others occupied sites in the neighborhood. Thus the group expectedly has the largest EMs but surprisingly does not have the highest ED.

Another well differentiated group is SC, that, besides having a low MI value, it has the shortest extinction time. Note that the spatial evaluation of SC is sequential so we expected a high MI, but we found the second lowest MI value. The other model implementation with a sequential spatial

ordering is SF, which only has the higher MI at low ED. Thus, the spatial evaluation order does not produce, per se, a higher spatial autocorrelation, which suggests that the combination of temporal and spatial orderings determines the behavior of the model implementations.

The implementations with time type 1 generally have higher density and EM than time type 2 because of the possibility of the colonization of a site that has not yet been evaluated. So this site will potentially trigger another C_{ev} , raising both the EM and the ED. The exception is the group SC, where the temporal sequence of events inverts the EM pattern. In SC1, when a recently colonized site is evaluated, an E_{ev} is first considered, so this new born site can become extinct before the end of the present time step. In the SC2 case the new born site can only become extinct in the next time step.

The group F1 has the highest density because we perform all the E_{ev} first and then all C_{ev} , and we always measure the density after all the C_{ev} , so we are measuring the maximum density. When C_{ev} and E_{ev} occur in an asynchronous way and we measure the average density of the model, it decreases, as in RR.

None of the spatial indices that we use can completely predict the persistence of the systems when the P_e is lower than the CP_e . Only the CP_e itself gives a rough idea of the EM, but in most cases this is not a measurable quantity of ecological systems. The relation of persistence and FD (Hastings et al., 1982; Sugihara and May, 1990) in the sense that more persistent systems (higher EM) have a lower FD, has not been confirmed here, because the more persistent models (RR) have the highest FD.

Some characteristics of the model implementations, like high density, high persistence, the development of small or big patches, can be a real ecological strategy for a particular system, so the finding that these different ecological strategies can be produced by merely changing the spatio-temporal order of events is very significant. The RR group has the most realistic features in both spatial and temporal order of evaluation for the vast majority of biological populations. The synchronizations imposed by the S spatial ordering

and by temporal sequences F and C, can be thought of as realistic only in high stress environments. But the RR implementations impose a considerably higher computational effort; we are presently considering another implementation that approximates the RR behavior with a much lower computational effort.

The results of this paper suggest that the timing of events in CA models can have a large impact on model predictions. It is important that timing reflects biological reasoning rather than programming expediency, which can often impose unrealistic assumptions on the timing of events. It is true that biological systems can sometimes have mechanisms which cause temporal correlation of events. For example, in many species, individuals tend to breed at around the same time of year. However, it is very unlikely that all young will be produced within a very short time interval during which no adults or young perish. Hence the model algorithm must allow for the possibility of such deaths. Temporal correlation of production of young can be induced by making birth events more probable in spring (say) than winter whilst still allowing some probability that other types of events can occur. In our simple model, this could be simulated by changing P_e from a constant to a time-varying function with a suitable period.

Recently Huberman and Glance (1993) demonstrated the importance of timing of events in CA models of social systems and the evolution of co-operation between individuals. In particular they observe that a recent study by Nowak and May (1992) of the 'Prisoner's Dilemma', contains the implicit assumption of complete synchrony between individuals. If this synchrony is broken, then simulations generate qualitatively different results. Strategies which persist in Nowak and May's simulations fail to survive in Huberman and Glance's when synchrony is broken. The effect of synchrony in the Nowak and May's model is perhaps more dramatic because they used deterministic rules, in our model, the stochastic rules partially mitigate the effects of synchronous updating of sites.

We have demonstrated that the output generated by a CA model depends critically on assumptions made about the ordering of events. Some

computer techniques and algorithms which hold information on single bits of computer memory but perform operation on whole words (e.g. McCauley et al., 1993) are very useful to speed the simulation of spatially explicit models. These techniques can often force synchronicity between sites. Care must be taken in specifying models so that the ordering properly reflects underlying biology rather than programming expedience or speed constraints. This increased care should produce models which better represent the system under consideration. Also, an explicit description of the timing mechanism should greatly aid other scientists who may wish to reproduce published simulations.

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