



Pattern Formation in a Patch Occupancy Metapopulation Model: a Cellular Automata Approach

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The explicit consideration of space in ecological research is of paramount importance to understand the structure and functioning of ecological systems. In this paper we develop a simple spatially explicit metapopulation model in which colonization is constant and independent of the number of occupied patches (i.e. propagule-rain effect, Gotelli, 1991). Extinction, on the other hand, is modelled as a stochastic process whose intensity depends on the number of occupied patches in the neighborhood of each focal patch. Our model is the CA counterpart of two classical patch occupancy metapopulation models. We analytically prove this by showing that our CA converges to the differential equation in the mean-field approximation. The asymptotic behavior of the system, expressed as the proportion of occupied patches, agrees with the equilibrium proportion of patches derived by using ODEs. In both models, the existence of a rescue-effect increases the range of extinction and colonization parameters over which the system attains complete occupancy of patches. However, in our model this result is strongly influenced by the degree of coupling among patches and is apparent only for local interactions. With local interactions and particular parameter values of colonization and extinction, self-organized spatio-temporal patterns emerge with a fractal-like clustering, even though the environment is spatially homogeneous. Our results point out that the importance of being spatial and discrete (Durrett & Levin, 1994a) in our model is a result of local interactions.

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Introduction

The explicit consideration of space and the development of theoretical approaches to study its effects upon the structure and functioning of ecological systems is currently recognized as one of the great advances in contemporary ecology (Levin, 1992; Durrett & Levin, 1994a; Kareiva, 1994; Tilman & Kareiva, 1997). The realization

that the behavior of ecological systems is closely linked to the spatial neighborhood of interaction has resulted in a proliferation of studies that consider the dynamical consequences of including space explicitly into models of behavior, genetics, and biotic interactions (e.g. Hassell *et al.*, 1991; Comins *et al.*, 1992; Nowak & May, 1992; Solé & Valls, 1992; Durrett & Levin, 1994b; May, 1994; Tilman *et al.*, 1994; Kareiva & Wennergren, 1995).

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Space, by itself, is capable of giving rise to global emergent self-organized spatial patterns with unexpected dynamical consequences (e.g. Rohani *et al.*, 1997). This has been seen in interactive particle systems (Durrett, 1988), coupled map lattices (Kaneko, 1989; Hassell *et al.*, 1991; Solé & Valls, 1991), and cellular automata models (Wolfram, 1983, 1984; Hogeweg, 1988; Dytham & Shorrocks, 1992; Caswell & Etter, 1993; Molofsky, 1994; Kusch & Markus, 1996). This latter class of models, originally developed by Ulam & Von Neumann (under the name of “cellular spaces”) has been widely applied in biology (see Ermentrout & Edelstein-Keshet, 1993) and recently in the study of ecological systems, including population dynamics (Caswell & Etter, 1993; Molofsky, 1994; Darwin & Green, 1996), community ecology (Czárán & Bartha, 1992), predator–prey dynamics (Van der Laan *et al.*, 1995), forest dynamics (Auger, 1995), competition (Green, 1989) and biogeography (Carey, 1996).

In this paper, we use a one-dimensional cellular automata model (CA) to explicitly incorporate space into a simple patch occupancy metapopulation model (Hanski, 1996). We analyse the dynamical consequences of local spatial interactions and the emergence of spatio-temporal patterns generated by colonization and extinction processes as a function of different spatial neighborhoods. We compare our results with those derived for analogous models that do not include space explicitly (e.g. based on ODEs).

THE MODEL

A metapopulation can be defined as an ensemble of local populations (i.e. subpopulations) which interact through the interchange of individuals through migration (Hanski & Simberloff, 1997). This concept, was originally introduced and formalized in ecology by Levins (1969, 1970) who developed a simple patch occupancy model:

$$\frac{d}{dt}p(t) = mp(1 - p) - ep \quad (1)$$

where $p(t)$ represents the proportion of occupied patches at time t . The dynamics of this system is driven by the migration (m) and extinction

(e) parameters, and the model generates a stable, internal equilibrium $p^* = 1 - e/m$. Assuming stochasticity in extinction rates, this model predicts a unimodal distribution of patch occupancy. This model was later modified by Hanski (1982), who introduced a decay in the extinction rate due to an increase in occupied patches, the rescue-effect (Brown & Kodric-Brown, 1977). The modified model is the following:

$$\frac{d}{dt}p(t) = mp(1 - p) - ep(1 - p). \quad (2)$$

The stochastic version of this model predicts the existence of two possible equilibrium solutions. One where species are regionally common and one where species are regionally rare (i.e. occur in a small fraction of patches). This is known as the “core-satellite” hypothesis (Hanski, 1982). In both models [eqns (1) and (2)] colonization ($mp(1 - p)$) is modeled as a quadratic function whose ecological meaning is that colonization depends on regional occurrence or number of both occupied and unoccupied patches within the metapopulation system. However, there are other possible formulations (e.g. MacArthur & Wilson, 1967) where migrants come from outside the system. In this scenario there is a “propagule rain” (Harper, 1977; Rabinowitz & Rapp, 1980) which implies that the colonization rate depends, in a linear way, on the fraction of empty patches only:

$$\frac{d}{dt}p(t) = m(1 - p) - ep \quad (3)$$

Incorporating rescue effects the above equation changes to:

$$\frac{d}{dt}p(t) = m(1 - p) - ep(1 - p) \quad (4)$$

Examples of situations in which the assumption of propagule rain might be appropriate include: (1) a collection of forest fragments separated from a larger expanse of forest which serves as a source of colonizers; (2) an archipelago of islands near a continental source of propagules; and (3) intertidal habitats for organisms which are sedentary as adults but have widely dispersed pelagic larvae.

Based on these two models [eqns (3) and (4)], we have developed spatially explicit stochastic models using cellular automata that in the mean-field approximation converge to their ODE's counterparts (see Appendix). We model a metapopulation system composed of a finite collection of N patches arranged in a one-dimensional lattice. Similar to the models considered above, each patch can be in only two states, occupied or empty. Each patch can be considered a finite automata (FA) whose state is a random variable that can take a value of 0 (empty) or 1 (occupied), with a probability distribution function determined by a local state transition rule which depends on its current state, and the state of the patches (FAs) in its neighborhood. Thus, our metapopulation is represented by a Cellular Automata composed by a collection of FA, a local transition rule, and a defined neighborhood.

The unidimensional space E is composed by the ordered set of all patches (FAs):

$$E = \{1, 2, \dots, (i-1), i, (i+1), \dots, N\} \quad (5)$$

We have assumed periodic boundary conditions. That is, the space can be seen as a discrete ring with N nodes, where each node represents a patch in the space (Fig. 1). The

neighborhood is defined as the r patches to the right and to the left of each focal patch located in the i position. Our neighborhood $\Omega(i;r)$ of radius r and around the i -patch will be defined by the set of the following patches:

$$\Omega(i;r) = \{(i-r), (i-r+1), \dots, (i-1), (i+1), \dots, (i+r-1), (i+r)\} \quad (6)$$

In our model, this neighborhood represents the degree of dynamical coupling among patches in the metapopulation. The state of the patches in this neighborhood at time t and its local state represents the inputs for each FA which through a transition rule compute in parallel and synchronously the probability distribution function which determines the future state of each patch in the metapopulation.

The proportion of occupied patches in the neighborhood $\Omega(i;r)$ is:

$$P'_{\Omega(i;r)} = \frac{1}{2r} \sum_{\theta \in \Omega(i;r)} a'_\theta \quad (7)$$

where a'_i represents the state of patch i at time t ($a'_i = 1$ if occupied, 0 if empty). Then, the probability of local extinction experienced by a patch i , which is in state 1 at time t , is:

$$P'_{E,i} = \begin{cases} (1 - p'_{\Omega(i;r)})e; & r \neq 0 \\ e; & r = 0 \end{cases} \quad (8)$$

where e represents the intrinsic extinction rate (or probability) for a patch. In case of considering rescue effects ($r \neq 0$), the extinction probability of each local patch will decay linearly with the proportion of occupied patches in its neighborhood $\Omega(i;r)$ at time t (Fig. 2). With no rescue effect ($r = 0$) the probability of local extinction of each patch at time t will be constant in time and space, and equal to e . In this case the dynamics of each patch is independent of its neighborhood. The size of the neighborhood is a measure of the spatial range over which the rescue-effect operates.

Colonization is assumed constant in both time and space. Thus, the probability that an empty patch at t becomes occupied at time $t+1$ is equal to c . This is because we assume a propagule rain scenario for migration.

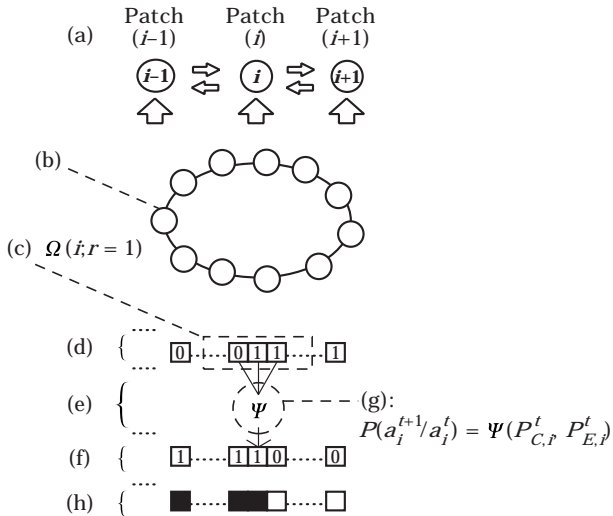


FIG. 1. Structure of the cellular automata model: (a) habitat patches; (b) spatial array; (c) neighborhood; (d) system configuration or state at time t ; (e) temporal transition, parallel computation on which extinction and colonization events take place; (f) system configuration for the next time step; (g) transition rule [eqn (9)]; (h) state of habitat patches, white = empty, black = occupied.

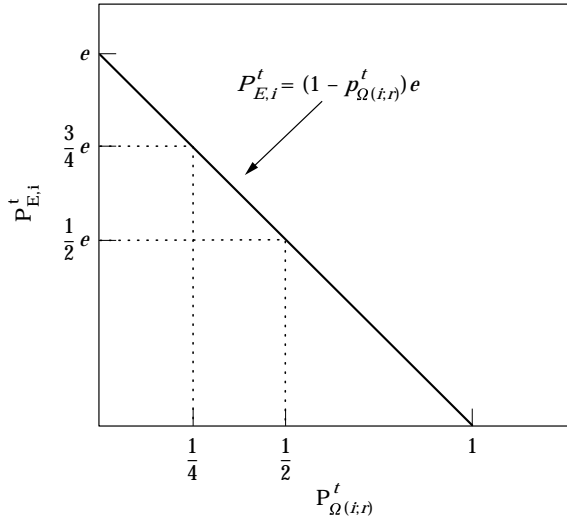


FIG. 2. Relationship between the local probability of extinction of a given patch and the proportion of occupied patches in its neighborhood under rescue effects.

Taking into account both the extinction and colonization processes as defined above, we can define the temporal transition rule, which will give the probability distribution of the random variable a_i^{t+1} , as:

$$P(a_i^{t+1}/a_i^t) = [a_i^t(1 - P_{E,i}^t) + (1 - a_i^t)c]^{a_i^{t+1}} [(1 - a_i^t)(1 - c) + a_i^t P_{E,i}^t]^{(1 - a_i^{t+1})}$$

where:

$$a_i^{t+1} \in \{0,1\}; a_i^t \in \{0,1\}, i = 1,2,3,4, \dots, N. \quad (9)$$

This equation allows us to compute the state of the FAs that constitute the CA and the transition probabilities between states. Thus, the probability that an empty patch at time t will be colonized at time $t + 1$ is:

$$P(a_i^{t+1} = 1 | a_i^t = 0) = c \quad (10)$$

The probability that an empty patch at time t will not be colonized at time $t + 1$ is:

$$P(a_i^{t+1} = 0 | a_i^t = 0) = (1 - c) \quad (11)$$

The probability that an occupied patch at time t will become extinct at the next time step is:

$$P(a_i^{t+1} = 0 | a_i^t = 1) = P_{E,i}^t \quad (12)$$

And the probability that an occupied patch at time t will not go extinct at time $t + 1$ is:

$$P(a_i^{t+1} = 1 | a_i^t = 1) = (1 - P_{E,i}^t) \quad (13)$$

These probabilities allow us to define the dynamics of our CA model. In general, with this kind of model we cannot arrive at an analytical expression for the equilibrium properties; hence we have to resort to simulations to detect the convergence of the model to a particular attractor. To do this we defined the following criteria for convergence:

Fixed-point attractor: we say that the dynamic converged to a fixed-point attractor if the system did not change in the frequency of occupied patches in two successive generations.

Statistical steady-state: we say that the dynamic converged to a statistical steady-state when the proportion of cells in each state, as measured by the Shannon entropy of the system, remain bounded to very small fluctuations around a fixed value, although the system changes with no apparent trend over time.

Non-convergent: we say that the system did not converge if after 10 500 generations we do not find any of the above mentioned attractors.

We explored the four-dimensional parameter space (N,r,c,e) of this model considering it as the cartesian product of a structural two-dimensional parameter space (N,r) with an ecological two-dimensional space (c,e) . We selected 200 (c,e) random vectors from the (c,e) parameter sub-space using a bivariate uniform distribution and used this set of points as our ecological scenario. We explored the (N,r) parameter sub-space by considering a fixed metapopulation size $N = 101$ patches. We explored two other metapopulation sizes (11 and 51) to assess the effect of N upon model dynamics. We found that the dynamics of models with 51 and 101 patches were essentially the same, thus the results reported here are indicative of the behavior for a large number of patches. Four different neighborhoods were used: no interaction between patches ($r = 0$), local interaction ($r = 1$), medium range interaction ($r = 25$), and global interaction ($r = 50$). Each N, r combination was simulated using the same 200 (c,e) random vectors.

Results

NEIGHBORHOOD SIZE AND RESCUE-EFFECTS

Our model converged to a fixed point attractor only in a few cases (10%) and only for certain combinations of the (c,e) parameter sub-space. In most cases (90%) the system did not converge. The distribution of these convergent points over the (c,e) parameter sub-space and the percentage of simulations that attain convergence depend on the spatial coupling among patches (i.e. on the neighborhood size). When we do not incorporate spatial coupling between the patches ($r = 0$), which means no rescue-effects, few cases converged to a fix-point attractor [Fig. 3(a)]. The fixed point attractors were of two types: metapopulation extinction or complete occu-

pancy. Extinction occurred for all simulations in which $c < 0.1$, whereas for $e < 0.1$ the metapopulation system attained complete occupancy. With local coupling between patches ($r = 1$), the area of the (c,e) parameter space where convergence was attained increased from 10% in the case of no interaction ($r = 0$) to 60% in this case [Fig. 3(b)]. This area of convergence includes all simulations in which $c \geq e$. In the cases of medium range ($r = 25$) and global interactions ($r = 50$) respectively, convergence decreased again to 10% and occupied the same area of the parameter space as seen in the previous cases [Fig. 3(c), (d)]. For those simulations in which the system did not converge to a fixed point or to a statistical steadystate, and for $r \neq 1$ the proportion of occupied patches

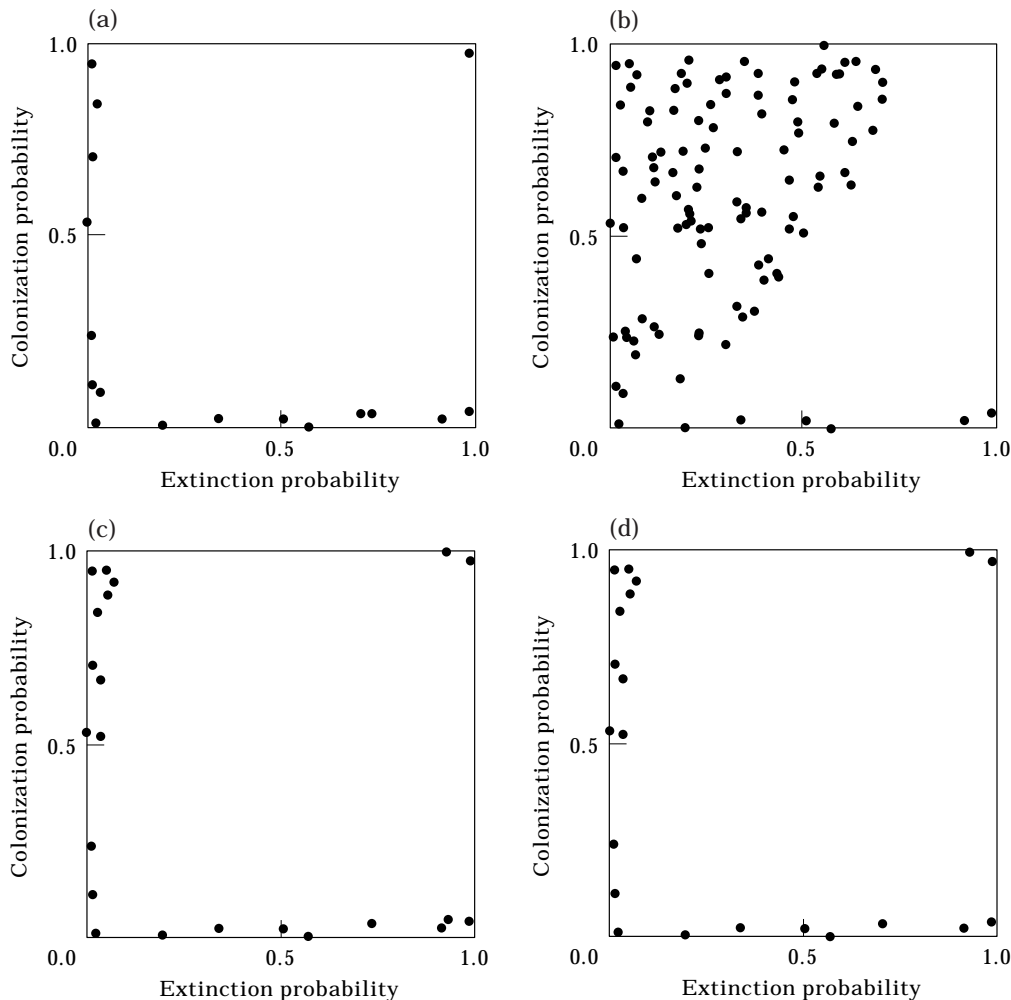


FIG. 3. Distributions over the (c,e) parameter space of those distributions that converged to a fixed-point attractor: (a) $r = 0$; (b) $r = 1$; (c) $r = 25$; (d) $r = 50$. $N = 101$ for all cases.

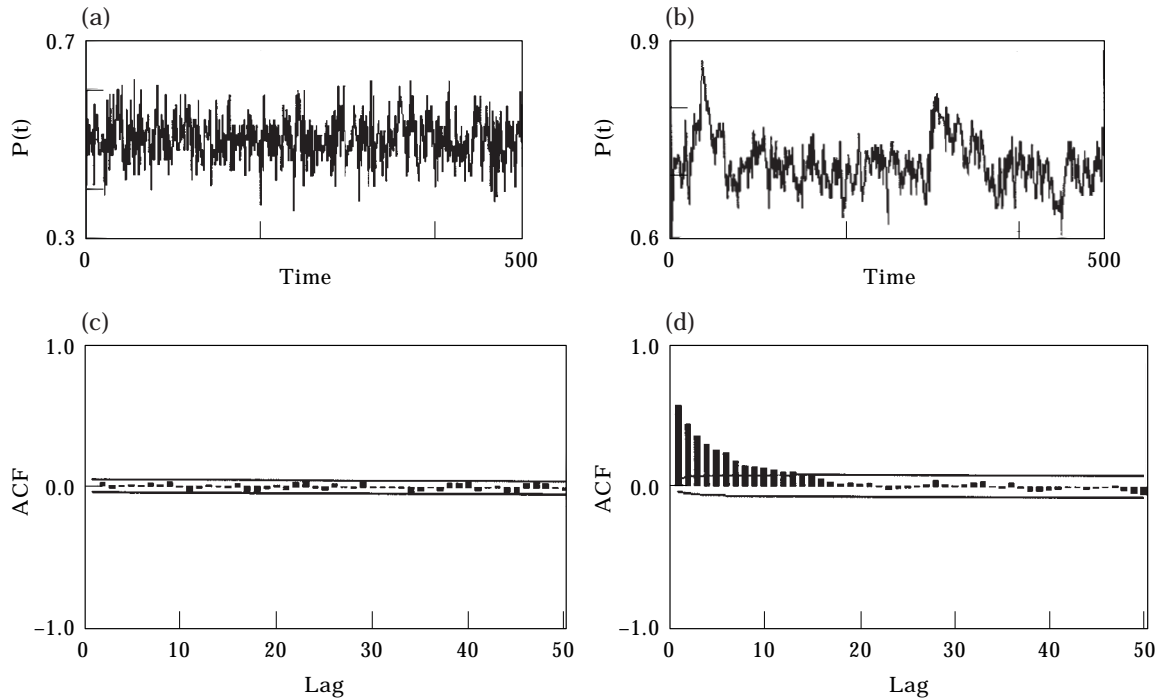


FIG. 4. Time series of the proportion of occupied patches in the metapopulation: (a) $r = 0$, $c = 0.4$, $e = 0.6$; (b) $r = 1$, $c = 0.4$, $e = 0.6$; (c,d) autocorrelation functions (ACF) of (a) and (b), respectively.

continuously changed over time, with a white-noise-like structure centered at $p^* = c/(c + e)$, which is the equilibrium proportion of patches expected for its ODE counterpart [eqn (3), Fig. 4(a)]. In contrast, for $r = 1$ [Fig. 4(b)] the time series of patch occupancy was significantly correlated for short temporal lags [Lag < 15; Fig. 4(d)]. This suggests the emergence of spatial structures (see below).

The analysis of the long term behavior of the system, taking all cases together, is shown in Fig. 5. Here it can be seen that the area of the parameter space where extinction occurs it is not affected by the existence of rescue-effects and does not change for different neighborhood sizes. However, the area of the parameter space where the system attains complete occupancy, as mentioned above, is greater when rescue-effect is present and depends on local interactions [$r = 1$; Fig. 5(b)]. For larger neighborhood sizes rescue-effects are not important [Fig. 5(c) and (d)]. In all cases the long term proportion of occupied patches is unimodal, with a mode centered at 100% occupancy (for $r = 1$) or at the

expected equilibrium proportion of occupied patches for the other cases (Fig. 6).

SPATIO-TEMPORAL PATTERNS

Three different spatio-temporal patterns characterized the dynamic behavior of our model. When convergence was attained, the transient behavior of the system gave rise to a spatio-temporal pattern in which extinction events propagated in time, resembling a diffusion limited aggregation pattern [Fig. 7(a)]. For the non-convergent cases, two spatio-temporal patterns were found, depending on the existence of rescue-effects and the scale of interaction (r). In the case of local interactions ($r = 1$) the system reached a dynamical attractor characterized by the emergence of a fractal-like self-similar pattern of occurrence over the space-time, with an aggregation of occurrence in clusters of all sizes and similar shapes [Fig. 7(b)]. For all other neighborhood sizes (including $r = 0$) the spatio-temporal pattern was characterized by a random mosaic of occupied and unoccupied patches [Fig. 7(c)].

Discussion

We presented a simple spatially explicit metapopulation model in which colonization is constant and independent of the number of occupied patches (i.e. propagule-rain effect; Gotelli, 1991) as assumed in island-mainland metapopulation models (Hanski & Simberloff, 1997). Extinction, on the other hand, is modelled as a stochastic process whose intensity depends on the number of occupied patches in the neighborhood of each focal patch. Our model is the CA counterpart, that in the mean-field approximation corresponds with two classical patch occupancy metapopulation models (see Gotelli, 1991). The analysis of this model allowed us to make the point that the spatial scale of the rescue-effect, measured through the extent of dynamical coupling among patches, has important implications for metapopulation persistence and long-term behavior.

In general, the long term behavior of the system, expressed as the proportion of occupied patches (Fig. 5) agrees with the equilibrium proportion of patches derived by using ODEs [eqns (3) and (4); Gotelli, 1991]. In both models the existence of a rescue-effect increases the range of extinction and colonization parameters over which the system attains complete occupancy of patches. However, in our model this result is strongly influenced by the degree of coupling among patches and is apparent only for local interaction (i.e. $r = 1$). This can be explained as follows. With no spatial coupling ($r = 0$), the future state of each patch depends on the assigned probabilities of extinction and colonization and is independent of its neighborhood. However, when rescue effects exist, and $r = 1$, the dynamics of each patch depends on the state of its two closest neighbors and its own state. This implies that each occupied patch in its neighborhood will decrease the extinction prob-

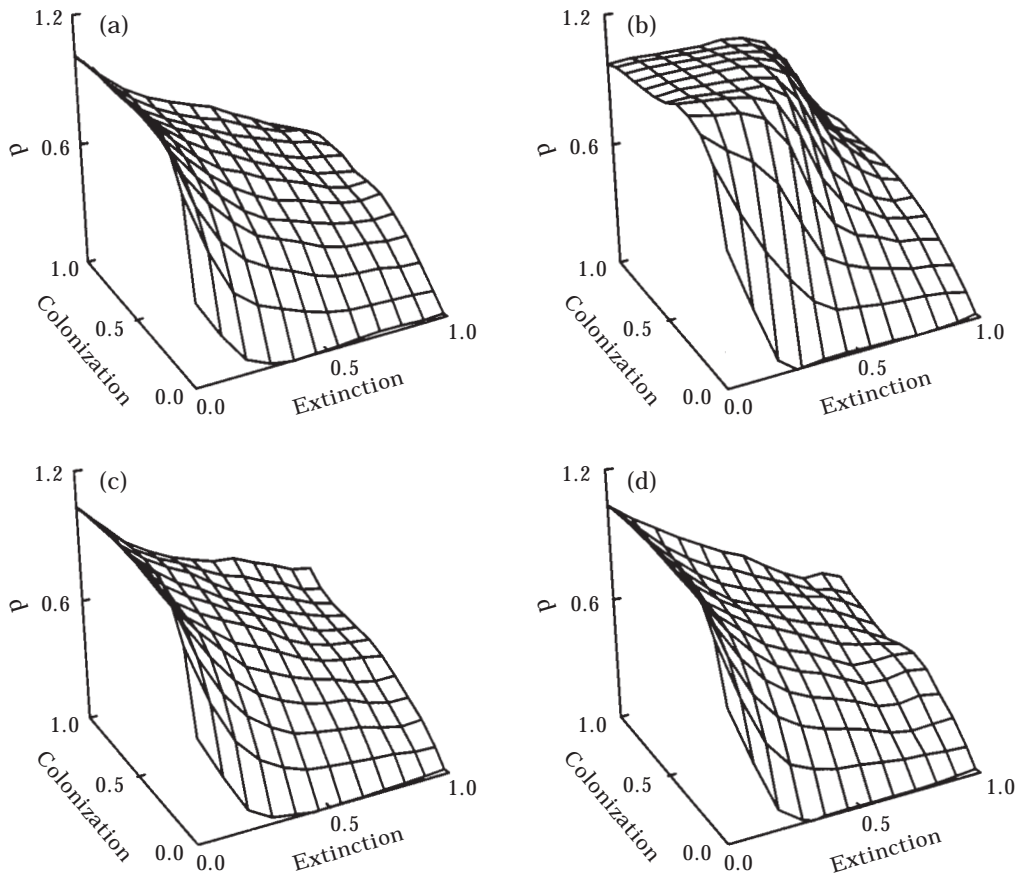


FIG. 5. Long-term proportion of occupied patches (p) over the (c, e) parameter space: (a) $r = 0$; (b) $r = 1$; (c) $r = 25$; (d) $r = 50$. $N = 101$ for all cases.

ability in a proportion equal to 50% [eqn (8), Fig. 2]. As r increases, the proportional contribution of each occupied patch decreases by a factor of $1/2r$ [eqn (7), Fig. 2]. Hence, for large neighborhoods, $1/2r$ tends to small values, approaching zero in the limit of large r . The net effect of this is a progressive dilution of rescue effects as r increases. This explains why the dynamical behavior of our model, expressed as the proportion of occupied patches, is the same for $r = 0$ and for large neighborhoods [Fig. 5(a), (c) and (d)]. Further exploration of our model for $r = 2, 3$ and 4 (Keymer *et al.*, unpubl. data) showed a progressive reduction of the total occupancy area ($p = 1$). Paraphrasing Durrett & Levin (1994a) the dynamics of our model underscore not only the importance of being

discrete and spatial, but also the importance of being local.

Patch occupancy models provide a simple way to illustrate the dynamical consequences of metapopulation structure. However, they usually make unrealistic assumptions. By assuming a fixed number of patches and by focusing on the proportion of occupied patches, patch occupancy models do not allow for dynamics of patches independent of that of the species occupying them (Marquet & Velasco-Hernández, 1997) and, as pointed out above, the per capita contribution of an occupied patch to the rescue effect decreases as the number of patches in the metapopulation (or neighborhood in our case) increases. Our eqn (8) implies that the probability of extinction equals zero when the

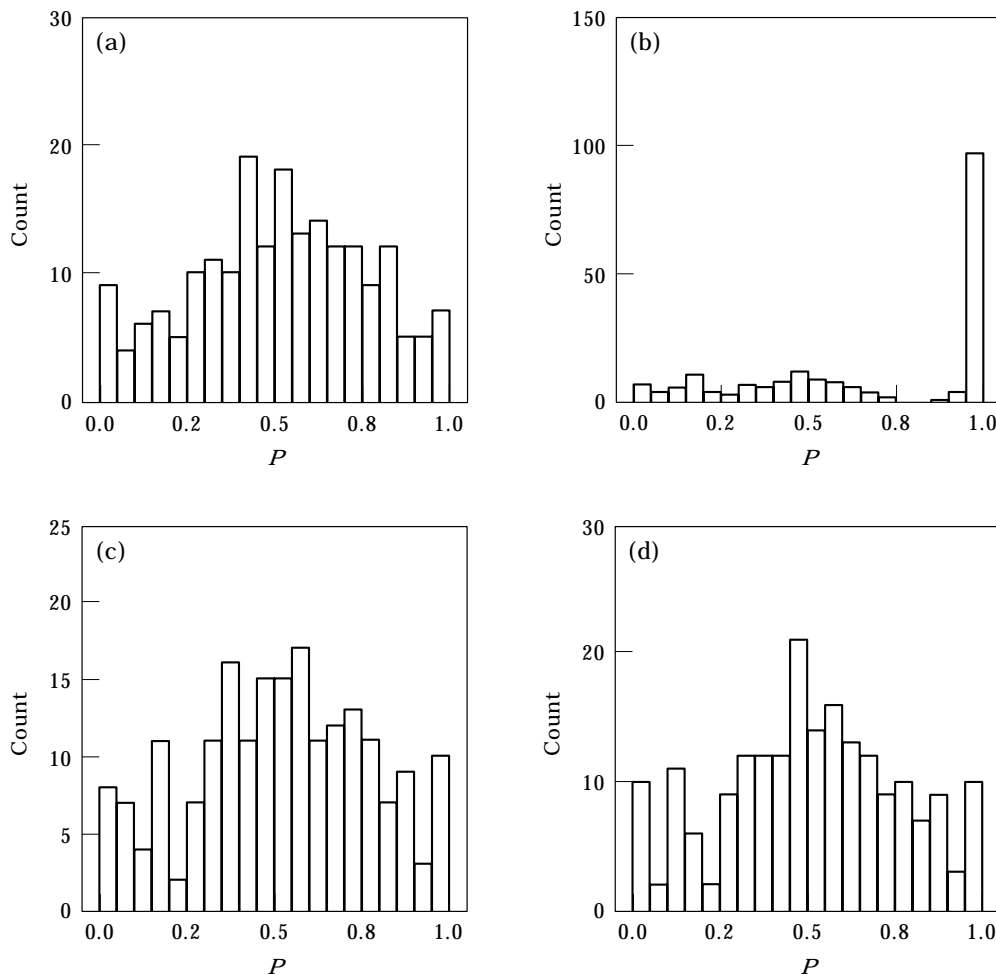


FIG. 6. Frequency distributions of the proportion of occupied patches: (a) $r = 0$; (b) $r = 1$; (c) $r = 25$; (d) $r = 50$. $N = 101$ for all cases.

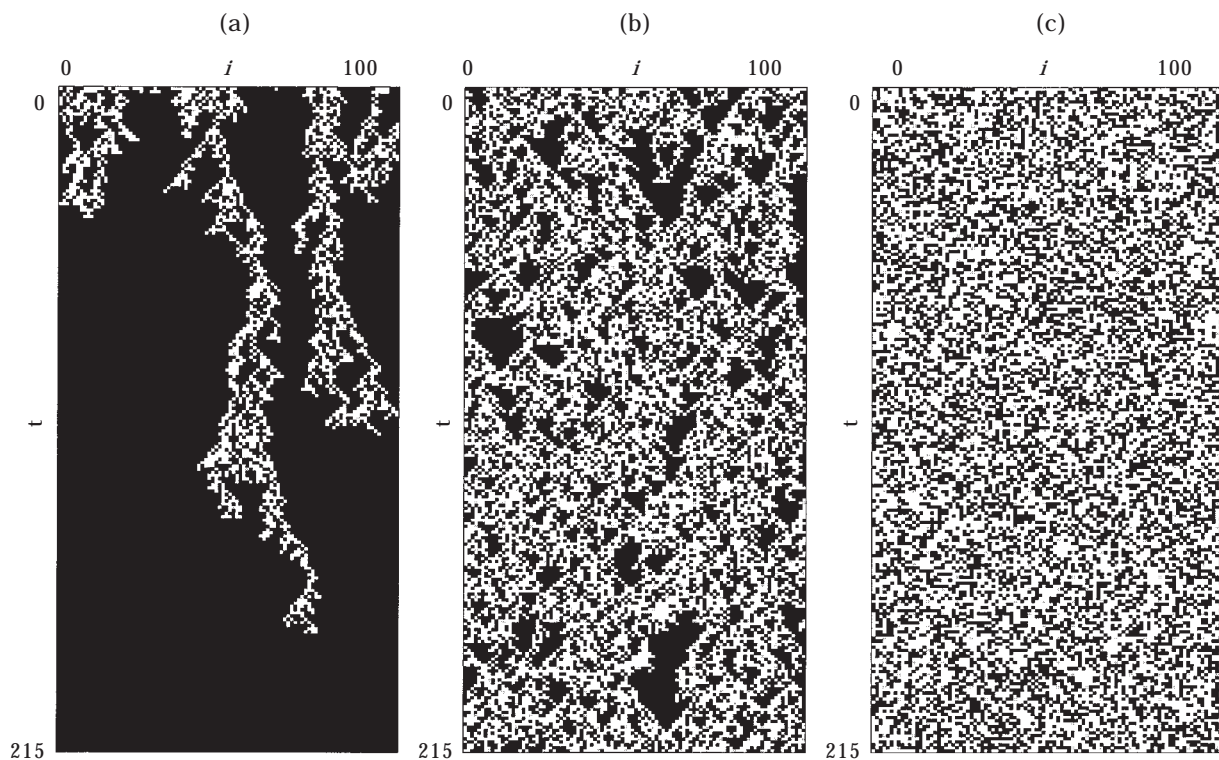


FIG. 7. Spatio-temporal patterns (occupied patches in black): (a) $r = 1$, $c = 0.5$, $e = 0.5$; (b) $r = 1$, $c = 0.4$, $e = 0.5$; (c) $r = 0$, $c = 0.4$, $e = 0.6$.

neighborhood is full. This same assumption is present in Hanski's (1982) rescue effect model. A more realistic way to model rescue effects would be to assume that extinction probability decreases with the proportion of occupied patches in such a way that, even when the neighborhood is full, there is still some intrinsic background probability of extinction (see Gotelli & Kelly, 1993). Similarly, for the sake of comparing our model with its ODE counterpart, we assumed that all patches are identical. The consequences of relaxing these assumptions, through the incorporation of differences in patch quality (e.g. a source-sink dynamics, Pulliam, 1988; see Marquet & Velasco-Hernández, 1997 for a patch occupancy approach) and a more realistic rescue-effect need further research.

The asymptotic behavior of our model converged to a fixed point attractor or did not converge at all. However, other behaviors are also possible, such as periodic attractors. We looked for this but did not find any periodic

attractor after examining correlograms for the time series of patch occupancy in each simulation. However, it can be shown analytically that a period two attractor exists when $c = e = 1$, and $r = 0$.

SPATIO-TEMPORAL PATTERNS

One-dimensional CAs are well known for giving rise to self-organized spatio-temporal patterns (e.g. Wolfram, 1983, 1984). Our model is not the exception. However, self-organized spatio-temporal structures with a fractal-like pattern emerge only under local ($r = 1$) interactions and for particular values of colonization and extinction. This pattern is verified in temporal autocorrelations in patch occupancy [Fig. 4(b) and (d)]. As shown in Fig. 7(b), the spatio-temporal pattern is characterized by the existence of occupancy clusters of different temporal and spatial extents. The important point here is the emergence of patterns of correlated occurrences without explicitly incorporating heterogeneity in our model.

Even in very simple models we can obtain important new information when we take space into account in our formulations. However, to make meaningful comparisons with differential equation models, it is important to demonstrate that the CA formulation truly corresponds to the ODE formulation. We have demonstrated such a correspondence through a mean-field approximation. This leads us to conclude that the CA model would exhibit the same dynamics as the ODE in the case where the system is homogeneous and well-mixed, such that every local neighborhood has the same statistical properties as the whole lattice. The fact that the CA model diverges from the behavior predicted by the ODE indicates the importance of spontaneous formation of spatial heterogeneity, where local neighborhoods have quite different properties depending on spatial location.

As mentioned earlier, our result agrees with that of Gotelli (1991) in relation to the importance of rescue effects in increasing regional occurrence of species. Nevertheless, we show that this importance depends also on the topological relationships among patches. We found that the rescue effect has its most important influence when the topological structure is the same in which self-organized spatio-temporal patterns appear.

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APPENDIX

Derivation of the Mean-field Approximation

One way of demonstrating correspondence between a cellular automata model and a classical differential equation is to show that the CA converges to the differential equation in the mean-field approximation. The fundamental assumption of a mean-field approximation is that all neighborhood configurations occur at random, with probabilities of occupancy equal to the overall proportions in the lattice as a whole. In particular, for our CA metapopulation

model we have to prove that it converges in the mean-field approximation to:

$$\frac{d}{dt}p(t) = c(1 - p) - ep(1 - wp)$$

which corresponds to eqn (3) when $w = 0$, and to eqn (4) when $w = 1$.

In order to generate the mean-field approximation, the overall probability of an empty cell being occupied should be c . This, when multiplied by $1 - p$ (the probability of having an empty cell), yields the colonization rate of the ODE. Similarly, the overall probability of an occupied cell going extinct should be $e(1 - wp)$, yielding an extinction rate of $ep(1 - wp)$.

For a given neighborhood, $\Omega(i,r)$ we define:

$$\Omega^*(i,r) = \{\alpha \in \Omega(i,r) / a_\alpha = 1\}$$

which is the set of occupied cells in the neighborhood $\Omega(i,r)$,

$$\eta = \#\Omega^*(i,r)$$

the number of occupied cells in the neighborhood, and

$$\#\Omega(i,r) = 2r$$

the total number of cells in the neighborhood.

For an empty neighborhood, $\eta = 0$, there is only one possible arrangement of $2r$ empty cells, which occur with probability $(1 - p)^{2r}$. For one occupied cell, $\eta = 1$, there are $2r$ possible arrangements, each of which occurs with probability $p(1 - p)^{2r-1}$. In general, for η occupied cells, there are

$$\frac{2r!}{\eta!(2r - \eta)!}$$

possible arrangements, each with a probability $p^\eta(1 - p)^{2r-\eta}$ of occurrence.

Given a focal cell, if it is empty, we assume a constant local colonization probability of c for any neighborhood configuration. To demonstrate that this converges to the desired colonization rate in the mean-field approximation, we must show that

$$c \sum_{\eta=0}^{2r} \frac{2r!}{\eta!(2r - \eta)!} p^\eta(1 - p)^{2r-\eta} = c$$

which follows directly from the binomial theorem.

If the focal cell is occupied, we assume that the local extinction probability is $(1 - w(\eta/2r))e$. To demonstrate that this yields the desired mean-field approximation, we must show that

$$\begin{aligned} e \sum_{\eta=0}^{2r} \frac{2r!}{\eta!(2r-\eta)!} (1 - w\frac{\eta}{2r}) p^\eta (1-p)^{2r-\eta} \\ = e(1 - wp) \end{aligned}$$

Canceling e from both sides, we get

$$\sum_{\eta=0}^{2r} \frac{2r!}{\eta!(2r-\eta)!} (1 - w\frac{\eta}{2r}) p^\eta (1-p)^{2r-\eta} = 1 - wp$$

We can separate the summation into two terms as follows

$$\begin{aligned} \sum_{\eta=0}^{2r} \frac{2r!}{\eta!(2r-\eta)!} p^\eta (1-p)^{2r-\eta} \\ - \sum_{\eta=0}^{2r} \frac{2r!}{\eta!(2r-\eta)!} w\frac{\eta}{2r} p^\eta (1-p)^{2r-\eta} = 1 - wp \end{aligned}$$

By the binomial theorem, the first sum equals 1, so the whole equation will be true if and only if the second sum equals wp .

$$\sum_{\eta=0}^{2r} \frac{2r!}{\eta!(2r-\eta)!} w\frac{\eta}{2r} p^\eta (1-p)^{2r-\eta} = wp$$

Simplifying and reordering terms, we get

$$\begin{aligned} wp \sum_{\eta=0}^{2r} \frac{(2r-1)!}{(\eta-1)!(2r-1-(\eta-1))!} p^{\eta-1} \\ (1-p)^{2r-1-(\eta-1)} = wp \end{aligned}$$

changing variables $\eta = \psi + 1$, the sum can be written as

$$\begin{aligned} wp \sum_{\psi+1=0}^{2r} \frac{(2r-1)!}{(\psi+1-1)!(2r-1-(\psi+1-1))!} \\ p^{\psi+1-1} (1-p)^{2r-1-(\psi+1-1)} = wp \end{aligned}$$

reordering and canceling vanish terms we get

$$wp \sum_{\psi=0}^{2r-1} \frac{(2r-1)!}{\psi!(2r-1-\psi)!} p^\psi (1-p)^{2r-1-\psi} = wp$$

Which, since the binomial theorem holds that the summation is 1, so the equation clearly holds.