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Measuring and Characterizing Spatial Patterns, Dynamics and Chaos in Spatially Extended Dynamical Systems and Ecologies

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Measuring and characterizing spatial patterns, dynamics and chaos in spatially extended dynamical systems and ecologies†

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In this paper I discuss space-time chaos in both locally mixing continuum systems (reaction-diffusion equations, coupled map lattices and functional maps) and individual-based models (probabilistic cellular automata and artificial ecologies). I particularly emphasize quantification and data-analysis and attempt to address the characterization of spatial structure and dynamics in such disordered systems. I discuss the relevance of these ideas to ecology, evolution and epidemiology. The artificial ecologies I consider motivate a new definition of space-time chaos for such systems and new data analysis techniques.

1. Introduction

In this paper I want to address a number of basic issues about the dynamics of spatially extended systems which are disordered in time or space. I am particularly interested in the characterization of spatial structure and its dynamics and how to quantify and measure this. In particular, I want to discuss the relevance of these ideas to fields such as ecology, evolution and epidemiology. These are areas where virtually all the real systems are spatially extended but where very few of the models take this into account. There are important practical implications for data collection and analysis.

Ecological models to study spatial effects fall into two broad categories. In the first, one assumes local mixing in space and models this using either a reaction-diffusion equation (Okubo 1980; Murray 1990), or a coupled map lattice (Hassell *et al.* 1991). Those 'patch' models which assume a large number of patches, homogeneous mixing within a patch and dispersal between patches (Hassell 1978; Reeve 1990; Hastings 1990; Levin *et al.* 1993) also fall into this class.

The other category of models are those which are individual-based. In these one models the stochastic behaviour of individuals which are distributed in space. Dynamics and competition are built into the model through the use of simple transition rules which only depend upon the local configuration. One is interested in the way in which the spatial dynamics are integrated to produce community behaviour. There are now a number of interesting applications of such systems to ecology and epidemiology. These include contact processes and spatial epidemics

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(Durrett 1993), host–parasitoid and host–pathogen dynamics (Comins *et al.* 1993; Rand *et al.* 1994*a*), ecological systems (Durrett & Levin 1994; DeRoos *et al.* 1991; Rand & Wilson 1994*a*) and game theory (Durrett & Levin 1993; Nowak & May 1992).

I want to discuss both these classes in this paper. I start by very briefly discussing some illustrative examples of continuum systems drawn from (i) mathematics and physics and (ii) ecology and epidemiology. Then I discuss some basic theory of disordered continuum systems and give a brief introduction to recent results on spatio-temporal chaos. Finally in this section, I consider some question of quantification and data analysis for these systems.

Then I move on to individual-based systems. After discussing some ecological examples and related general theory, I consider some new ideas about the data analysis of such systems. I describe a new method for identifying spatial scales. I outline a method (Rand & Wilson 1994*a*) for immense data compression in such systems and discuss its application to detecting structural change in ecosystems. I apply this approach to a resource–predator–prey system and a spatial model of succession in a forest community.

These examples motivate a new definition of space-time chaos for such individual-based systems. This is given in § 3 *e*.

In the discussion I will consider several basic questions of general applicability. A basic problem is to understand when such spatially extended systems admit a good description in terms of low-dimensional dynamics. How can we understand, describe and characterize the spatio-temporal behaviour of systems for which this low-dimensional description does not hold? How should we characterize spatial order and disorder? What is the nature of (*a*) the continuum limit (see § 2 *b* (ii)) and (*b*) the thermodynamic limit (see § 2 *b* (iii)) in such systems? How do we deal with the immense amounts of data in the states of these models and maximize the information gained from this data? Are there general techniques for identifying appropriate spatial and temporal scales?

2. Locally mixing continuum systems

In this half of the paper I will be concerned with systems which are modelled either by reaction-diffusion equations, functional maps or coupled map lattices. Reaction-diffusion equations have the following general form: $\partial_t u = D\nabla^2 u + X(u)$. Here $u = u(x,t) \in \boldsymbol{R}^m$ or $\boldsymbol{C}^m$ and the diffusion matrix D may be complex. An example is the complex Ginzburg–Landau (CGL) equation below.

Coupled map lattices (CMLs) are defined as follows. Let Λ be $\boldsymbol{Z}^\nu$ or a finite rectangle in $\boldsymbol{Z}^\nu$. The state $u = (u_x)_{x\in\Lambda}$ associates to each point x in Λ an element u_x of a vector space V. The simplest CMLs are mappings Φ of the form

$$\Phi : (u_x)_{x\in\Lambda} \mapsto \left(\sum_{y\in\Lambda} s_\varepsilon(|y-x|) f(u_y)\right)_{x\in\Lambda}.$$

Here f is a mapping from V to V and the interaction s_ε satisfies (i) $s_\varepsilon(n)$ is exponentially small in $|n|$, (ii) $s_\varepsilon(n) < \varepsilon$ for all $n \neq 0$ and (iii) $s_\varepsilon(0) \in [1-\varepsilon, 1]$. A much studied example is that for nearest-neighbour coupling where $s_\varepsilon(0) = 1-\varepsilon$, $s_\varepsilon(1) = \varepsilon/N$ (where N is the number of immediate neighbours) and $s_\varepsilon(n) = 0$ for all other n. A CML $\Phi = \Phi_\varepsilon = A_\varepsilon \circ L$ is a composition of two maps where the

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Table 1. *Some examples of the CMLs, functional maps and PDEs used to illustrate the theoretical discussion*

(They are (i) coupled logistic maps, (ii) the complex Ginzburg–Landau (CGL) equation, (iii) the CGL map, (iv) the resource–predator–prey system and (v) the host–parasitoid system.)

	local (reaction) dynamics L	coupling A_g
$x \in [0,1]$	$x' = 4ax(1-x)$	$x'_i = x_i + g\nabla^2(\underline{x})_i$
$u = r\mathrm{e}^{\mathrm{i}\phi} \in \boldsymbol{C}$	$\partial_t u = \varepsilon u + (1+\mathrm{i}c_1)\nabla^2 u - (1-\mathrm{i}c_2)\lvert u\rvert^2 u$	
$u = r\mathrm{e}^{\mathrm{i}\phi} \in \boldsymbol{C}$	$f(r\mathrm{e}^{\mathrm{i}\phi}) = \surd(\mu r^2/(\lambda\mu + (1-\lambda)r^2))$ $\times \exp(\phi - \tau\alpha r^2)$	$(1 + \tau_0(1+\mathrm{i}\beta)\Delta/M)^M$ $\approx \exp(\tau_0(1+\mathrm{i}\beta)\Delta)$
prey v	$v' = v(1+b_1)$ $\times \exp(-\alpha p/r - c_1 p/(1+h_1 v))$	$v'_i = v_i + g_v\nabla^2(\underline{v})_i$
predator p	$p' = p(1-d)\exp(c_2 v)$	$p'_i = p_i + g_p\nabla^2(\underline{p})_i$
resource r	$r' = r(1+b_3)\exp(-r/k - c_3 p)$	$r'_i = r_i + g_r\nabla^2(\underline{r})_i$
host h	$h' = \lambda h\mathrm{e}^{-p}$	$h'_i = h_i + g_h\nabla^2(\underline{h})_i$
parasite p	$p' = qh(1-\mathrm{e}^{-p})$	$p'_i = p_i + g_p\nabla^2(\underline{p})_i$

local map is $L((u_x)) = (f(u_x))$ and A_ε is the *interaction* or *coupling map* defined by s_ε. For the nearest neighbour example above

$$A_\varepsilon(u)_x = u_x + \varepsilon\nabla^2(u)_x$$

where

$$\nabla^2(u)_x = \sum_{\text{nbrs } y \text{ of } x} (u_y - u_x).$$

Weak coupling means $\varepsilon \approx 0$.

The natural phase space for a CML is usually an open subset $\ell^\infty(E)$ of the ℓ^∞-space $\ell^\infty(V)$. Here $\ell^\infty(V)$ is the Banach space of all $u = (u_x)$ such that $u_x \in V$ for all x and $\|u\| = \sup_x \|u_x\| < \infty$. And $\ell^\infty(E) = \{u : u_x \in E \text{ for all } x\}$.

Functional maps are similarly defined but in this case x is continuous and ranges over a rectangle in $\boldsymbol{R}^\nu$. For the interaction A_ε we take standard smoothing operators such as $\exp(\varepsilon\Delta)$, truncations of this or operators defined by related kernels. For example, the CGL map (see table 1) gives a functional map with closely analogous behaviour to the CGL equation in one and two dimensions (Bohr *et al.* 1989, 1990*a*, *b*).

In general we use CMLs to probe the thermodynamic limit and functional maps to probe the continuum limit.

(*a*) *Some illustrative examples*

For my theoretical discussion I want to refer to the following examples. The mathematical formula for each example is given in table 1.

(i) *Mathematical and physical examples*

Because of limitations of space, for the mathematical and physical examples I just refer the reader to the indicated sample references. Further references can be found in these.

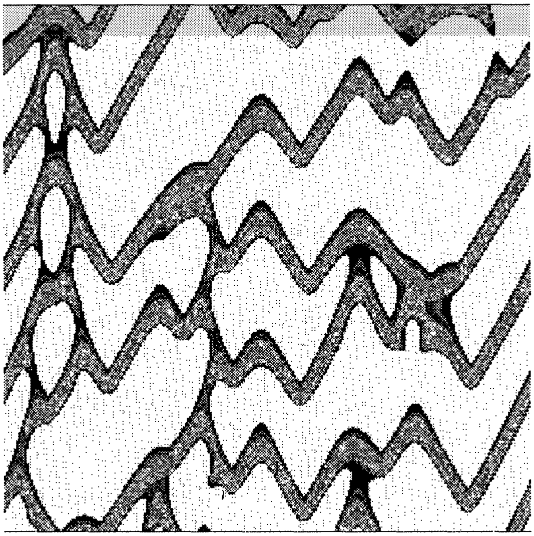

Figure 1. A typical space-time plot of the prey in the one-dimensional resource–predator–prey system. It shows how the bursts of prey nucleate and convect across the system.

1. *Coupled logistic maps.* Kaneko 1991.

2. *Hyperbolic CMLs.* Bunimovich & Sinai 1988, Pesin & Sinai 1991, Gundlach & Rand 1993*a–d*, Campbell & Rand 1994*a–c*.

3. *The complex Ginzburg–Landau (CGL) equation and map.* Schraiman *et al.* 1992, Chaté 1994, Bohr *et al.* 1989, 1990*a*, *b*, Aranson *et al.* 1991*a*, *b*, Weber *et al.* 1992.

(ii) *Biological examples*

4. *A resource–predator–prey system.* The local dynamics for this system are chaotic (Rand *et al.* 1994*b*).

The corresponding diffusively coupled CML displays space-time intermittency. The background state has zero prey and plentiful resource. From this state one gets random nucleation of prey outbreaks followed by predators waves. These structures then propagate with a characteristic velocity across the ecology. This is shown in the space-time plot in figure 1. We discuss quantifiers of this state below (e.g. in § 2 *c*).

5. *Host–parasitoid system* (Comins *et al.* 1992). The local dynamics for this involve diverging Lotka–Volterra cycles which always lead to extinction. However, in large two-dimensional systems they can survive for a very long time and there are attractors with infinite lives. In not too small one-dimensional systems, by initially adding a very small random number of parasites at the boundaries one can put the system into an attractor which for infinitely long times has a relatively large minimum population size. The states in this model are space-time intermittent rather than fully developed space-time chaotic. They are similar to those in the resource–predator–prey system above. The background state is that where both parasite and host is absent. From this one gets nucleation of bursts of infection that are then convected across the system.

(*b*) *Mathematical theory*

(i) *Basic length scales: dissipation, excitation and correlation length scales*

Let us suppose that our system is defined over a region of ν-dimensional physical space represented by a rectangle of length L. We shall be particularly interested in the behaviour of our systems as the volume $V = L^{\nu}$ of the system is increased.

Since all the systems we consider are dissipative, there is a length scale ℓ_D below which all modes are damped. This is the *dissipation length.* For typical low-dimensional systems $\ell_D \approx L$ and there are only a few excited modes. However, in large systems $\ell_D \ll L$ and this would appear to be the case in many ecological and epidemiological situations. This scale is very important for data analysis. In general one expects that it is not necessary to resolve the spatial structure at scales well below ℓ_D. I discuss the mathematical meaning of ℓ_D in § 2 *b* (ii) below.

Consider the correlation $C_{ij}(\tau, r) = \langle (u_i(x,t) - \bar{u}_i)(u_j(x+r, t+\tau) - \bar{u}_j) \rangle$ where the averaging $\langle \cdot \rangle$ is over both space x and time t. In many spatio-temporal chaotic systems $C_{ij} \sim \exp(-r/\xi - \tau/\gamma)$. This defines the *spatial correlation length* $\ell_C = \xi$ and the *temporal correlation time* γ.

(ii) *The continuum limit and the dissipation length*

We consider systems with a finite spatial domain. Suppose that the phase space of our dynamical system is a Hilbert space $\boldsymbol{H}$. For some systems such as the CGL equation it can be proved (Doering *et al.* 1988) that on the attractor A there is a cone condition of the form $||Q_n u|| \leqslant ||P_n u||$ where $P_n u$ is the projection of $u \in H$ onto the space $\boldsymbol{H}_{\leqslant n}$ spanned by the first n generalized Fourier modes and $Q_n = 1 - P_n$ is the complementary projection onto $\boldsymbol{H}_{>n}$. It follows from this that if $A' = P_n(A)$ then there is a Lipshitz map $a : A' \subset \boldsymbol{H}_{\leqslant n} \to \boldsymbol{H}_{>n}$ such that every $u \in A$ is of the form $u = u' + a(u')$ for $u' = P_n(u) \in A'$. In other words, the high modes $a(u')$ are *slaved* to the low modes u'.

If this holds, we can identify the dissipation length ℓ_D as the longest wavelength λ of the modes in $\boldsymbol{H}_{\leqslant n}$.

When there is slaving on the attractor, it is natural to ask if there is a finite-dimensional dynamical system that mirrors the non-transient behaviour of the full system. Thus the problem becomes one of extending the slaving function a to some sort of open set U in the space of low Fourier modes $\boldsymbol{H}_{\leqslant n}$. This can be done if we can extend the cone condition. In this case, standard invariant manifold techniques can be used to prove the existence of an *inertial manifold* which is the graph of a mapping $a : U \subset \boldsymbol{H}_{\leqslant n} \to \boldsymbol{H}_{>n}$.

For a wider class of systems, such as two-dimensional Navier–Stokes, one can prove that attractors are finite-dimensional. This can be done when one can show that near to the attractor small round balls in phase space are transformed by the dynamics into 'pancakes' which are very thin in all but m dimensions. When this holds one can define ℓ_D in a similar way to that described above.

(iii) *The thermodynamic limit and extensive chaos*

I would like to start this section by proposing a definition of space-time chaos for such continuum systems. (I give the corresponding definition for individual-based systems in § 3 *e*.) For this definition it is important to keep in mind that we are interested in large systems. Mathematically we are interested in the large

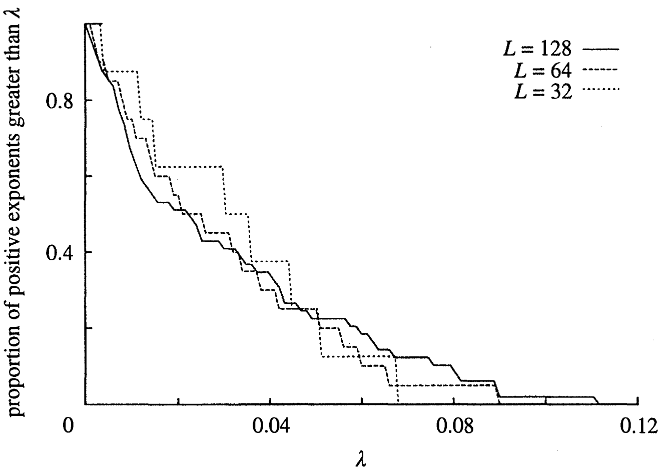

Figure 2. An approximation of the Lyapunov density for the host–parasitoid system with parameters $\lambda = 2$, $q = 1$ and $g_{\mathrm{h}} = g_{\mathrm{p}} = 0.25$. The graphs are for $L = 32$, $L = 64$ and $L = 128$.

volume limit $V \to \infty$. Thus I consider the systems of interest to be parametrized by V or equivalently by the length of the system L.

Definition. A system is *space-time chaotic* if (i) it has a thermodynamic limit at $V = \infty$; and (ii) the number of positive Lyapunov characteristic exponents is $\mathcal{O}(V)$.

All the example systems of § 2 *a* contain régimes that satisfy this definition. It should be noted that the notion of space-time chaos described here can be further subdivided. For example, in the CGL equation one finds régimes of space-time intermittency and amplitude turbulence, and both of these can satisfy our definition. I discuss these distinctions below.

Let me discuss (ii) first. Of course, the main characteristics of low-dimensional chaos are the existence of an attractor and at least one positive Lyapunov characteristic exponent (LCE) for this attractor. In a spatially extended system we expect that the number of active degrees of freedom grows roughly linearly in the system's volume V. For a system that is both chaotic in space and time we also expect that a roughly constant proportion of these will correspond to unstable modes with a positive exponent. Thus we want the condition (ii).

In many systems a stronger condition holds: there is a limiting *Lyapunov density* $\lambda(\chi) = \lim_{V\to\infty} \lambda_V(\chi)$. Here $\lambda_V(\chi)$ is the ratio of the number of exponents which are $> \chi$ to the number of the positive exponents for the system of volume V. An example of such a Lyapunov density is shown in figure 2 where I draw approximations to that for the host–parasitoid model. All our examples have a Lyapunov density in the appropriate régimes.

We note now that if (ii) holds then it defines a new length scale ℓ_L by the relation: number of positive exponents $\sim (L/\ell_L)^{\nu}$. The density of positive characteristic exponents is $\ell_L^{-\nu}$. Since the Lyapunov dimension is determined by the Lyapunov exponents, from the Lyapunov spectrum on can determine a density $\ell_{LD}^{-\nu}$ for the Lyapunov dimension via the relation: Lyapunov dimension of attractor $\sim$

$(L/\ell_{LD})^{\nu}$. For the logistic system with the coupling $g = 0.3$ this is approximately 0.67.

The thermodynamic limit. Now I want to turn to the question of what is the thermodynamic limit for such systems. I will discuss this for coupled map lattices, but it will be clear to the reader how to generalize this to other systems. Consider a CML $\Phi : \ell^{\infty}(E) \rightarrow \ell^{\infty}(E)$. This is the infinite volume system and has associated with it the finite volume systems Φ_V.

We say that Φ has a *thermodynamic limit* if it satisfies the following requirements:

(i) Φ has an attracting invariant set A with open basin $B = B(A)$ in $\ell^{\infty}(E)$. This restriction on the basin can be relaxed somewhat.

(ii) For typical initial conditions $u(\cdot)$ in B the spatio-temporal statistics are described by a single spatio-temporal ergodic natural measure μ on A.

(iii) If μ_V is the corresponding natural measure for the system of finite volume V, then $\mu_V \rightarrow \mu$ as $V \rightarrow \infty$ and the number of positive LCE of μ_V is $\mathcal{O}(V)$.

Here typical has the following meaning: Let $\pi_V : \ell^{\infty}(E) \rightarrow \ell^{\infty}_V(E)$ be the projection onto the corresponding V sites. Typical means that $u(\cdot) \in B_0$ where B_0 is a subset of B such that $\pi_V(B_0)$ has full Lebesgue measure in $\pi_V(B)$ for all V. Space-time ergodic means that for all continuous $v : \ell^{\infty}(E) \rightarrow \boldsymbol{R}$

$$\langle v(S^x(u))\rangle_x = \langle v(\Phi(u)\rangle_t = \int_A v \, \mathrm{d}\mu,$$

where S^x is the spatial translation: $(S^x u)(y) = u(x + y)$.

It is proved in Bunimovich & Sinai (1988), Pesin & Sinai (1991), Gundlach & Rand (1993*a*–*d*) and Campbell & Rand (1994*a*, *b*) that weakly coupled map lattices with hyperbolic local dynamics have a thermodynamics limit.

(iv) *Extensive chaos*

Recall the definition of the exponent length ℓ_L and the density for Lyapunov dimension. Analogously, we can define the following related length scales:

ℓ_F: fractal dimension of $A \sim (L/\ell_F)^{\nu}$ as $L \rightarrow \infty$;

$\ell_{R,q}$: order q Renyi entropy of $A \sim (L/\ell_{R,q})^{\nu}$ as $L \rightarrow \infty$.

When these quantities and the length scales ℓ_L and ℓ_{LD} for the Lyapunov exponents and Lyapunov dimension are well defined and finite we say the we have *extensive chaos*. Then, in the language of physics, each of the classical dynamical quantities (fractal dimension, Lyapunov dimension, order q Renyi entropy and number of positive LCEs) is extensive.

It should be noted that these various lengths ℓ are independent of the correlation length ℓ_C. For example, there are examples of one and two-dimensional systems (L. A. Bunimovich, personal communication; Miller & Huse 1993) where $\ell_C \rightarrow \infty$ as the coupling is increased to some finite critical value while ℓ_L remains finite.

It should not be too difficult to use the results of Campbell & Rand (1994*a*–*c*) to show that weakly coupled map lattices with hyperbolic local dynamics have extensive chaos. All the examples of § 2 *a* are extensive in the appropriate régimes.

(*c*) *Space-time intermittency*

Space-time intermittency is characterized by a competition between two states. The first state, the 'laminar' or background state acts as an absorbing state and typically, but not necessarily, is linearly stable. The 'turbulent' active state is usually made up of localized objects. These carry the disorder. They erupt from the background state in a chaotic fashion. However, note that it is not necessary for the background state to be truly laminar or for the active state to be chaotic.

In the one-dimensional CGL equations the localized objects are 'holes'. In the resource–predator–prey system they are prey-predator booms which also correspond to holes in the resource. In the host–parasitoid system they are localized lump-like parasite outbreaks. In this system it can be shown (M. Keeling 1994, personal communication) that if the host and parasite are both low then the system will become extinct. This state (both populations low) is therefore the stable absorbing state. In the one-dimensional system most initial conditions will give you just this state and the populations go extinct. However, you can excite the active state by tickling the system with some very small localized random noise. It is easily excited and once active stays present even when the noise is turned off.

In this régime these localized nucleating objects which carry the disorder are the building blocks for a statistical theory. For example, two interesting quantities are the distributions $P(\xi)$ and $P(\tau)$ of the sizes ξ and lifetimes τ of the laminar regions separating the localized objects (Chaté & Manneville 1988). It is expected that in the intermittent régime these will be exponential, i.e. $P(\xi) \sim \exp(-\xi/\ell_1)$ and $P(\tau) \sim \exp(-\tau/\ell_2)$ and this then defines spatial and temporal coherence lengths ℓ_1 and ℓ_2. The length distribution for the host–parasitoid system is shown in figure 3. In this case $\ell_1 \approx 5.4$ and $\ell_2 \approx 2.33$. Note that ℓ_1^{-1} corresponds to a spatial entropy since we are using a symbolic coding into laminar and turbulent states. Then, assuming that the localized objects do not vary too much, ℓ_1^{-1} and ℓ_2^{-1} are related to the spatial and temporal KS-entropies of this system.

(*d*) *Stabilization of chaotic repellers*

Consider the coupled logistic map example of § 2 *a* and suppose that the parameter of the logistic map is chosen so that the uncoupled logistic maps have a stable 3-cycle. Then the coupled system has an attractor which is the homogeneous state corresponding to this 3-cycle. However, if the system is reasonably large and started from random initial conditions then this attractor is never seen. For the individual maps there is a horseshoe repeller around the 3-cycle and there is a corresponding horseshoe in the coupled system (at least for weak coupling (Campbell & Rand 1994*a*)). The states get tangled up in this repeller and the escape time for this grows exponentially or faster with the system size. Thus, for large V, the repeller acts effectively as an attractor while for the infinite system it is an attractor.

This is a very common phenomenon in a wide range of systems. Moreover, there are examples, where these escape times become infinite at finite system sizes. An example for the CGL map is given in Bohr *et al.* (1989, 1990*a*, *b*).

(*e*) *Reconstruction of attractors for spatially extended systems*

Recall the various embedding theorem for a time-series coming from a low-dimensional dynamical system (Takens 1980). Clearly, it is not sensible to at-

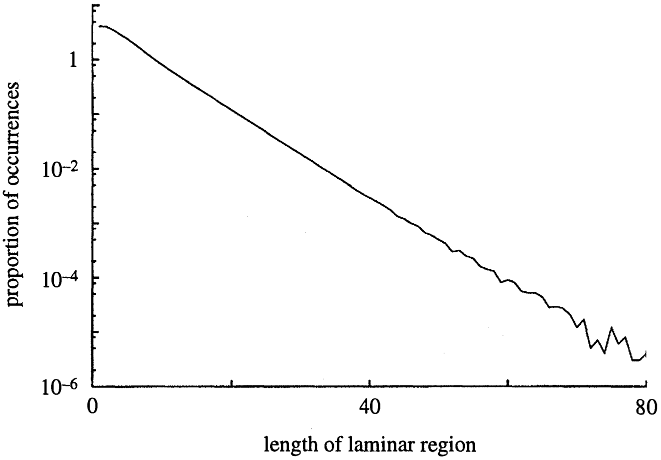

Figure 3. The distribution $P(\xi)$ of the sizes ξ of the laminar regions separating the localized objects in the host–parasitoid system with parameters $\lambda = 2$, $q = 1$ and $g_h = g_p = 0.25$.

tempt reconstruction for large spatially extended systems using a single scalar observable. However, it has been shown that this does give rise to a practicable method when the observable is a spatially extended field (Rand & Wilson 1994*b*). For example in the resource–predator–prey system of § 2 *a* for the observable one can take the spatially extended state of just one of the species and reconstruct the other two from this. If the coupling is strong one can even only monitor the observed state on a sublattice provided that it is well-distributed. This result is of interest for ecology since it offers the possibility of monitoring observable species using remote sensing and then reconstructing the invisible species from the spatially extended time-series of some observable species.

3. Individual-based systems: artificial ecologies

I now discuss some non-equilibrium individual-based systems. I will concentrate on questions concerned with the data analysis of spatial and temporal patterns in non-equilibrium systems. The main ideas are taken from Rand & Wilson (1994*a*).

Artificial ecologies (AEs) are a slight generalization of probabilistic cellular automata (PCAs). Physical space is represented by a two-dimensional $L \times L$ lattice Ω of sites. Each site x can be in any one of a number of discrete states $s_1, \ldots, s_d$. Therefore, the state of the system is given by a configuration $S = \{S_x\}_{x \in \Omega}$. The state $S(t)$ at time t determines a probability distribution on the potential future states in the following way.

In a PCA each site is updated independently. This is not appropriate for many ecological applications because an event at one site can determine a specific change at another neighbouring site. Thus, in an AE the state of each neighbourhood determines a probability distribution on a finite set of admissible events. This set is called the *event set*. Each of these events is a transformation of the state on the neighbourhood.

There are two possibilities for the updating:

Synchronous updating where the state of each neighbourhood determines a probability distribution on the event set. Thus the state $S(t)$ at time t determines a probability distribution of the states at time $t+1$. The whole configuration is then updated synchronously.

Asynchronous updating where the state of each neighbourhood determines the rates at which the various events in the event set occur in the neighbourhood. If event i has rate r_i in a neighbourhood then the probability of it occuring in $[t, t+h]$ is $r_i h + o(h)$ where $o(h)/h \rightarrow 0$ as $h \rightarrow 0$. Once it occurs, the neighbourhood's state may change leading to a change in the rates r_i associated with the neighbourhood.

Note the difference between PCAs and AEs. Wheras in a PCA all events only change the central site, in an AE other sites in the neighbourhood can be changed.

The examples I discuss here are synchronously updated. It appears that for the particular systems I am discussing this does not matter and the corresponding asynchronously updated systems have similar spatial and temporal statistical properties. However, this is not always the case and there are systems where the synchronously and asynchronously updated versions have very different behaviour (Huberman & Glance 1993).

(*a*) *Two basic examples*

In this paper I will consider two examples: a resource–predator–prey system (Rand & Wilson 1994*a*) and a model for the Middle-European beech forest cycle (Wissell 1991). These examples are chosen for their intermediate-scale non-equilibrium dynamics.

(i) *Resource–predator–prey model*

Each site can be in one of five states; *resource*, *predator*, *predator in a resource*, *prey* or *empty*. A predator in a resource is effectively both and its evolution can be described by what happens to each separately. Hence we will ignore this as a separate state. The boundary conditions are periodic.

Because of limitations of space we do not give the precise rules or parameter values here. They can be found in Rand & Wilson (1994*a*). However, we note that they are chosen to implement the following intuitive rules. (*a*) A resource site can grow into any adjacent empty site with a given probability g. (*b*) A prey will move into and eat an adjacent resource site. (*c*) If there is no resource in adjacent sites a prey will move randomly into one of its adjacent sites. (*d*) There is a certain probability of a prey giving birth $p_{V,b}$ into an adjacent empty site. This probability is zero if a prey individual has not eaten for a certain amount of time. (*e*) A prey will die with probability one if it has not eaten for a certain amount of time. (*f*) For the predators there are similar rules to the prey for giving birth and dying. (*g*) If there are no neighbouring prey then a predator has a hunting ability in that it can sense prey further away than it can actually move. If it does then it can move one step in that direction.

A typical spatial state for this model is shown in figure 4. Note the spatial heterogeneity. For these parameter values there is a majority of resource. For different parameter values this can change to be a minority. To obtain this spatial state and in the example used in the following discussion we use the parameter values as given in Rand & Wilson (1994*a*).

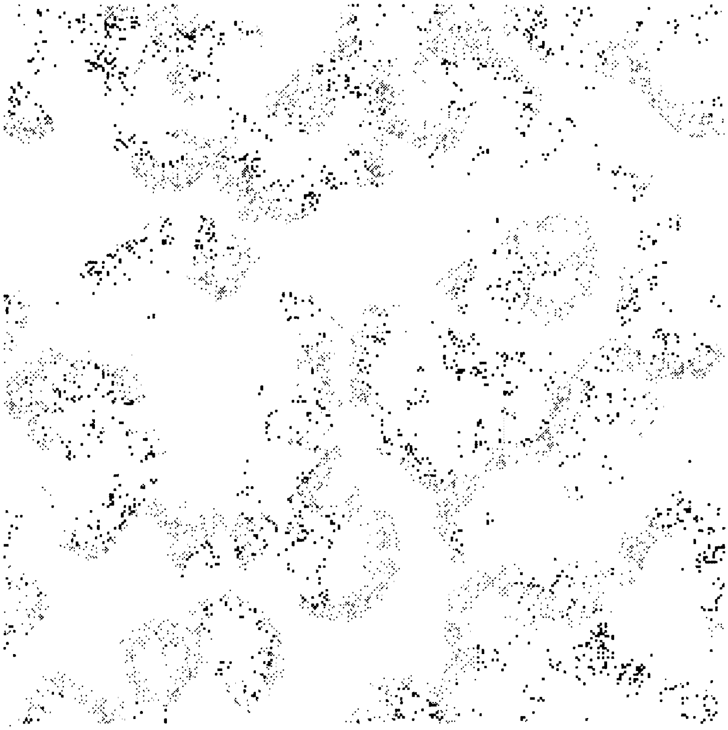

Figure 4. A typical spatial configuration of the resource–predator–prey AE for the given parameter values. The lattice size shown is 300×300. The colour-coding is as follows: lightest grey, empty; medium grey, prey; black, predator.

(ii) *Wissel's Middle European beech forest cycle*

This attempts to model the spatial patterns associated with the natural cycles in the Middle European beech forest (Wissell 1991). The rules for this are given in figure 5 and a typical spatial state is shown in figure 6. All my comments on this model are taken from Hendry & McGlade (1994).

(*b*) *Dynamics and attractors*

These AEs determine a Markov process on the space of configurations $\underline{S}$. Associated with this is the following transition operator L which acts on probability measures ρ_n on configuration space:

$$\rho_n(d\underline{S}_n) = \int \rho_{n-1}(d\underline{S}_{n-1})P(d\underline{S}_n|\underline{S}_{n-1}), \tag{3.1}$$

where $P(d\underline{S}_n|\underline{S}_{n-1})$ is the conditional probability of the configuration $\underline{S}_n$ given that the previous one was $\underline{S}_{n-1}$. There is a lot of interest in the limiting behaviour of ρ_n as $n \to \infty$. However, this concerns the large-scale behaviour of the system and, as we will see, we will be considering how to extract information from the intermediate scales as well. In our case the latter information will be more interesting.

Note that for some finite systems the resulting attractor is trivial and consists of an absorbing state $\underline{0}$. However, the expected time for absorbtion is often very large (typically $\mathcal{O}(e^{cV})$) and the system has approached a 'statistical stationary

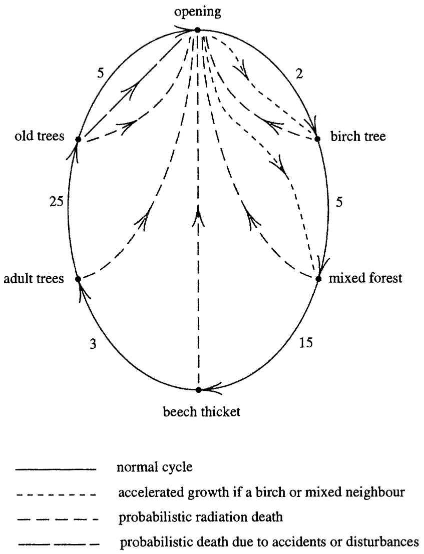

Figure 5. The rules for the beech forest mosaic cycle system. The transition around the normal cycle occur at the rates shown in units of a decade. There is an accelerated transition to birch tree or mixed forest if a neighbour is of this type. Exposed trees can die from radiation exposure to East, South or West if it is not protected by a neighbour. The probabilities for these transitions are p_{E}, p_{S} and p_{W}. Old trees can also die from accidents or disturbances. This occurs with probability p_D.

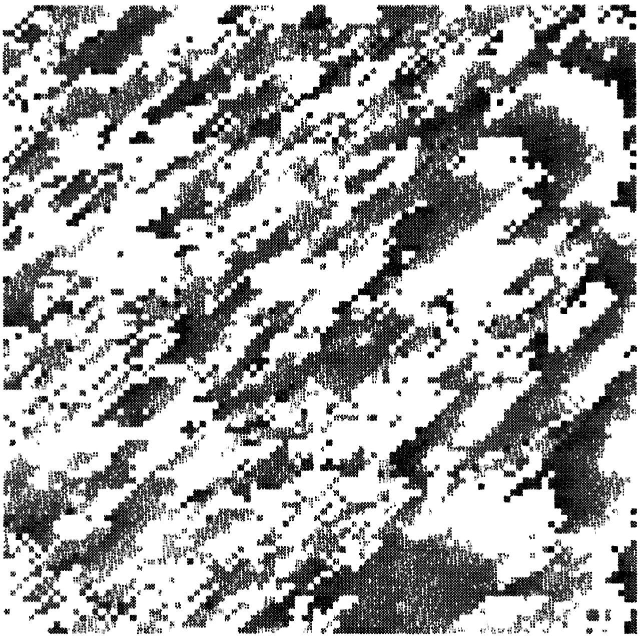

Figure 6. A typical spatial configuration of the beech forest cycle system. The lattice size is 150×150. The colour-coding is as follows: white, opening; lightest grey, birch; light grey, mixed forest; dark greys, beech (with darker shades representing older trees).

state' long before absorbtion destroys it. If this is the case, then one should modify the above approach to be conditioned on the fact that the absorbing state is not reached. In the following discussion we ignore these complications.

The first point to note is that both the above models appear to have attractors onto which they settle once transients have died away. By an *attractor* I mean a subset A of configuration space with the following properties:

Attractiveness: With probability one, as $t \to \infty, S_t \to A$. For finite systems this means that $S_t \in A$ for t large.

Invariance: Once the system is on the attractor it almost surely doesn't leave it, i.e. if $S_t \in A$ then $S_{t'} \in A$, for all $t' > t$.

Ergodicity: If i and j are two states in A then for some $n \geqslant 1$ there is a positive probability of state changing from i to j in n steps.

Moreover, we expect that these attractors are small in the sense that the fraction of states ρ which are in them is small. Analytical arguments and simulation leads us to believe that $\rho \leqslant \exp -cL^2$ for some constant $c > 0$. This observation is related to the fact that relatively small subpatterns of the state have interactions that are exponentially small in their mutual separation in space.

(*c*) *Characterizing the spatial structure associated with the attractor*

An important tool for characterizing the patterns in such systems is given by the *pattern measures*. These describe the spatial structure statistically. They determine the probabilities $P(S_{x_1} = i_1, \ldots, S_{x_m} = i_m)$ of patterns when the state is $\underline{S} = (S_x)$.

A remarkable observation is that for this system and for the states on the attractor, on intermediate length scales, these pattern measures vary within some low-dimensional set. Thus suggests that in principle it is possible to achieve a large amount of data-compression by using this low-dimensional parametrization. After discussing spatial scales we return to describe a remarkably effective data-compression technique which depends upon the near-determinism of the system at intermediate length scales.

We now use these ideas to address several questions. In particular, I want to consider how to (*a*) characterize spatial structure, (*b*) quantify the dynamics, (*c*) deal with the immense amounts of data in the states of these models, (*d*) identify appropriate spatial and temporal scales, (*e*) maximize the information gained from this data and (*f*) use these ideas to detect change in ecosystems. To facilitate this, I will describe a correspondence between the set of pattern measures in the attractor and a set of low-dimensional vectors.

A crucial idea of our analysis is to look for spatial scales where the ratio of 'deterministic' information to stochastic fluctuations is maximized. Another, slightly different, way of saying this is that we search for a length scale which maximizes non-trivial determinism.

(*d*) *Window time-series*

To understand this we consider the time series $x(t) = x_V(t)$ obtained by counting the total number of one of the species (say the resource) inside a fixed window of size $V = \ell \times \ell$. If the window is too small then the time-series is dominated by stochastic effects. If it is too large the interesting effects are averaged out and all we observe is small stochastic fluctuations about a constant mean value.

However, in each of our systems there is a clearly defined intermediate length scale ℓ_{S} on which to observe the dynamics which gives us the maximum amount of information about the system and its dynamics relative to the amount of data and work necessary to describe it. This scale is an inherent characteristic of the ecosystem and is also the appropriate scale of measurement. Roughly speaking it is characterized by the following properties: (i) non-overlapping ℓ_{S}-windows are nearly independent, and (ii) the dynamics of any two points in an ℓ_{S}-window are significantly correlated. This raises the question of whether there is a systematic method for finding this scale. We discuss one which uses the time-series.

Consider an V-window W_V where $\ell = \sqrt{V}$ is large compared to any correlation length. Divide this into $m = V/V_{\mathrm{S}}$ V_{S}-windows. Then the time-series for W_V is the sum of the time series for the ℓ_{S}-windows. Let $\mathrm{Var}(V)$ denote the variance of the time-series in a ℓ-window. Then (Rand & Wilson 1994*a*) we expect that if V_{S} is large enough

$$\mathrm{Var}(V)/V = \mathrm{Var}(V_{\mathrm{S}})/V_{\mathrm{S}} + C_0 + C_1 V, \tag{3.2}$$

where $C_0 + VC_1$ is a small error term due to the correlations between windows due to the fact that the time-series are finite and are all acting out dynamics on the same attractor. As the length T of the time series is increased $C_1 \to 0$. If $\mathrm{Var}(V)/V$ is plotted for our resource–predator–prey model then one clearly sees the crossover from small-scale behaviour to the scaling behaviour given by equation (3.2). This is shown in Rand & Wilson (1994*a*). It occurs around $V = 10\,000$. Therefore, we take $\ell_{\mathrm{S}} = 100$.

(*e*) *Determinism and dimension*

Let $x(t)$ be the time-series from a V_{S}-window. If this is plotted it appears smooth. Therefore, it is natural to ask whether the population dynamics are deterministic. By this I mean that there is some time-independent functional relationship of the form

$$x(t) = f(x(t - d\tau), x(t - (d-1)\tau), \ldots, x(t - \tau)) + \xi(t-1), \tag{3.3}$$

where $\xi(t)$ represents a very small stochastic fluctuation whose magnitude is so small that $\xi(t) \ll x(t)$ and is below the scale at which f is linear. This last condition is very important because when it holds there are practical techniques to detect determinism. In stable equilibrium, periodic or quasi-periodic systems the noise will be stabilized by the local linear contraction and in chaotic systems the Lyapunov exponents can be probed. The techniques of Wilson & Rand (1993) provide a tool for checking for this separation of scales, i.e. that the stochastic scale is smaller than the nonlinearity scale.

For our models we verify (3.3) by using singular value decomposition (SVD) techniques (Bertero & Pike 1982) and direct inspection of the data. For the former, it would be natural to use a version of this that is local in phase space, but it turns out that for this example it suffices to use global techniques.

Firstly, form the time-delayed vectors

$$\underline{x}(t) = (x(t - d\tau), x(t - (d-1)\tau), \ldots, x(t - \tau)).$$

The first piece of evidence comes from the low dimension of the resulting vector time-series. Using SVD techniques we search for an orthogonal basis of $\boldsymbol{R}^d$ with the following property: Let $e_1, \ldots, e_d$ be any orthogonal basis $\underline{e}$ of $\boldsymbol{R}^d$ and consider the 'error':

$$e_k(\underline{x}, T) = T^{-1} \int_0^T ||\underline{x}(t) - \underline{y}_k(t)||^2 \, \mathrm{d}t$$

of the projection $\underline{y}_k(t) = \sum_{i=1}^{k} \langle \underline{x}(t), e_i \rangle e_i$ onto the subspace spanned by $e_1, \ldots, e_k$. Define

$$\sigma_i(\underline{e}) = T^{-1} \int_0^T \langle \underline{x}(t), e_i \rangle^2 \, \mathrm{d}t.$$

Then $e_k(\underline{x}, T) = \sum_{i \geqslant k} \sigma_i(\underline{e})$. We seek a basis $\underline{e}$ that minimizes the error $\sum_{i \geqslant k} \sigma_i(\underline{e})$ for all k. If the dynamics of $\underline{x}$ is ergodic then we can also expect that the basis found in this way will be largely independent of the vector time-series $\underline{x}(t)$. This basis can be found using the SVD techniques described in Rand & Wilson (1994*a*). The important point is that all but 6% of the variation is in the projection $\underline{x}^{\mathrm{proj}} = \underline{y}_4$ onto $e_1, \ldots, e_4$ (i.e. $\sum_{i=1}^{4} \sigma_i(\underline{e}) / \sum_{i=1}^{\infty} \sigma_i(\underline{e}) \geqslant 0.94$). Thus, even globally in phase space, our system is largely four-dimensional and we can project the time-series onto the first four eigenvectors to reconstruct the time-series minus most of the noise. This means that virtually all the dynamics in the original signal are occurring in a four-dimensional embedded space. Such a result is a strong indicator of determinism. It is also surprising considering the high-dimensionality of the original spatial system.

We can now perform an extra direct test of determinism. Choosing some state at time t, $\underline{x}(t)$, we find a previous state, $\underline{x}(t - t')$, very close to our original state. We check that, as in a deterministic system, the evolution of these two states will be very similar. We can also perform this test on the projections $\underline{x}^{\mathrm{proj}}(t)$ of these vectors onto $e_1, \ldots e_4$.

In our case the deterministic part of the population dynamics are chaotic. This means that nearby states diverge from each other exponentially fast at a rate determined by the largest Lyapunov exponent. We check that this is the case (Rand & Wilson 1994*a*).

The fact that the time-series are chaotic is of some general interest because there has long been a controversy about whether ot not cellular automata could be chaotic. Here is an example of an AE which is chaotic on time-series in V_{S}-windows and which we therefore expect has a Lyapunov density in the sense given above. Thus I would like to suggest the following definition of space-time chaos for PCAs and AEs.

Definition. A PCA or AE is *space-time chaotic* if it has an attractor satisfying the properties of § 3 *b* and an invariant stationary measure ρ (where $\rho_n \to \rho$ as $n \to \infty$ whenever ρ_n is as in equation (3.1)) and for ρ-typical realizations (i) there is a volume V_{S} such that the V_{S}-window time-series are deterministic in the sense of equation (3.3) with the appropriate separation of stochastic and nonlinear scales and (ii) there are positive Lyapunov characteristic exponents associated with the V_{S}-window and the values of these exponents have a dependence upon the realizations of the dynamics in far-away windows which is exponentially weak in their separation distance.

(*f*) *Application 1. Detecting structural change in ecosystems*

I outline a technique to detect long-term structural change or drift in an ecosystem (Rand & Wilson 1994*a*). This is an important problem in the management of ecosystems because one wants to detect degradation of the ecosystem before it's too late. The point is to be able to distinguish between structural change, by which we mean change in the parameters governing the dynamics, and the natural dynamical variation of the ecosystem. The detection of change is also important in the analysis of ecological data because nearly all data analysis techniques assume stationarity in the time series being analysed. Our method can detect drift of the order of one part in a thousand per period (i.e. about 10^{-6}–10^{-5} per iteration).

Two different problems are of interest. In the first, we are given a continuous time series from an ecology and wish to detect change occurring within it. In the second we have two different time-series and we wish to identify if there is a significant difference between the two. We only consider the second here. For the first see Rand & Wilson (1994*a*).

The idea for both problems is to combine our data reduction techniques described above with a technique introduced in Eckmann *et al.* (1987) for detecting non-stationarity in data-sets. This uses *recurrence plots.* To address the second problem, we count the recurrences within one of the time series and compare this with cross-recurrences that occur between the two. We expect the latter to be fewer and therefore check for a significant difference between the two.

Given the projection $\underline{x}^{\mathrm{proj}}(t) = \underline{y}_4(t)$ introduced above of the time-delayed vectors $\underline{x}(t)$ we look for pairs t, t' with such that $\| \underline{x}^{\mathrm{proj}}(t) - \underline{x}^{\mathrm{proj}}(t') \| < \varepsilon$. We calculate the fraction $N_{\varepsilon,\mathrm{within}}(s)$ of such pairs t, t' with $|t' - t| = s$ and where $\underline{x}^{\mathrm{proj}}(t)$ and $\underline{x}^{\mathrm{proj}}(t')$ are taken from just within the same time-series. For ε small these correspond to recurrences in the dynamics. We then compare this with the fraction $N_{\varepsilon,\mathrm{cross}}(s)$ of such pairs but where $\underline{x}^{\mathrm{proj}}(t)$ and $\underline{x}^{\mathrm{proj}}(t')$ are taken from different time-series.

For example if we change the parameter g that determines the rate at which empty sites are colonised by the resource from 0.4 to 0.6, an inspection of the phase space indicates that the attractor has only moved by a very small amount. Moreover, inspection of the spatial patterns by eye reveals no obvious changes in the spatio-temporal patterns. Nevertheless, there is a significant difference between the internal recurrence plots and the cross-recurrence plot between the differing time-series. These plots are shown in Rand *et al.* (1994*a*).

(*g*) *Application 2. Reconstructing invisible species*

In principle this approach to representing patterns can also be used to reconstruct invisible species from the visible ones. I have in mind here a situation where say the resource in our resource–predator–prey model could be monitored but one could not see the predators and prey.

The determinism implies that our four-dimensional vector $\underline{x}^{\mathrm{proj}}(t)$ determines the pattern measure not only of the visible species but also of the other species. One way to check this is to do the SVD analysis on time-delayed vectors of the form,

$$(x(t-d\tau),\ldots,x(t-\tau),y(t-d\tau),\ldots,y(t-\tau)),$$

where x is the visible species as discussed above and y is the invisible species. If this has similar σ_k as for the single species then this suggests that the second species is slaved to the first. Thus if we know the first then in principle we can predict the second. This slaving appears to be present in the forest model and should be present in the resource–predator–prey system if the window size is increased so that the prey and predator numbers are not too small. Note, however, that even if the species are slaved together, it will require a lot of work to approximate the actual slaving function.

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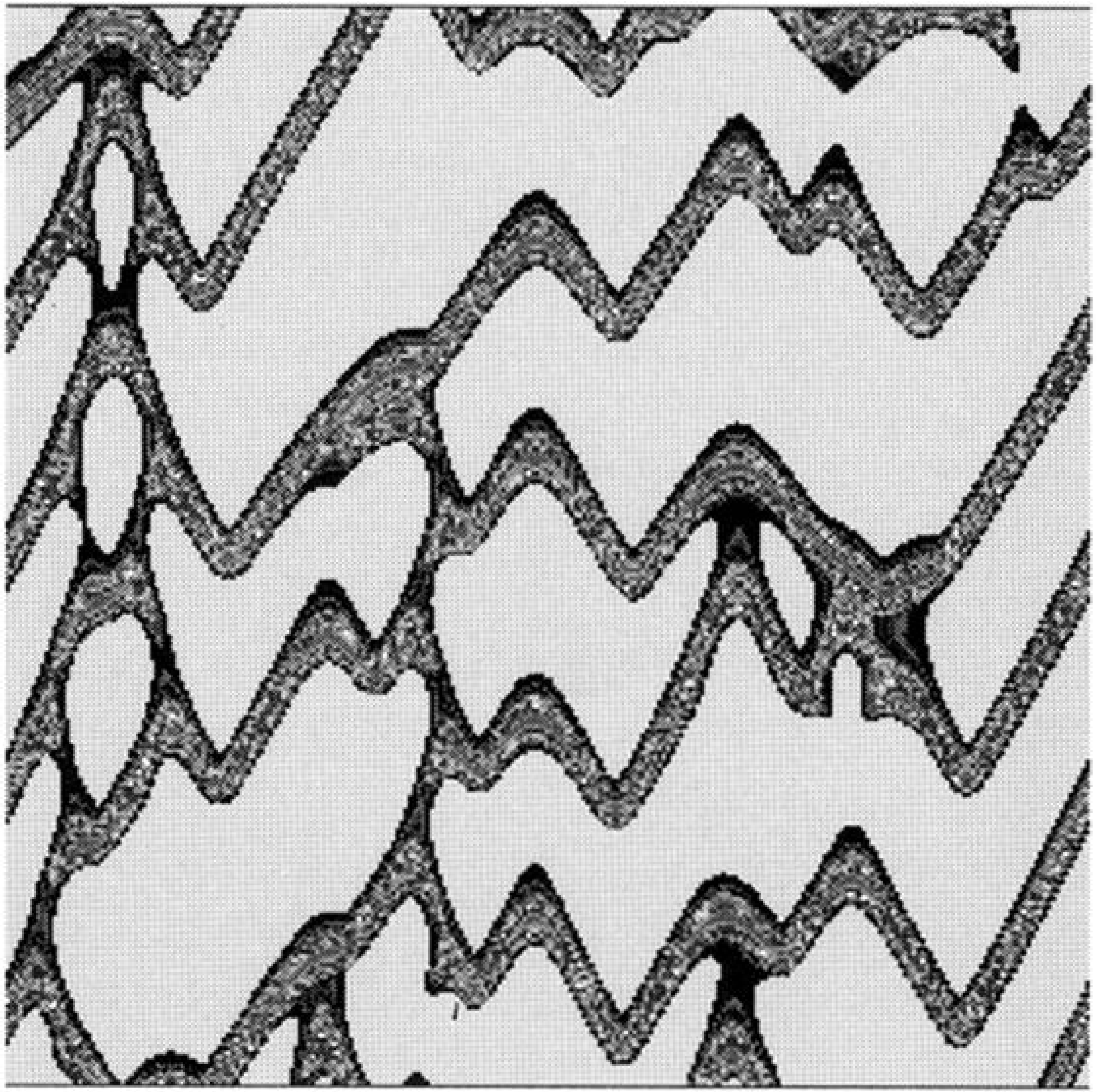
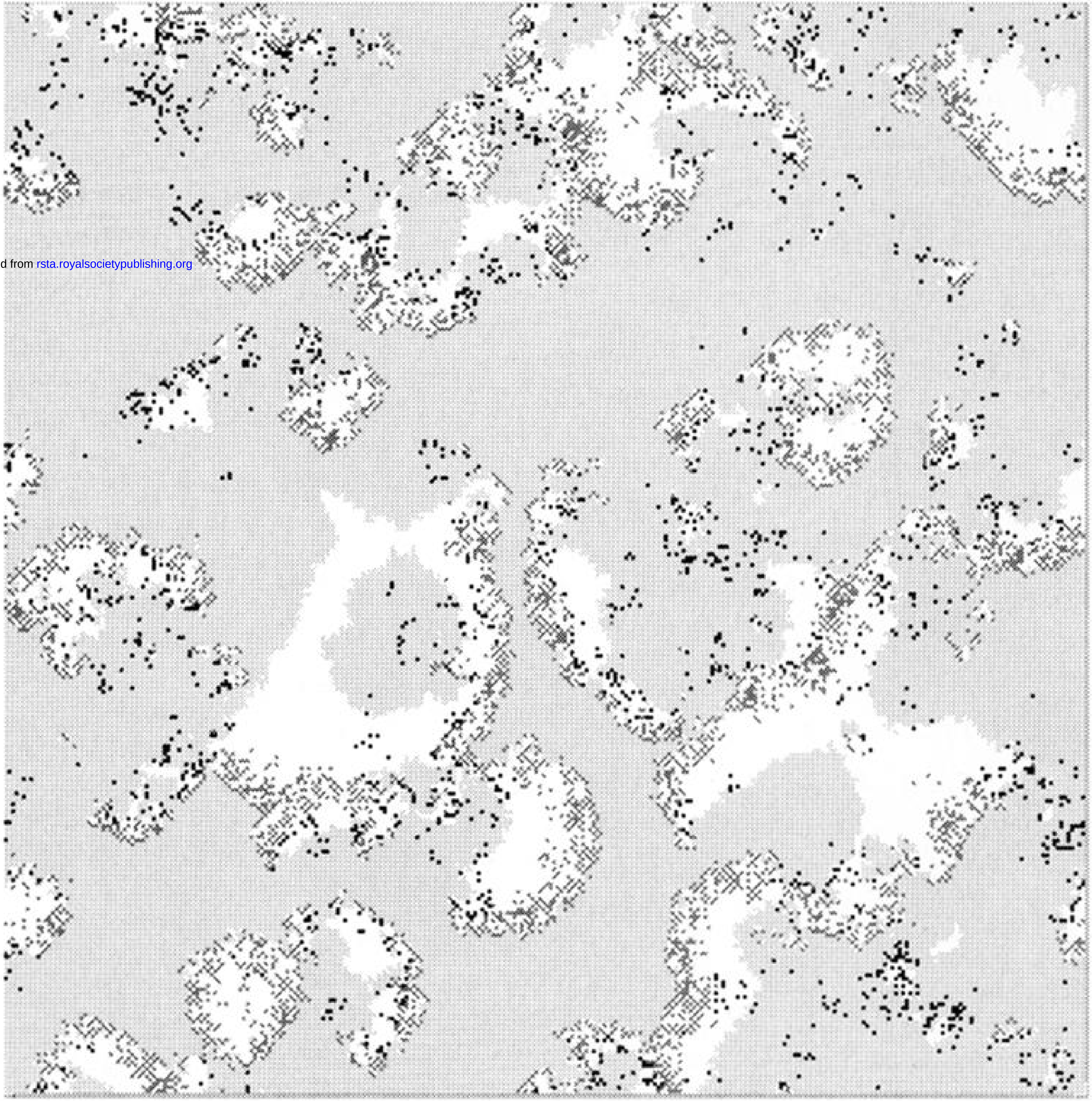
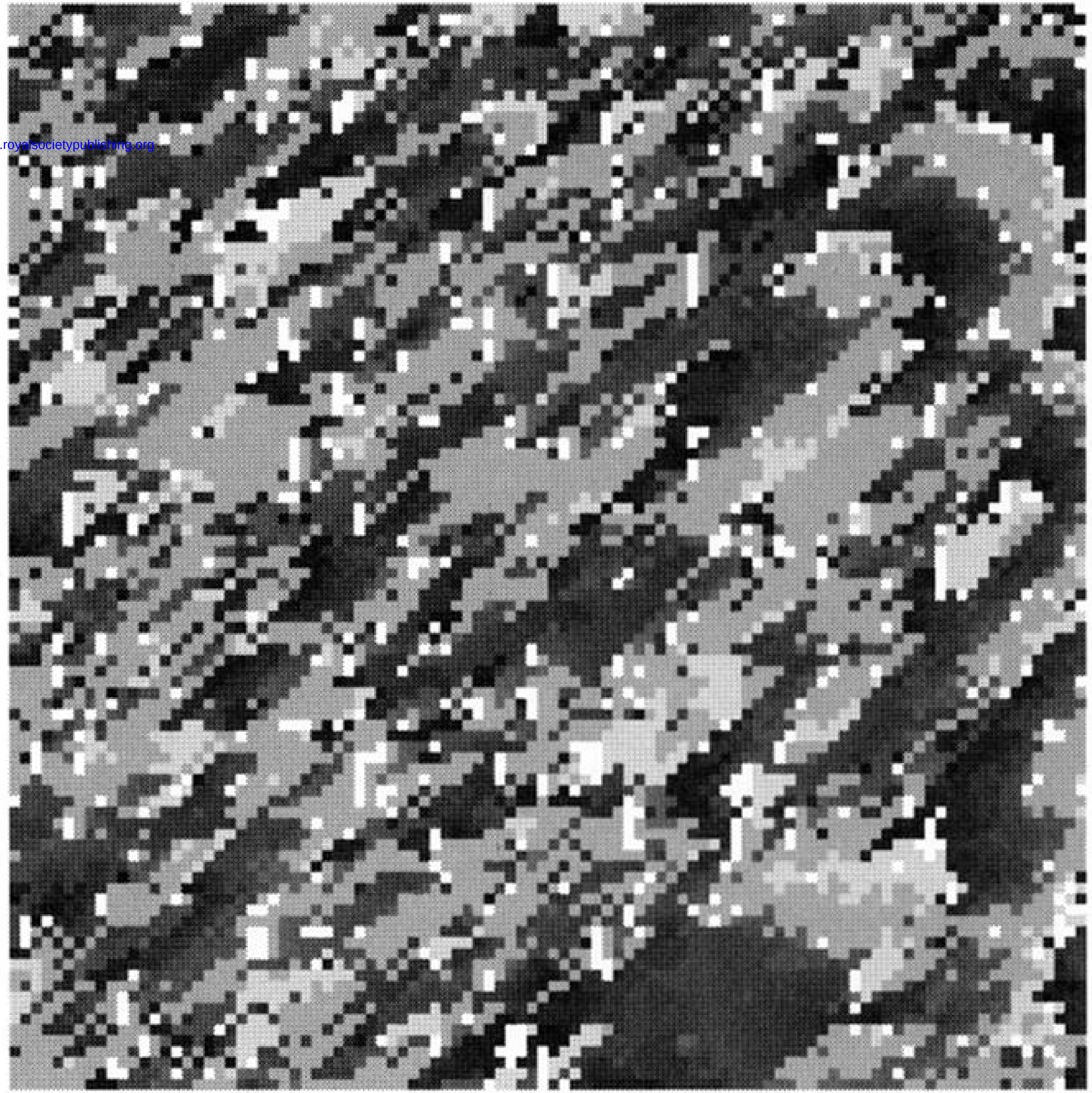


igure 1. A typical space-time plot of the prey in the one-dimensional resource–predator–prey system. It shows how the bursts of prey nucleate and convect across the system.



igure 4. A typical spatial configuration of the resource–predator–prey AE for the given parameter values. The lattice size shown is 300×300. The colour-coding is as follows: lightest grey, mpty; medium grey, prey; black, predator.



igure 6. A typical spatial configuration of the beech forest cycle system. The lattice size is 50 × 150. The colour-coding is as follows: white, opening; lightest grey, birch; light grey, mixed orest; dark greys, beech (with darker shades representing older trees).