Reconstructing the dynamics of unobserved variables in spatially extended systems

H. B. WILSON¹ AND D. A. RAND²

¹*Department of Biology, Imperial College of Science, Technology and Medicine, Silwood Park, Ascot, Berkshire SL5 7PX, UK (h.b.wilson@ic.ac.uk)*

²*Nonlinear Systems Laboratory, Mathematics Institute, University of Warwick, Coventry CV4 7AL, UK*

SUMMARY

Attractor reconstruction using embedding techniques is a widely used tool when analysing data from real systems. It allows reconstruction of the system dynamics from only one observable and is thus extremely powerful. We show here that this reconstruction is also possible from spatially coupled systems. We use a common host–parasitoid model as an example as ecological systems are virtually always spatially extended. Additionally, data from ecological systems has often only one observable, e.g. population density, from a potentially much higher-dimensional system. Singular value decomposition is used to show the existence of a functional relationship mapping the time delayed coordinates of one variable to the full spatially coupled system. We investigate the effects of noise and indicate two important spatial scales. Finally, we illustrate that a reconstruction can be obtained from a system that is only partially sampled.

1. INTRODUCTION

Takens (1981) demonstrated that it is possible to reconstruct a multi-dimensional state space from a scalar time series. This reconstructed state space is qualitatively equivalent to the original one in the sense that the original and the reconstructed attractors have the same differentiable structures. In particular, important properties such as the topology and dimension of the original attractor are preserved. Hence it is possible to analyse qualitative system properties even when state space variables are missing. In ecological systems populations are nearly always embedded in higher-dimensional systems, and so Takens's theorem is potentially of great use. However, there are two properties of ecological systems which are ubiquitous but are not considered by the theorem. These are the effects of noise and space.

Takens's theorem is valid for the limit of noise free data. By noise we mean either: (i) small random fluctuations in state space variables that may potentially be propagated through the system, *dynamical noise*; or (ii) errors in determining the position of state space variables, *measurement noise*. The problems caused by noise have been addressed in some detail by various authors (e.g. Casdagli *et al.* 1991). They show that reconstruction becomes impossible due to noise when the attractor dimension and Lyapunov exponents are large. Hence, at least for small amounts of noise, we are able to use reconstruction methodology only for low-dimensional systems.

The problems posed by space have been less well addressed. Spatial systems tend to be complex, analytically intractable, and are potentially extremely

high-dimensional systems. This means they are often very difficult to analyse. However, ecological systems are nearly always spatially extended and space has important consequences for dynamics and persistence (e.g. Gilpin & Hanski 1991; Comins *et al.* 1992; Rand & Wilson 1995). Additionally, many authors have pointed out the capability for non-trivial, emergent dynamics in spatially extended systems where the relationship between the local biological mechanisms and the resultant dynamics is often extremely complex (e.g. Wolfram 1984). Thus, the presence of coupling, or migration, between populations is potentially a non-trivial problem.

We wish to show here that reconstruction of the dynamics of a spatially extended biological system is possible even when only one species can be observed within it. The original motivation behind this work was reconstructing biological dynamics from satellite images. Satellite images contain a great deal of spatial information and are able to pick out certain biological habitats, such as forests, whereas they cannot distinguish other features, such as individual animals. Given a close dynamical relationship between an unobserved variable (such as the population size of an animal) and an observed feature (its habitat) is it possible to make predictions about the unobserved species? The methodology outlined could also apply to other systems with spatial information. For example, epidemiological systems where the number of infectives from different but coupled populations are known (e.g. the number of people with measles in major cities in England), or spatial host–parasitoid systems.

In the next section we introduce the theory of embedding and in §3 we introduce the spatial model. We combine the two in §4 and investigate the effects of noise and under-sampling.

2. EMBEDDING

We consider the case where we have only an observed one-dimensional time series $\{x_i\}_{i=1}^{N'}$ where N' is the number of points in the time series. In population dynamics studies this observable is typically the population density of one species. Often the time series will come from a much higher-dimensional system, e.g. one involving other species. We attempt to analyse and understand the system by making use of embedding theorems (Whitney 1936) as first applied to time series by Packard *et al.* (1980) and put on a firm mathematical basis by Takens (1981). The basic idea supporting this methodology is that the past and future of a time series contain information about the present unobserved state variables. This information can be used in the form of a *delay vector*. In fact there are many choices of possible coordinate system, e.g. successive time derivatives, but the easiest and most widely used are delay coordinates. Takens studied the delay reconstruction map Φ ,

$$\Phi(\mathbf{y}) = (v(\mathbf{y}), v(f^1(\mathbf{y})), \dots, v(f^{2m}(\mathbf{y}))),$$

where $v(\mathbf{y})$ corresponds to a value of a measurement made on the system in state $\mathbf{y}$. He proved that generically Φ is an embedding when $m \geq 2d + 1$, where d is the dimension of the original attractor. An embedding is a smooth, one-to-one coordinate transformation with a smooth inverse (i.e. Φ is a *diffeomorphism*). Hence the reconstructed attractor is topologically equivalent to the attractor for the whole system and thus preserves important geometrical invariants such as the dimension of the attractor and the Liapunov exponents of a trajectory (see Eckmann & Ruelle 1985). This means that, given time-delayed coordinates of one observable, it is possible to reconstruct the dynamics for the full system.

For the observed scalar time series, $x_i = v(f^t(\mathbf{y}))$, the function v corresponds to measuring one state variable of the system at a particular time, $t = \alpha i$ (where α is the sampling time between successive measurements). Hence the delay coordinates are

$$\mathbf{x}_i = (x_i, x_{i-\tau}, \dots, x_{i-(E-1)\tau}), \quad (1)$$

where E is known as the *embedding dimension* and τ the *delay time*, which is conventionally taken to be an integer here. Given appropriate choices of E and τ , the vector $\mathbf{x}_i$ is a faithful reconstruction of the full state of the system at time i . The theorem does not tell us what the appropriate choices are for E and τ . In addition the theorem is proved for a system without noise.

3. COUPLED MAP LATTICES

Various models have been used to approximate and simulate spatial systems. These include reaction–

diffusion equations, coupled map lattices and cellular automata. In this paper coupled map lattices are used as a convenient model although the technique could also be applied to the other models.

A coupled map lattice is a dynamical system with discrete space and time. Space is represented by an array, or lattice, of sites. This array is usually in one or two dimensions but any number are theoretically possible. In this paper we use a two-dimensional $L = l \times l$ lattice. At each site a map represents the dynamics. Sites are then coupled together by diffusion (or, analogously, dispersal) between neighbouring sites. The neighbourhood, $\mathcal{N}(x)$, of a site x is predetermined but can be of various different types. We choose the eight immediately adjacent sites: $\mathcal{N}(x) = \{x + z : |z_1| \leq 1, |z_2| \leq 1, z \in \mathbf{Z}^2, z \neq (0, 0)\}$.

Boundary conditions describe what happens at the edges of the array. These can either be reflective, absorbing or cyclic. Reflective boundaries mean that dispersing individuals are prevented from crossing the boundary and so remain in the edge site. Absorbing boundaries mean dispersing individuals are lost to the system. Cyclic conditions are when opposite edges are effectively joined and individuals leave one edge and come on at the opposite. This means that all sites are dynamically equivalent and so cyclic conditions have been chosen throughout the simulations that follow. We note that the particular boundary conditions chosen do not qualitatively change any of our results.

At each site, x , in the lattice we have a discrete generation map which describes the dynamics at that site. Our methodology is appropriate for a large class of systems but as an illustrative example we have chosen a commonly used host–parasitoid model,

$$\left. \begin{aligned} N_{x,t+1} &= \lambda N_{x,t} e^{-a_P P_{x,t}}, \\ P_{x,t+1} &= c H_{x,t} [1 - e^{-a_P P_{x,t}}], \end{aligned} \right\} \quad (2)$$

where $N_{x,t}$ and $P_{x,t}$ are, respectively, the population size of hosts and parasitoids in site x at time t . The quantity λ is the host reproductive rate, a_P is the per capita parasitoid attack rate and c is the conversion efficiency of parasitized hosts into adult female parasitoids in the next generation. By scaling the population densities, the parameters a_P and c can be set to one.

After the local dynamics at each site there is a dispersal phase. A fraction μ_N of hosts and μ_P of parasitoids disperse equally to the eight neighbouring sites leaving a fraction $(1 - \mu_N)$ and $(1 - \mu_P)$ in each site. Hence equation (2) becomes:

$$\left. \begin{aligned} N_{x,t+1} &= (1 - \mu_H) \lambda N_{x,t} e^{-a_P P_{x,t}} + \mu_N \bar{N}_{x,t}, \\ P_{x,t+1} &= (1 - \mu_P) c H_{x,t} [1 - e^{-a_P P_{x,t}}] + \mu_P \bar{P}_{x,t}, \end{aligned} \right\} \quad (3)$$

where $\bar{N}_{x,t}$ and $\bar{P}_{x,t}$ are the average number of hosts and parasitoids in the neighbourhood of site x after the local dynamics have occurred. Equation (3) is used in many spatially extended host–parasitoid models (e.g. Comins *et al.* (1992) and very similar to Sole *et al.* (1992)).

After initial transients have died away, the dynamics given by equation (3) settle onto an attractor Λ . Depending on the dispersal parameters μ_H and μ_P (and given reasonable lattice sizes, $l \geq 20$) this attractor can have very different spatial patterns. Either a 'crystal lattice' structure, spirals or a spatially chaotic pattern occurs (Hassell *et al.* 1991).

4. EMBEDDING IN SPACE

Let $\mathbf{S}_H(t)$ and $\mathbf{S}_P(t)$ be vectors representing the population densities of the host and parasitoid at each site in the lattice. Thus they are L ($= l \times l$)-dimensional vectors. We wish to explore whether we can reconstruct the dynamics of the parasitoid given the dynamics of the host, or vice versa. Let $\underline{\mathbf{S}}_H(t)$ be the time-delayed vector

$$(\mathbf{S}_H(t), \mathbf{S}_H(t - \tau), \dots, \mathbf{S}_H(t - (E - 1)\tau)).$$

If this is an embedding there exists a one-to-one function F which maps the time-delayed vector to the true state of the system,

$$(\mathbf{S}_P(t), \mathbf{S}_H(t)) = F(\underline{\mathbf{S}}_H(t)). \quad (4)$$

Locally, the function F is approximately linear; i.e. higher order terms are negligible. Thus, linear analysis techniques can be used to test whether $(\mathbf{S}_P(t), \mathbf{S}_H(t))$ is linearly dependent on $\underline{\mathbf{S}}_H(t)$. Here we use a technique called singular value decomposition (SVD). This is used to test whether a matrix composed of vectors $(\mathbf{S}_P(t), \mathbf{S}_H(t), \underline{\mathbf{S}}_H(t))$ has rank equal to the dimension of $\underline{\mathbf{S}}_H(t)$. If this is true it indicates the local linear dependence of $(\mathbf{S}_P(t), \mathbf{S}_H(t))$ on $\underline{\mathbf{S}}_H(t)$ and the existence of a function F .

We choose a vector $\underline{\mathbf{S}}_H(t)$ which is in our attractor Λ . Let $\mathbf{z}$ be the vector $(\mathbf{S}_P(t), \mathbf{S}_H(t), \underline{\mathbf{S}}_H(t))$. We construct an ϵ -neighbourhood matrix, $\mathbf{B}_\epsilon(\mathbf{z})$, whose rows consist of vectors $\{(\mathbf{z}_j - \mathbf{z}) : |\mathbf{z}_j - \mathbf{z}| < \epsilon\}$, where $\mathbf{z}_j$ are vectors within a ball of radius ϵ centred at $\mathbf{z}$. $\mathbf{B}_\epsilon(\mathbf{z})$ is an $N_r \times (L + L + (L * E))$ matrix where $N_r \geq (L + L + (L * E))$ is the number of rows.

If a linear function exists then the dynamics will be occurring in an $(L \times E)$ -dimensional space, the dimension of the embedded vector. Hence the rank of $\mathbf{B}_\epsilon(\mathbf{z})$, as indicated by the number of non-zero singular values, will equal $L \times E$. In practice we do not expect singular values to be precisely zero as there is always some noise in the system due to numerical effects. The singular values reflect this noise level.

As discussed by previous authors (Broomhead *et al.* 1987, 1991; Read 1992), for small enough ϵ the rows of $\mathbf{B}_\epsilon(\mathbf{z})$ are approximately the tangent vectors to Λ at $\mathbf{z}$. Since the rank of $\mathbf{B}_\epsilon(\mathbf{z})$ is the number of its linearly independent columns, the dimension of the tangent space is given by the rank of $\mathbf{B}_\epsilon(\mathbf{z})$. The singular values corresponding to this tangent space measure the root mean square radius of the neighbourhood projection onto this tangent space. Thus they scale linearly with ϵ until saturation (when ϵ is of the order of the attractor width) or until the effects of curvature of the attractor become apparent (when we are no longer working in a linear regime).

Figure 1. The singular spectrum from the spatially coupled host-parasite model (equation (3)). The parameters used in the model are $\lambda = 2$, $u_N = 0.2$, $u_P = 0.6$ and the lattice size is 20×20 . We discard the first 1000 iterates to remove transient effects so as to ensure we are on the attractor Λ . These parameters give a chaotic spatial pattern and are used in all the simulations that follow. The matrix is formed using $E = 2$, $\tau = 1$, $N_r = 1200$ and the radius used is $\epsilon = 0.01$.

The other singular values measure how the rows of $\mathbf{B}_\epsilon(\mathbf{z})$ deviate from representing the tangent space due to the curvature of the attractor at $\mathbf{z}$. These singular values will scale as ϵ^2 , or faster, until they also saturate.

5. RESULTS

Equation (3) is iterated to remove any effects of initial conditions (transient effects) so that we are on the attractor Λ . We then take a vector $\mathbf{S}_H(t)$ and form the time-delayed vector $\underline{\mathbf{S}}_H(t)$. In this case the time delay, τ , is one iteration and the embedding dimension, E , is two. Choosing appropriate values of E and τ can be difficult. Here the underlying biology (discrete generations and a two-dimensional system) motivates our choice. In practice, one can often use a range of values and check the robustness of the result (e.g. see Sole & Bascompte 1995). The vector $\underline{\mathbf{S}}_H(t) = ((\mathbf{S}_H(t - 1), \mathbf{S}_H(t)))$ already includes the vector $\mathbf{S}_H(t)$. Therefore, we need only investigate whether $\mathbf{S}_P(t)$ is linearly dependent on $\underline{\mathbf{S}}_H(t)$ as the dependence of $\mathbf{S}_H(t)$ on $\underline{\mathbf{S}}_H(t)$ is trivial (it is exactly given). The first row in our matrix $\mathbf{B}_\epsilon(\mathbf{z})$ is $\mathbf{z} = (\mathbf{S}_H(t), \mathbf{S}_P(t), \underline{\mathbf{S}}_H(t))$. Using the equations of motion (equation (3)) arbitrarily close vectors can be generated, $\mathbf{z}_j$ (instead of waiting until an orbit comes close to our original vector $\mathbf{S}_H(t)$). To do this the lattice is perturbed a time $E\tau\alpha$ in the past, by a very small amount, proportional to ϵ . This perturbed vector is then iterated E times. A nearby vector has now been generated with which we can form the next row, $\mathbf{z}_j$, in our matrix. This is repeated N_r times in order to form an $N_r \times 3L$ matrix. When the SVD procedure is performed, $3L$ singular values are obtained of which $2L$ are expected to be non-zero and the rest zero. Figure 1 shows the singular spectrum. The value of each eigenvalue in this

Figure 2. The singular spectrum in the presence of noise. The parameters are as for figure 1. Note that the magnitude of the singular value floor reflects the noise level in the system ($\ln(e_i) \approx \ln(a)$ for singular values within the noise floor).

spectrum is the projection of the dynamics onto the eigenvector associated with that eigenvalue. Large eigenvalues (relative to the whole spectrum) therefore indicate the dimensions (given by the associated eigenvectors) which dominate the dynamics. In this case, as predicted, there are $2L$ significant (i.e. non-zero) singular values. The other singular values are of the order 10^{-16} which is effectively zero. The absolute value of these singular values reflect the (numerical) noise within the system. This is outlined for the global case (rather than the local situation, as here) by Broomhead & King (1986; see also Wilson & Rand 1993).

6. NOISE

The above results are for a deterministic system. Clearly real systems will all include some form of noise. To investigate the effects of noise, uniformly distributed noise is added to equation (3). This is done by an additive noise process,

$$\left. \begin{aligned} N_{x,t+1} &= (1 - \mu_H) \lambda N_{x,t} e^{-a_P P_{x,t}} \\ &\quad + \mu_N \bar{N}_{x,t} + \xi_1(t), \\ P_{x,t+1} &= (1 - \mu_P) c H_{x,t} [1 - e^{-a_P P_{x,t}}] \\ &\quad + \mu_P \bar{P}_{x,t} + \xi_2(t), \end{aligned} \right\} \quad (5)$$

where $\xi_1(t)$ and $\xi_2(t)$ are random numbers taken from a uniform distribution between 0 and a . In order to test for the existence of the function F we need to operate at a distance scale ϵ (which defines our ball) which is within two boundaries. These define the scale at which nonlinearities enter the system, d_{nonlin} , and the noise scale, d_{noise} . Hence $d_{\text{noise}} < \epsilon < d_{\text{nonlin}}$. This is exactly as outlined in Wilson & Rand (1993). Hence trajectories are generated that are consistent with these boundaries.

In figure 2 the singular spectrum for several noise scales is shown. When the noise is relatively small the last 400 singular values solely reflect noise in the system. The magnitude of this noise floor directly measures the amount of noise within the system. Something qualitatively different occurs when the noise is

large ($a = 0.1$). This is illustrated in figure 3. Figure 3a shows the phase plot for the mean amount of hosts and parasitoids per site for equation (5) with $a = 0.001$.

As discussed above, the scaling of the singular values as a function of the radius ϵ also characterizes the geometry of the local dynamics. This can be investigated by generating nearby vectors, as before, but at different scales, ϵ . In figure 3b we see that between the scales d_{noise} and d_{nonlin} singular values corresponding to the tangent direction scale linearly with ϵ . Shown on the figure is a line of gradient one for comparison. The other singular values, associated with noise, do not scale with ϵ . Indicated are the two scales d_{noise} and d_{nonlin} . The first scale, d_{noise} , comes directly from the noise amplitude and d_{nonlin} is estimated from where the singular values begin scaling at higher orders.

Figure 3c shows a similar phase plot as above except with a noise level of $a = 0.002$. The attractor has qualitatively changed. We now see large amplitude oscillations on a single limit cycle. This indicates the presence of an unstable manifold in the deterministic system, equation (3). In the purely deterministic system, trajectories converge onto the original attractor. However, large amplitude noise pushes the system off this attractor and onto the unstable manifold, which in this case is a limit cycle. This is similar to behaviour in epidemic models that have chaotic repellers (see Rand & Wilson 1991). In figure 3d we show the scaling of the singular values. Indicated are the two scales, d_{noise} and d_{nonlin} . Between these two scales the system is fully determined by knowing only the host or parasitoid densities, $S_H(t)$ or $S_P(t)$, at one time as only one set of eigenvalues scales linearly with ϵ . This reflects the system collapsing onto a lower-dimensional object than with the deterministic system. When noise is added to dynamical systems, the attractor dimension usually increases as noise is state space filling. In this case we get the opposite effect due to the presence of the unstable manifold. This is interesting as the magnitude of noise needed to push the system onto this manifold is not large compared to what is observed in nature. As the noise level is increased the amplitude of the limit cycle decreases until it becomes centred at a point.

We also note two additional points. In figure 3d we see that the noise eigenvalues (plotted are the 900th and 1100th) scale linearly with $\log(\text{radius})$ at scale below d_{noise} . We expect this to be the case because at such scales the data points are distributed uniformly in reconstruction space, i.e. their distribution is described by a smooth measure at this scale. If this is the case, the eigenvalues scale linearly with $\log(\text{radius})$ (as is shown in §3.2 of Broomhead *et al.* 1991). Secondly, the effects of curvature become apparent at a smaller scale in figure 3d than in figure 3b. This reflects that the curvature is greater at the point chosen to perform the local scaling analysis in the second case. The points were randomly chosen and are indicated in figure 3a, c.

Figure 3. (a) Phase space plot of the mean number of hosts and parasitoids per site for equation (3) with noise amplitude, $a = 1.0 \times 10^{-3}$. The parameters for the model are as in figure 1. Plotted are 100 iterations before and after the point used (arrowed) for the local scaling analysis in (b). This point was chosen by randomly choosing an initial starting condition and then iterating equation (5) 1000 times. (b) The scaling of the singular values as a function of the radius ϵ . We plot the two singular values corresponding to the tangent space (the 300th and 600th) and two singular values corresponding to noise (the 900th and 1100th). For each value of ϵ we generate a matrix using $E = 2$, $\tau = 1$ and $N_r = 1200$ centred around the point arrowed in (a). Also shown is a line of gradient one for comparison. (c) As for (a) except the noise level is, $a = 2.0 \times 10^{-3}$. (d) As for (b) except the noise level is, $a = 2.0 \times 10^{-3}$.

7. SAMPLING RATE

It is difficult, often because of practical limitations, to make enough samples in space to fully represent a system. Given that the system is under-sampled, therefore, is it still possible to reconstruct the dynamics of unobserved species?

For the system (system size L) given by equation (3) the dimensionality of the state space is $2L$. Using the host species at every site we form an L -dimensional vector, $\mathbf{S}_H(t)$. As a surrogate for the other L unknown quantities (the number of parasitoids at each site, $\mathbf{S}_P(t)$), the past state of the hosts is used, $\mathbf{S}_H(t-1)$, i.e. the embedding dimension used is two. The vector $(\mathbf{S}_H(t-1), \mathbf{S}_H(t))$ can then be used to represent the system. What happens to the existence of a functional relationship, F , where $\mathbf{S}_P(t) = F(\mathbf{S}_H(t-1), \mathbf{S}_H(t))$, when only a fraction of the sites are sampled? Let $\mathbf{S}_H^f(t)$ be the vector of host densities when we sample a fraction f , $0 < f \leq 1$

of the sites, e.g. when $f = 0.5$ every second site is sampled. The dimension of $\mathbf{S}_H^f(t)$ is thus fL . The dimension of the state space, however, remains $2L$. As before, past states of the sampled vector can be used as surrogates for the missing dimensions. In this case, however, the embedding dimension E , the number of past states needed, will be $2/f$. Thus if $f = 0.5$, the vector

$$(\mathbf{S}_H^f(t-3), \mathbf{S}_H^f(t-2), \mathbf{S}_H^f(t-1), \mathbf{S}_H^f(t))$$

should be an embedding.

This is demonstrated by generating the matrix, $\mathbf{B}_\epsilon(\mathbf{y})$, where $\mathbf{y}$ is the vector

$$(\mathbf{S}_H^f(t-3), \mathbf{S}_H^f(t-2), \mathbf{S}_H^f(t-1), \mathbf{S}_H^f(t)).$$

In figure 4 we show the singular values of $\mathbf{B}_\epsilon(\mathbf{y})$. The rank of the matrix is the same as the matrix with only the sampled embedded vectors. This indicates, as before, that the embedded sampled vector determines the full state of the system. When the sample rate is

Figure 4. The singular spectrum for the sampled system, i.e. the singular values associated with the matrix $\mathbf{B}_\epsilon(\mathbf{y})$. The sampling rate is every other column from the lattice, i.e. $f = 0.5$. The other parameters are $E = 4$, $\tau = 1$, $\epsilon = 1.0 \times 10^{-4}$ and $N_r = 1200$.

decreased further, the non-sampled sites can still be reconstructed if the dimension of the embedded vector is increased, i.e. more past states are used. The more a system is under-sampled the higher the embedding dimension needed, i.e. the less information is known about the present state of the system, then the more information is needed about past states.

8. CONCLUSIONS

Time-delayed vectors are commonly used to study time series of population densities in ecological systems. Takens's theorem is cited as justification for this methodology. However, whether using such time delays is justified when populations are spatially coupled together by dispersal and immigration has not previously been formally studied. This work shows that it is possible to understand (at least for locally low-dimensional systems) the full spatial dynamics of a population by measuring only one variable (in this case the host population). This begins a more formal study into how to optimally reconstruct spatial populations.

REFERENCES

Broomhead, D. S. & King, G. P. 1986 Extracting qualita-

- tive dynamics from experimental data. *Physica D* **20**, 217–236.
- Broomhead, D. S., Jones, R. & King, G. P. 1987 Topological dimension and local coordinates from time series data. *J. Phys. A* **20**, L563–L569.
- Broomhead, D. S., Indik, R., Newell, A. C. & Rand, D. A. 1991 Local adaptive Galerkin bases for large dimensional dynamical systems. *Nonlinearity* **4**, 159–197.
- Casdagli, M., Eubank, S., Farmer, J. D. & Gibson, J. 1991 State space reconstruction in the presence of noise. *Physica D* **51**, 52–98.
- Comins, H. N., Hassell, M. P. & May, R. M. 1992 The spatial dynamics of host–parasitoid systems. *J. Anim. Ecology* **61**, 735–748.
- Eckmann, J.-P. & Ruelle, D. 1985 Ergodic theory of chaos and strange attractors. *Rev. Mod. Phys.* **57**, 617.
- Gilpin, M. & Hanski, I. 1991 *Metapopulation dynamics: empirical and theoretical investigations*. London: Academic.
- Hassell, M. P., Comins, H. N. & May, R. M. 1991 Spatial structure and chaos in insect population dynamics. *Nature, Lond.* **353**, 255–258.
- Packard, N. H., Crutchfield, J. P., Farmer, J. D. & Shaw, R. S. 1980 Geometry from a time series. *Phys. Rev. Lett.* **45**, 712.
- Rand, D. A. & Wilson, H. B. 1991 Chaotic stochasticity: a ubiquitous source of unpredictability in epidemics. *Proc. R. Soc. Lond. B* **246**, 179–184.
- Rand, D. A. & Wilson, H. B. 1995 Using spatio-temporal chaos and intermediate scale determinism to quantify spatially extended ecosystems. *Proc. R. Soc. Lond. B* **259**, 111–117.
- Read, P. L. 1992 Applications of singular systems analysis to ‘Baroclinic chaos’. *Physica D* **58**, 455–468.
- Sole, R. V. & Bascompte, J. 1995 Measuring chaos from spatial information. *J. Theor. Biol.* **175**, 139–147.
- Sole, R. V., Valls, J. & Bascompte, J. 1992 Spiral waves, chaos and multiple attractors in lattice models of interacting populations. *Phys. Lett. A* **166**, 123–128.
- Takens, F. 1981 Detecting strange attractors in turbulence. In *Dynamical systems and turbulence* (ed. D. Rand & L.-S. Young), Springer Lecture notes in Mathematics, pp. 366–381. Berlin: Springer.
- Whitney, H. 1936 Differentiable manifolds. *Ann. Math.* **37**, 645.
- Wilson, H. B. & Rand, D. A. 1993 Detecting chaos in a noisy time series. *Proc. R. Soc. Lond. B* **253**, 239–244.
- Wolfram, S. 1984 Cellular automata as models of complexity. *Nature, Lond.* **311**, 419–424.

Received 6 November 1996; accepted 6 December 1996