

# Synchrony and second-order spatial correlation in host–parasitoid systems

OTTAR N. BJØRNSTAD\* and JORDI BASCOMPTE†

\*Departments of Entomology and Biology, 501 ASI Building, Penn State University, University Park, PA 16802, USA; and †Estación Biológica de Doñana, CSIC. Apdo. 1056, E-41080 Sevilla, Spain

## Summary

1. Recent theoretical studies on population synchrony have focused on the role of dispersal, environmental correlation and density dependence in single species. Trophic interactions have received less attention. We explored how trophic interactions affect spatial synchrony.

2. We considered a host–parasitoid coupled map lattice to understand how the self-organizing spatial patterns generated by such dynamics affect synchrony. In particular, we calculated the spatial correlation functions (SCF) associated with travelling waves, spatial chaos and crystal lattices.

3. Travelling waves were associated with cyclic SCF (called second-order SCF) that differed greatly from those seen in spatial chaos or crystal lattices. Such U-shaped patterns of spatial synchrony, which have not been predicted by single-species models, have been reported recently in real data. Thus, the shape of the SCF can provide a test for trophically generated spatiotemporal dynamics.

4. We also calculated the cross-correlation function between the parasitoid and the host. Relatively high parasitoid mobility resulted in high within-patch synchrony of the dynamics of the two species. However, with relatively high host mobility, the parasitoid dynamics began to lag spatially behind those of the host.

5. We speculated that this spatial lag between the host and parasitoid is the ultimate source of travelling waves, because the spatial cross-correlation in turn affects host dynamics.

6. A new method to estimate the spatial cross-correlation function between two species was developed as an integral part of the study.

*Key-words:* coupled map lattice models, cross-correlation, non-parametric covariance function, reaction–diffusion, spatial dynamics.

*Journal of Animal Ecology* (2001) **70**, 924–933

## Introduction

The way ecological interactions generate population synchrony has received much attention recently in theoretical ecology (reviewed in Bjørnstad, Ims & Lambin 1999). So much so that we can now see the outlines of a general theory for how dispersal, environmental correlation and density dependence mould synchrony in single-species systems. Generically, such theoretical populations tend to share the correlation of the environment. Dispersal enhances synchrony locally so that the level of correlation in dynamics drops with distance (Lande, Engen & Saether 1999; Bjørnstad & Bolker

2000). Population regulation, however, affects synchronization. Synchrony may be enhanced if density dependence is strong enough to induce cycles (Bjørnstad 2000), but will otherwise decrease synchrony (Kendall *et al.* 2000). Chaotic populations are hard to synchronize (Bjørnstad *et al.* 1999). The theory of population synchrony is less complete for systems of interacting species. Ims & Steen (1990) studied trophically induced synchrony and noted that migratory predators could induce region-wide synchrony in prey populations. Ranta, Kaitala & Lindström (1997a), in contrast, found that the trophic interaction between Canadian lynx (*Lynx canadensis* Kerr) and snowshoe hares (*Lepus americanus* Erxleben) exhibited a U-shaped relation between synchrony and distance. Generally, reaction–diffusion systems involving two species, such as a predator and a prey, have the potential of

Correspondence: Ottar N. Bjørnstad, Department of Entomology, 501 ASI Building, Penn State University, University Park, PA 16802, USA (e-mail onb1@psu.edu).

generating a wide range of spatial dynamics including travelling waves and stable patch formation (reviewed in Bascompte & Solé 1995; Rohani *et al.* 1997). However, a gap still exists between these theoretical predictions and field studies (see, however, Hastings, Harrison & McCann 1997; Maron & Harrison 1997). An important step prior to exploring the possible existence of self-organizing spatial patterns in nature is to understand the relationship between the theoretical patterns and the statistical measures of population synchrony used in data analysis. In this study we help bridge the gap between theory and data by studying the shape of the spatial correlation function (SCF) and spatial cross-correlation function (SCCF) in spatially extended trophic interactions. We used a spatially extended host–parasitoid system as a focal case (Hassell, Comins & May 1991).

The common way of studying spatial synchrony in theoretical systems is by quantifying the spatial covariance (or correlation) in abundance (reviewed in Bjørnstad *et al.* 1999; Koenig 1999). A detailed understanding of population synchrony is achieved by analysing how the correlation is a function of spatial distance: the SCF. In addition to being a common way of quantifying spatial synchrony, our focus on SCF is motivated by recent work on moment equations for spatially extended ecological systems (Bolker & Pacala 1999; Keeling, Wilson & Pacala 2000; Snyder & Nisbet 2000; Bascompte 2001). These studies show how complicated spatiotemporal dynamics can be approximated by considering the spatial mean and spatial correlation. This work recasts the complicated spatial dynamics in terms of how local density affects spatial correlation ('the pattern') and how this spatial pattern in turn affects the local interactions ('the process'); the analogy to the present setting is obvious.

We followed the convention of focusing on spatial correlation in abundance in our study. In addition, we characterized the pattern of spatial cross-correlation between the interacting species (Bolker & Pacala 1999). As indicated above, several of the detailed predictions about synchrony in single-species systems diverge when local dynamics bifurcate to cyclicity or chaos (Bjørnstad *et al.* 1999; Bjørnstad 2000). However, across the divergent predictions, there are a few unifying features: synchrony in single-species systems is predicted to be (i) positive and (ii) non-increasing with distance. We showed these predictions to be violated in spatially extended systems of interacting species.

Parasitoids engage in very intimate interactions with their hosts. In uncoupled populations, the dynamics of these systems relate to the way the parasitoids induce delays in the regulation of the host. This delay causes population cycles because it induces second-order temporal autocorrelation (lagged density-dependence; Royama 1992). The second-order temporal autocorrelation is characterized by the correlation cycling from initially positive through an interval of negativity back to positive correlation with increasing time lag.

We conjectured that the second-order temporal autocorrelation in trophic systems is the cause of the cyclic spatial correlation. This motivated us to call the cyclic (U-shaped) synchrony in reaction–diffusion systems second-order spatial correlation. We used a coupled map lattice model (Hassell *et al.* 1991; Bascompte & Solé 1995) in combination with the non-parametric covariance function (Bjørnstad *et al.* 1999) to clarify the presence of second-order spatial correlation in trophic reaction–diffusion systems.

In order to discuss the patterns of synchrony in spatially extended trophic systems, we first briefly outline our prototypical model and its dynamics. We then outline the relationship between synchrony and SCF, and sketch out the non-parametric covariance function that allows us to quantify the shape of the SCF. In addition to studying the spatial correlation within each species, we study the spatial cross-correlation between the species and develop the non-parametric cross-correlation function. In the Results we explore the classes of correlation functions that arise from trophic interactions and detail the emergence of second-order correlation.

### A host–parasitoid coupled map lattice

In order to study patterns of synchrony in trophic systems, we use a well-known model of spatially extended host–parasitoid interactions (Hassell *et al.* 1991; Comins, Hassell & May 1992). The model describes a two-dimensional universe comprising discrete patches. Generations are non-overlapping. We start with an initial condition consisting of all but one patch empty, and we follow the Hassell *et al.* (1991) formulation. The dynamics at each generation consist of two phases: dispersal and interaction. In the first phase, a fraction  $\mu_h$  of adult hosts and a fraction  $\mu_p$  of adult parasitoids leave the patch where they were born and distribute into the eight surrounding patches. The equations for the dispersal stage can be written as:

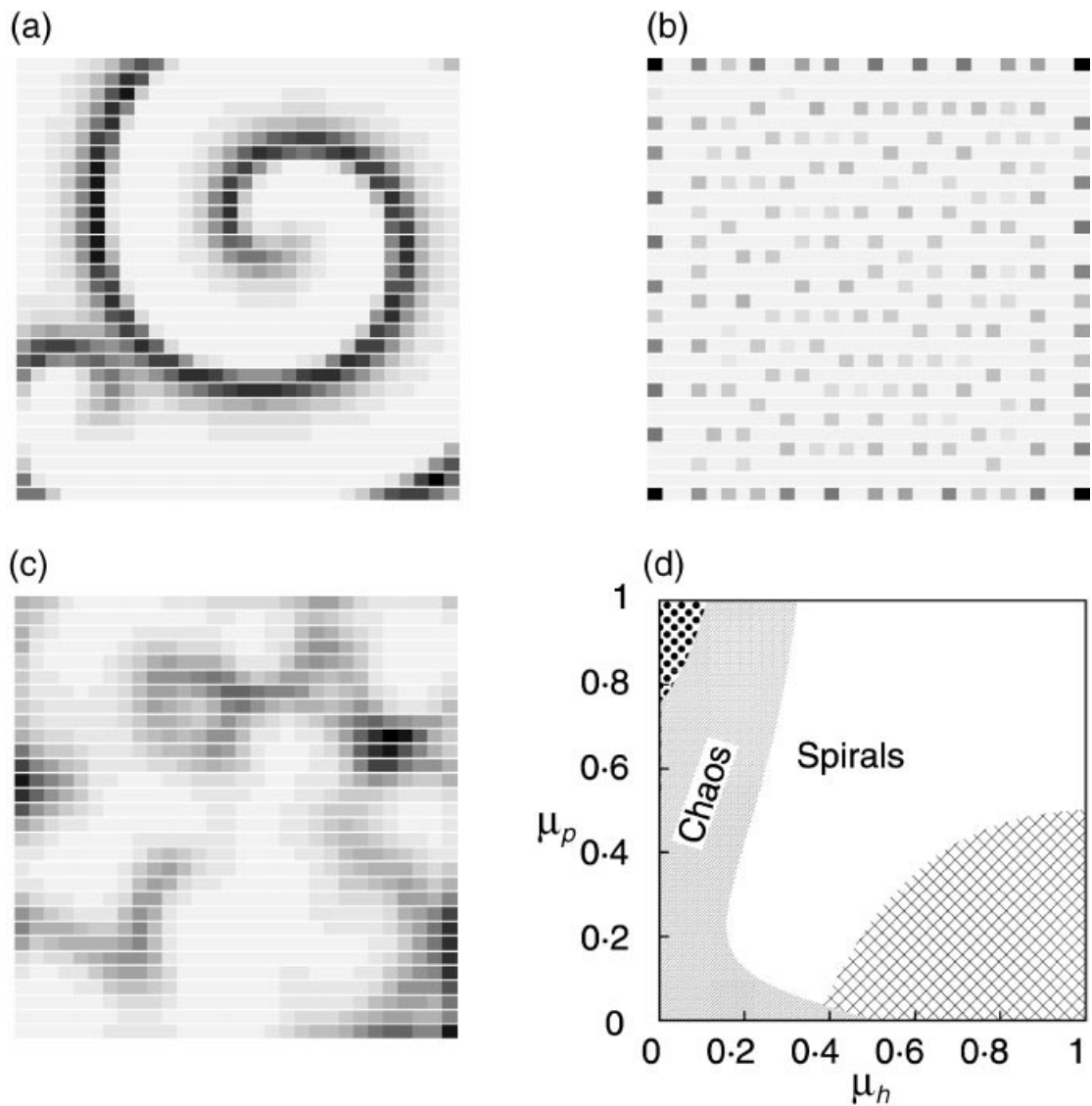
$$H'_{i,t} = (1 - \mu_h)H_{i,t} + \mu_h \bar{H}_{i,t} \quad \text{eqn 1}$$

$$P'_{i,t} = (1 - \mu_p)P_{i,t} + \mu_p \bar{P}_{i,t} \quad \text{eqn 2}$$

where  $H_{i,t}$  and  $P_{i,t}$  denote the densities of adult host and parasitoids at patch  $i$  and generation  $t$  prior to dispersal, and  $H'_{i,t}$  and  $P'_{i,t}$  denote post-dispersal densities. The quantities  $\bar{H}$  and  $\bar{P}$  are the neighbourhood host and parasitoid densities (mean over the eight nearest neighbouring patches). We use absorbing boundaries, i.e. we assume that the boundary is surrounded by a ring of permanently empty patches to which dispersers are lost.

The second phase to the dynamics is host reproduction at *per capita* rate,  $\lambda$ , and parasitoid *per capita* emergence rate,  $c$ . We assume the second phase to follow the Nicholson–Bailey model (Hassell *et al.* 1991), such that the densities at the beginning of generation  $(t + 1)$  are:

$$H_{i,t+1} = \lambda H'_{i,t} e^{-aP'_{i,t}} \quad \text{eqn 3}$$



**Fig. 1.** Self-organized spatial patterns in host density based on the model (equations 1–4). (a) Spiral wave; (b) crystal lattice; (c) spatial chaos. Each figure corresponds to a snapshot of host density at generation 5000. Light shading represents low density and dark shading represents high density. Simulation started with 20 hosts and parasitoids in a single patch with all the other patches empty. Boundary conditions are absorbing and dispersal is to the eight nearest neighbours (see text). The lattice size is  $30 \times 30$ , and the parameters are as follows:  $\lambda = 2$ ,  $a = 1$ ,  $c = 1$ , and (a)  $\mu_h = 0.5$ ,  $\mu_p = 0.3$ , (b)  $\mu_h = 0.05$ ,  $\mu_p = 1$ , (c)  $\mu_h = 0.2$ ,  $\mu_p = 0.9$ . (d) The qualitative types of spatial dynamics as a function of host and parasitoid mobility (adapted from Hassell *et al.* 1991). The dotted areas represent crystal lattices. The hatched area represents ‘hard to start spirals’ (Hassell *et al.* 1991) where the system either goes globally extinct or exhibits spiral waves (depending on parameters and initial conditions).

$$P_{i,t+1} = cH'_{i,t}(1 - e^{-aP'_{i,t}}) \quad \text{eqn 4}$$

where  $H'_{i,t}$  and  $P'_{i,t}$  are as defined in equations 1 and 2 and  $a$  is the *per capita* parasitoid attack rate.

The non-spatial Nicholson–Bailey model gives rise to divergent parasitoid–host cycles that eventually lead to the extinction of the parasitoid or both the parasitoid and the host. It is easy to see (Nisbet & Gurney 1982) that the parasitoid induces a delay in the regulation of the host. Indeed, in the vicinity of the unstable equilibrium ( $H^* = \lambda \log \lambda / a (\lambda - 1)$ ,  $P^* = \log \lambda / a$ ), the regulation of the host is according to:

$$h_t = \left(1 + \frac{\log \lambda}{\lambda - 1}\right) h_{t-1} - \frac{\lambda \log \lambda}{\lambda - 1} h_{t-2} \quad \text{eqn 5}$$

where  $h = \log H$ . This represents a second-order temporal autocorrelation that is cyclic (but divergent) through time.

Once the spatial dimension is introduced and the lattice is big enough (Hassell *et al.* 1991), the full model (equations 1–4) will more often than not result in indefinite persistence of the parasitoid–host interaction. Persistence is secured through the space–time interaction of the two species (Hassell *et al.* 1991; see also Wood & Thomas 1996; Bolker & Pacala 1999). This persistence is induced through a range of self-organized spatial dynamics. Hassell *et al.* (1991) studied the spatial dynamics of the model (equations 1–4) and showed that persistence is achieved through three qualitatively different self-organized spatial patterns (Fig. 1):

(i) spiral waves, (ii) crystal lattices and (iii) spatial chaos. The key parameter is partly, as indicated by equation 5, the growth rate  $\lambda$  but, more importantly (Hassell *et al.* 1991), the dispersal rates  $\mu_h$  and  $\mu_p$ . With high host dispersal rates, population densities form evolving spiral waves (Fig. 1a). The corresponding local dynamics are periodic, quasiperiodic or chaotic (Solé, Valls & Bascompte 1992). Crystal lattices, which are stable patterns characterized by patches with high densities surrounded by lower density patches (Fig. 1b; Hastings *et al.* 1997; Maron & Harrison 1997), arise from extreme mobility of the parasitoid relative to that of the host. Spatial chaos represents spatiotemporal fluctuations that lack both spatial and temporal periodicity (Fig. 1c). The latter resembles spatial randomness in that densities vary in space and time without any clear pattern, although the model is deterministic (Hassell *et al.* 1991; Comins *et al.* 1992). In Fig. 1d we detail the parameter combinations that lead to the different types of spatial dynamics.

In the following, we use  $30 \times 30$  cell lattices and analyse 200 generations of data (from the 900 local populations) after allowing for a transient period of 1000 generations. We have checked, using larger lattices, that the results we present below are not unduly influenced by the extent and grain of the lattice, nor by edge effects.

### Spatial correlation functions

Spatial correlation has attained much recent focus from two different angles. First, it is the central measure for quantifying spatial synchrony, a topic that has received much attention during the last few years (reviewed in Bjørnstad *et al.* 1999). Secondly, spatial correlation is a quantity of central importance to understanding, and approximating, spatiotemporal ecological interactions (Bolker & Pacala 1999; Keeling *et al.* 2000). We therefore follow recent efforts (Bjørnstad & Bolker 2000) and consider the SCF of the spatially extended system. We denote the space–time (marginal) average host and parasitoid abundance by  $\langle H \rangle$  and  $\langle P \rangle$ , respectively. The synchrony between the two time series  $\underline{H}_i$  and  $\underline{H}_j$  of host populations at locations  $i$  and  $j$  are then given by:

$$\rho_{ij} = (\underline{H}_i - \langle H \rangle) \times (\underline{H}_j - \langle H \rangle)^T / \sigma_H^2 \quad \text{eqn 6}$$

where underscored symbols represent vectors (time series),  $\times$  denotes matrix multiplication,  $^T$  denotes matrix transposition, and  $\sigma_H^2$  represents the space–time (marginal) variance in the host abundance. The definition in equation 6 is, thus, the algebraic shorthand notation for the pairwise correlation of different time series (with identical means and variances). In self-organized ecological systems, the correlation typically depends on the spatial distance,  $r_{ij}$ , separating the populations  $i$  and  $j$ . The function  $\rho(r)$  that governs this dependence is called the SCF.

Under the anticipation that the SCF should be a tractable function for simple dynamical systems, Bjørnstad & Bolker (2000) pursued an analytic solution to the SCF of a spatially extended single-species system. They assumed density-independent dispersal and stable dynamics. However, even for this simplest case it was difficult to find a closed-form solution to the SCF. (In the limit of frequent dispersal, the SCF is approximately Gaussian locally but with exponential or Bessel tails). In order to elucidate the SCF in more complicated spatially extended systems, we therefore rely on recent techniques to estimate the SCF numerically, without assuming any a priori functional form (such as the Gaussian or the Bessel). The non-parametric covariance function (NCF) effectively attains this estimate by employing a non-parametric regression of  $\rho_{ij}$  against  $r_{ij}$  (Hall & Patil 1994; Bjørnstad & Falck 2001) according to:

$$\tilde{\rho}(r) = \frac{\sum_{i=1}^n \sum_{j=i+1}^n K(r_{ij}/h) \rho_{ij}}{\sum_{i=1}^n \sum_{j=i+1}^n K(r_{ij}/h)} \quad \text{eqn 7}$$

where  $K()$  is a kernel function (Härdle 1990) and  $h (> 0)$  is its bandwidth. The bandwidth is a parameter that adjusts the smoothness of the fitted curve. The estimated function,  $\tilde{\rho}(r)$ , is non-parametric in the sense of not assuming any specific class of a priori parametric models for the relation (Härdle 1990). Details are given in Bjørnstad & Falck (2001). In all our calculations we use smoothing splines with 25 ‘equivalent’ degrees of freedom to estimate the correlation function.

Understanding synchrony in multispecies systems also involves the spatial correlation between species (as a function of distance; Bolker & Pacala 1999). We therefore used a new non-parametric method to estimate the spatial cross-correlation function (SCCF). We denote the space–time parasitoid mean and variance by  $\langle P \rangle$  and  $\sigma_P^2$ , respectively. All other notation is as given in the previous paragraphs. The cross-correlation,  $w_{ij}$ , between the host population at location  $i$  and the parasitoid population at location  $j$  (either at similar or different locations) is then given by:

$$w_{ij} = (\underline{H}_i - \langle H \rangle) \times (\underline{P}_j - \langle P \rangle)^T / \sigma_H \sigma_P. \quad \text{eqn 8}$$

We measured within-patch synchrony of the parasitoid and host as the average correlation between the two species in each patch (= mean  $w_{ii}$  for all  $i$ ). More generally,  $w_{ij}$  will depend on the spatial distance,  $r_{ij}$ , according to the SCCF,  $C(r)$ . By an extension of existing methodology (Hall & Patil 1994; Bjørnstad & Falck 2001), we can estimate the SCCF non-parametrically according to:

$$\tilde{C}(r) = \frac{\sum_{i=1}^n \sum_{j=i+1}^n K(r_{ij}/h) w_{ij}}{\sum_{i=1}^n \sum_{j=i+1}^n K(r_{ij}/h)}. \quad \text{eqn 9}$$

The derivation follows directly that of Hall & Patil (1994) and Bjørnstad & Falck (2001). However, the

exact numerical properties of this estimator, in the face of finite sample size, deserve future study. A library of S-plus and R functions to calculate the non-parametric SCCF is available from the authors upon request.

We can provide a crude summary statistic of the spatial pattern by calculating the spatial correlation length in the parasitoid–host model. We use the  $L_c$  correlation length, i.e. the distance at which the correlation falls to  $1/e$  ( $\approx 0.37$ ). As a summary statistic for the cross-correlation between species, we focus on the distance at which the SCCF peaks. This reflects the distance over which parasitoid build-up lags behind that of the host.

## Results

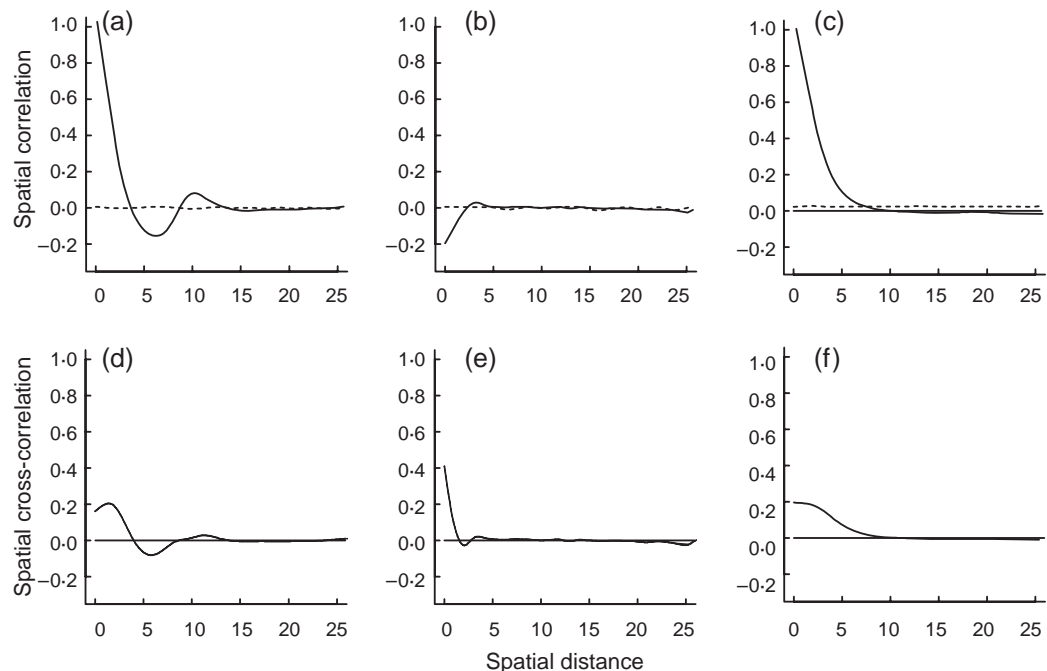
Figure 1 shows snap-shots of the three different spatial dynamics that are generated by the model (equations 1–4). The SCF reveals that each of the dynamic types is associated with a distinct pattern of spatial synchrony (Fig. 2a–c). Spatial chaos (Fig. 2c) is the only pattern with SCF comparable with those described from single-species systems (Bjørnstad & Bolker 2000; Bjørnstad 2000). The correlation function is initially high and tails off towards zero correlation with distance.

Spiral waves resemble, initially, the decline from locally high correlation that is seen in spatially chaotic systems. However, for intermediate distances the SCF diverges markedly by exhibiting conspicuous negative correlation, which cycles back to positive at twice the spatial lag (Fig. 2a). A randomization test reveals that the negative correlation is highly significant in all sys-

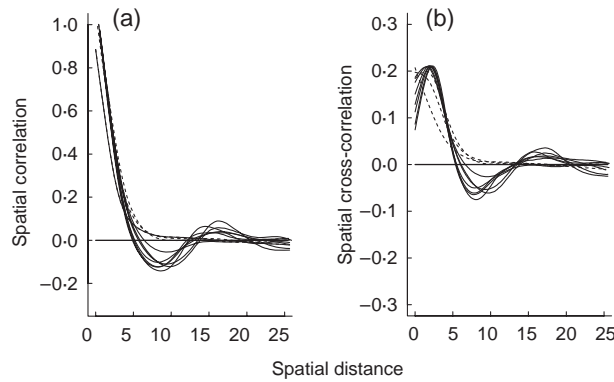
tems with spiral waves. These cyclic SCF for dynamic spatial waves bear an intriguing resemblance to the cyclic temporal correlation function that results from second-order (delayed density-dependent) processes (Royama 1992; see the Discussion).

The last type of dynamics, the crystal lattices, is associated with strong negative correlation between neighbouring populations. We have, through an extensive analysis across parameter space, confirmed that each of the three different spatial dynamics (Fig. 1a–c) is generally associated with the unique families of SCF (Fig. 2a–c). For any given parameter value, the correlation functions in parasitoid abundance are near identical to those of the host. We have therefore elected not to show these.

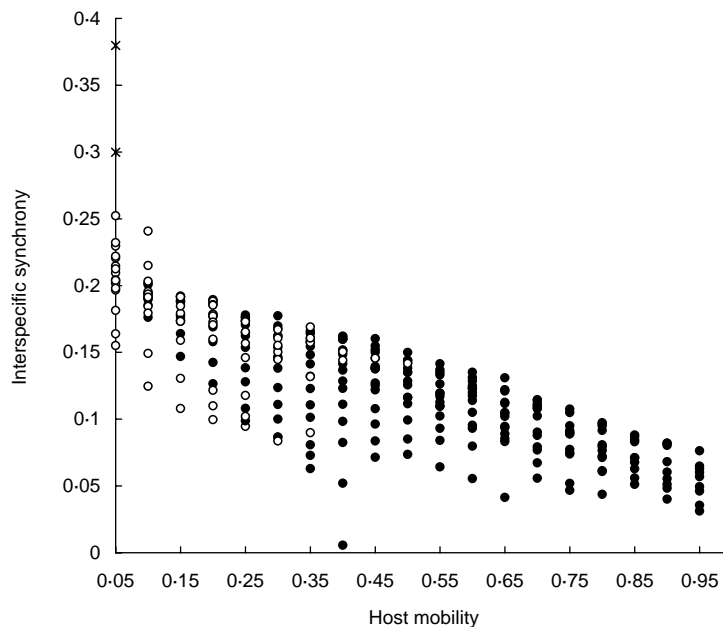
In addition to the unique SCF, each of the three spatial dynamics (Fig. 1a–c) is associated with particular SCCF between the host and its parasitoid. All types exhibit positive SCCF at short spatial lags. However, spiral waves are associated with cyclic SCCF, i.e. SCCF that are positive at short spatial lags and then cycle through negative and positive cross-correlations thereafter (Fig. 2a). Note, also, how the cross-correlation increases initially. Spatially chaotic populations, in contrast, have SCCF that start off positive but the SCCF does not become negative with distance (Fig. 2c). Crystal lattices, finally, are characterized by locally high cross-correlations. Through explorations of parameter space we have confirmed that spatially chaotic systems may have cross-correlation functions that show a non-zero distance mode, i.e., as for spiral waves, the SCCF may initially increase with distance (Fig. 3b). We summarize the SCF and SCCF across a



**Fig. 2.** Spatial correlation functions (SCF) (top row) and spatial cross-correlation functions (SCCF) (bottom row). Correlation and cross-correlation is plotted as a function of distance. Each function corresponds to each of the patterns of Fig. 1. (a, d) Spiral wave; (b, e) crystal lattice; (c, f) spatial chaos. All patterns have very distinct correlation and cross-correlation functions (see text). The dotted lines (near the  $y = 0$  line) in (a–c) represent a typical correlation function under complete spatial randomization.



**Fig. 3.** (a) Spatial correlation functions (SCF) and (b) spatial cross-correlation functions (SCCF) along a transect of host mobility. Parasitoid mobility is taken to be  $\mu_p = 0.7$  throughout. Host mobility is incremented from 0.05 to 0.95 by 0.1. The three lowest levels of host mobility (dotted lines;  $\mu_h = 0.05, 0.15$ , and  $0.25$ ) represent spatial chaos, neither the SCF or SCCF fall below zero. Higher host mobility results in travelling waves, as apparent from cyclicity in both the SCF and SCCF. Note how increased host mobility is associated with the mode of the SCCF being further away from zero.



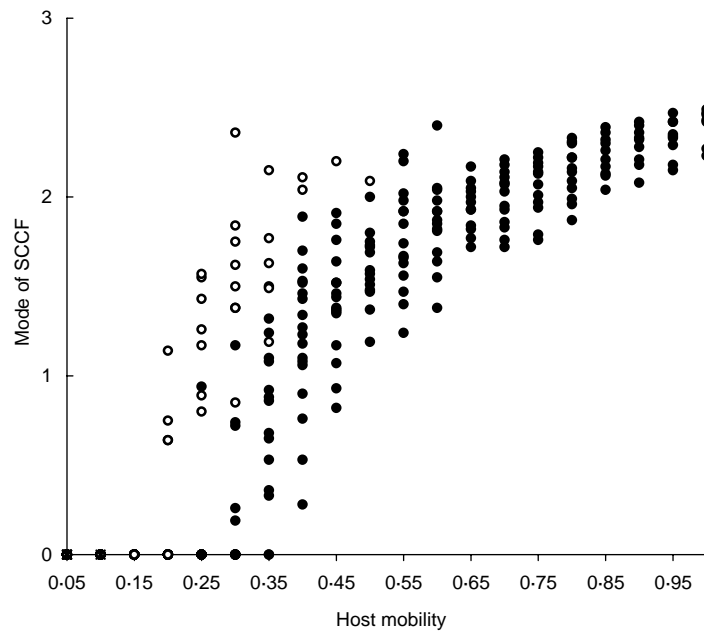
**Fig. 4.** Interspecific synchrony as a function of host mobility. Highest synchrony is associated with the crystal lattices (★). The synchrony scales inversely with host mobility,  $\mu_h$ , in spiral waves (●) and spatial chaos (○).

transect of different host dispersal rates (parasitoid dispersal is kept constant at  $\mu_p = 0.7$ ) in Fig. 3. The transect illustrates that the SCF and SCCF are in many ways similar in shape; however, the functions never go negative for spatially chaotic systems, while they cycle through negative and positive for spiral waves.

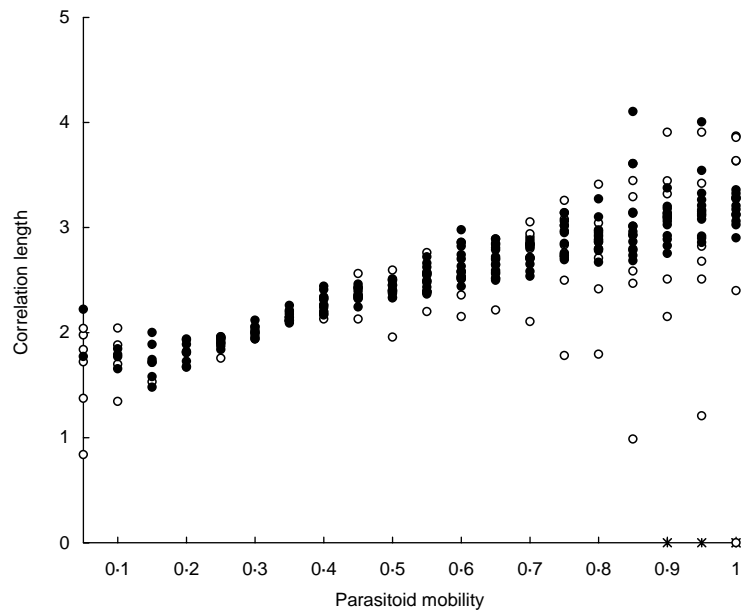
We used the cross-correlation to quantify the within-patch synchrony between the parasitoid and the host. When we increment host and parasitoid dispersal rates by 0.05 across parameter space we find a mean within-patch cross-correlation of 0.14 (minimum = 0.00, maximum = 0.99). This is highest in crystal lattices (mean 0.67, range 0.30, 0.99) and lowest in spiral waves (mean 0.12, range 0.00, 0.20). Spatial chaos has intermediate cross-correlation (mean 0.18, range 0.08, 0.62). A casual inspection shows that the local cross-correlation is negatively affected by the host dispersal rate (Fig. 4).

The synchrony is, however, also positively affected by parasitoid mobility. The partial correlation of local cross-correlation and host and parasitoid mobility is  $-0.69$  (SE = 0.05) and  $0.39$  (SE = 0.05), respectively.

The decline in local cross-correlation is associated with a shift in the mode of the SCCF away from zero. For low host mobility, the mode is at zero, signifying that the parasitoid abundance peaks in each patch at the same time as the host. However, as host mobility increases the parasitoid dynamics begin to lag the host in space (Fig. 5; see also Fig. 3b). The lag is zero for crystal lattices. The mean lag is 0.5 (units = number of cells) for spatial chaos (note, however, that the median is zero). The average mode in the SCCF of spiral waves is 1.4 (median 1.7). A casual inspection of the mode reveals that the spatial lag is most strongly determined by the host mobility (Fig. 5) but it is also influenced by



**Fig. 5.** The mode of the spatial cross-correlation function (SCCF) as a function of host mobility. The mode is zero for low host mobility ( $\mu_h < 0.2$ ), and increases with host mobility thereafter. Stars represent crystal lattices, filled circles represents spiral waves and open circles represent spatial chaos.



**Fig. 6.** The  $L_e$  correlation length as a function of parasitoid mobility,  $\mu_p$ . The SCF for crystal lattices ( $\star$ ) is singular at the origin, the correlation length is thus zero (or undefined). Higher parasitoid mobility results in greater correlation length for both spatial chaos ( $\circ$ ) and travelling waves ( $\bullet$ ).

the parasitoid mobility. The partial correlation of this lag against host and parasitoid mobility is 0.80 (SE = 0.02) and 0.26 (SE = 0.02), respectively. Note, thus, that the dependence on the host mobility is opposite to that of the local synchrony.

The  $L_e$  correlation length measures the scaling of the pattern within each species. The mean host correlation length across parameter space is 2.5 (range 0, 4) (units = number of cells). Crystal lattices have zero (or undefined)  $L_e$ , as the correlation function is negative

between neighbouring populations (Fig. 2b). The  $L_e$  correlation length is very similar for spatial chaos and spiral waves, with means of 2.5 (range 0, 3.9) and 2.6 (range 1.5, 4.1), respectively. The parasitoid correlation lengths (not shown) are almost identical to those of the host. In contrast to the mode of the SCCF, the correlation length is most strongly influenced by the parasitoid mobility (Fig. 6; partial correlation = 0.53, SE = 0.05). However the  $L_e$  also depends significantly on host mobility (partial correlation = 0.22, SE = 0.05).

A complication is that the correlation length appears to scale nearly perfectly with parasitoid mobility in spiral waves (correlation = 0.93) while it is more strongly influenced by the host mobility in spatially chaotic populations (partial correlation = 0.67).

## Discussion

This paper reports on a theoretical discussion of the patterns of intra- and interspecific spatial synchrony that result from the interaction between a host and its parasitoid. We have used a coupled map lattice to model the spatially extended trophic interaction, and used spatial correlation and cross-correlation functions to describe the patterns of synchrony. The results can be summarized as follows.

1. Spatially extended host–parasitoid interactions can lead to spatial chaos, spiral waves or crystal lattices depending on the relative and absolute mobility of the interacting species. Each type of behaviour is characterized by distinct patterns of spatial synchrony within and between species.
2. Spiral waves result in cyclic correlation and cross-correlation functions, a result that differs qualitatively from what can be obtained with single-species interactions.
3. With increased host mobility, the parasitoid population dynamics increasingly lag the host dynamics in space. This is reflected in the SCCF having its mode away from zero.
4. Crystal lattices exhibit negative synchrony between neighbouring populations.

It is natural to ask whether the results obtained by coupled map lattices are robust when considering individual-based interactions and models. Bascompte, Solé & Martínez (1997) show the presence of the same self-organized spatial patterns in individual-based models. Similarly, Rohani *et al.* (1997) have specifically addressed the question of whether spatial self-organizing patterns persist in the presence of noise. We are therefore confident that our results should generalize to other types of models. Note, though, that much work remains to be done on how the interaction between spatial dynamics and demographic stochasticity affects host–parasitoid dynamics (Wilson & Hassell 1997).

Bolker & Pacala (1999) showed, using moment equations, how spatiotemporal dynamics can be understood by considering how local interactions affect patterns of spatial correlation and cross-correlation, and how these in turn affect local dynamics (see also Keeling *et al.* 2000). Their perspective is a very valuable tool in order to interpret both the pattern of synchrony and the patterns of dynamics seen in our theoretical model. The local dynamics of the Nicholson–Bailey model in the absence of any coupling show a divergent cycle. Persistence can therefore only be achieved due to spatial interactions. Because of the inherent local instability, mobility of the host and

parasitoid introduces spatially transient associations between the host and parasitoid. This eventually ends in local extinction. If the spatial dimension is large enough (Wood & Thomas 1996), however, indefinite global persistence can be achieved through the movement of this unstable interaction through space. Low to moderate mobility of both species induces spatial aggregation of both species as well as positive local cross-correlation of the two, leading to a space–time interaction, called spatial chaos (Figs 1c, 2c,f) (Hassell *et al.* 1991).

Keeping in mind that in the absence of any local interactions dispersal will increase the extent of spatial correlation in abundance, it is intuitive that if parasitoid dispersal is very high relative to that of the host, the parasitoid can effectively embrace patches of high host abundance, leading to a cross-correlation that extends further in space than the spatial correlation in the host itself (Fig. 2b,e). This results in a *per capita* parasitization rate that increases as one moves away from high-density host patches. Because any host that attempts moving will rapidly fall victim to the increased parasitization rates, and any parasitoid that ventures too far away from a patch will run out of resources, the spatial pattern gets effectively frozen (Hastings *et al.* 1997; Maron & Harrison 1997).

In contrast, with increasing mobility of the host relative to the parasitoid, the parasitoid build-up begins to lag spatially behind the build-up of the host. This results in the spatial cross-correlation between the two species, having a maximum away from zero (Figs 3 and 5). The *per capita* parasitization rates thus become relatively lower in high host density patches and relatively higher in the patches where the host density used to be high (Fig. 2a,d). Effectively this pattern of cross-correlation results in negative spatial correlation in host density at intermediate distances, due to the increased rates of parasitization in the wake of the host build-up. This intricate feedback of the trophic interaction on the spatial correlation, which in turn affects the trophic interaction, is the cause of travelling waves in abundance (Fig. 1a).

We have found that each of the three types of spatial dynamics, spiral waves, spatial chaos and crystal lattices, is connected with very distinct spatial correlation and cross-correlation functions. One may therefore be able to test for complex spatial dynamics through a combined use of SCF and SCCF. In particular, two of the three patterns are associated with SCF very different from what can be found in single-species systems (Bjørnstad *et al.* 1999). In particular, spiral waves entertain a cyclic correlation function that has a minimum (which in the present case is always negative) at intermediate distances. Ranta *et al.* (1997a), who studied synchrony in the Canadian snowshoe hare, called this a U-shaped pattern of synchrony. As cyclic temporal autocorrelation results from second-order interactions (see equation 5), we call the cyclic SCF second-order spatial correlation. Ranta *et al.* (1997b)



and Bascompte *et al.* (1997) both took the U-shaped pattern in synchrony of the snowshoe hares as possible evidence for travelling waves in abundance. At a first glance the present study supports this notion. Note, however, that the second-order SCF seen in the present model cycles around zero, while the U-shaped synchrony in the snowshoe hare never drops below 0.5. We have explored whether regionally correlated stochastic forcing on the parasitoid–host system could serve to raise the SCF above zero (cf. the Moran effect; Royama 1992). However, we have not found any case in which the SCF becomes positive in its entire domain due to the effect of global noise. Whether this is a general feature of host–parasitoid travelling waves remains to be investigated.

Spatial chaos is a deterministic, random-like pattern of variation in population abundance through space. An important task that remains to be done is to develop rigorous statistical methods to distinguish self-organizing deterministic spatial chaos from spatial randomness (Bascompte & Solé 1995; May 1999). If we compare the SCF in the self-organized dynamical systems with comparable SCF of spatially randomized systems (Fig. 2c), we see a startling contrast. This suggests that we should be able to develop a test based on the SCF. However, distinguishing self-organized spatial chaos (Fig. 2c) from more simple dispersal-induced synchronization of stochastic systems (Bjørnstad & Bolker 2000) will be a more serious challenge.

Lambin *et al.* (1998) recently provided a dedicated statistical test for travelling waves in abundance. The method is fine-tuned to analyse data from directed travelling waves going through a study area (rather than radial waves or entire spirals). For such data, their method is likely to be more powerful and less ambiguous than inspecting correlation functions. They furthermore point out a very interesting phenomenon: when the study area is only a small portion of the entire dynamic area, the data may be anisotropic. That is, the SCF will drop more quickly in one direction (perpendicular to the wave) than in others (more parallel to the wave). This is an important point worthy of further study.

The local association between the parasitoid and its host is only high when the host mobility is low (Fig. 4). This is because when the host becomes more mobile, the parasitoid dynamics begin to lag spatially behind that of the host. This raises an important cautionary note for the study of a parasitoid and its ‘habitat’. A naive correlational analysis of the spatial relationship between a parasitoid and its host may falsely indicate a low association between the two (whenever the host is mobile).

The number of studies of spatial synchrony has increased dramatically over the last few years. At the same time the focus of the studies has gone through a natural progression, asking first what are the patterns of synchrony, then focusing on potential causes of synchrony. The challenge for the years to come is to ask what the consequences of spatial synchrony, or, more

generally the feedback of patterns of spatial correlation, are on the temporal dynamics of populations.

## Acknowledgements

Both authors received postdoctoral fellowships from the National Center for Ecological Analysis and Synthesis, a center funded by NSF (grant DEB-94–21535), the University of California at Santa Barbara, and the State of California. We thank Big Bull Cafe for providing a nice and relaxing setting for our lunch talks, where the ideas of this paper took shape. Ben Bolker and one anonymous referee provided valuable comments and discussion.

## References

- Bascompte, J. (2001) Aggregate statistical measures and metapopulation dynamics. *Journal of Theoretical Biology*, **209**, 373–379.
- Bascompte, J. & Solé, R.V. (1995) Rethinking complexity – modeling spatiotemporal dynamics in ecology. *Trends in Ecology and Evolution*, **10**, 361–366.
- Bascompte, J., Solé, R.V. & Martínez, N. (1997) Population cycles and spatial patterns in snowshoe hares: an individual-oriented simulation. *Journal of Theoretical Biology*, **187**, 213–222.
- Bjørnstad, O.N. (2000) Cycles and synchrony: two historical ‘experiments’ and one experience. *Journal of Animal Ecology*, **69**, 869–873.
- Bjørnstad, O. & Bolker, B. (2000) Canonical functions for dispersal-induced synchrony. *Proceedings of the Royal Society of London Series B*, **267**, 1787–1794.
- Bjørnstad, O.N. & Falck, W. (2001) Nonparametric spatial covariance functions: estimation and testing. *Environmental and Ecological Statistics*, **8**, 53–70.
- Bjørnstad, O.N., Ims, R.A. & Lambin, X. (1999) Spatial population dynamics: analysing patterns and processes of population synchrony. *Trends in Ecology and Evolution*, **11**, 427–431.
- Bolker, B. & Pacala, S.W. (1999) Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *American Naturalist*, **153**, 572–602.
- Comins, H.N., Hassell, M.P. & May, R.M. (1992) The spatial dynamics of host–parasitoid systems. *Journal of Animal Ecology*, **61**, 735–748.
- Hall, P. & Patil, P. (1994) Properties of nonparametric estimators of autocovariance for stationary random fields. *Probability Theory and Related Fields*, **99**, 399–424.
- Härdle, W. (1990) *Applied Nonparametric Regression*. Cambridge University Press, Cambridge, UK.
- Hassell, M.P., Comins, H.N. & May, R.M. (1991) Spatial structure and chaos in insect population dynamics. *Nature*, **353**, 255–258.
- Hastings, A., Harrison, S. & McCann, K. (1997) Unexpected spatial patterns in an insect outbreak match a predator diffusion model. *Proceedings of the Royal Society of London Series B*, **264**, 1837–1840.
- Ims, R.A. & Steen, H. (1990) Geographical synchrony in microtine population cycles: a theoretical evaluation of the role of nomadic avian predators. *Oikos*, **57**, 381–387.
- Keeling, M.J., Wilson, H.B. & Pacala, S.W. (2000) Re-interpreting space, time lags and functional responses in ecological models. *Science*, **290**, 1758–1761.
- Kendall, B.E., Bjørnstad, O.N., Bascompte, J., Keith, T. & Fagan, W. (2000) Ecological interactions, environmental

- correlation and spatial synchrony. *American Naturalist*, **155**, 628–636.
- Koenig, W.D. (1999) Spatial autocorrelation of ecological phenomena. *Trends in Ecology and Evolution*, **14**, 22–26.
- Lambin, X., Elston, D.A., Petty, S.J. & MacKinnon, J.L. (1998) Spatial asynchrony and periodic travelling wave in cyclic field vole populations. *Proceedings of the Royal Society of London Series B*, **265**, 1491–1496.
- Lande, R., Engen, S. & Saether, B.E. (1999) Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. *American Naturalist*, **154**, 271–281.
- Maron, J.L. & Harrison, S. (1997) Spatial pattern formation in an insect host–parasitoid system. *Science*, **278**, 1619–1621.
- May, R. (1999) Unanswered questions in ecology. *Philosophical Transactions of the Royal Society of London Series B*, **354**, 1951–1959.
- Nisbet, R.M. & Gurney, W.S.C. (1982) *Modelling Fluctuating Populations*. Wiley, Chichester, UK.
- Ranta, E., Kaitala, V. & Lindström, J. (1997a) Dynamics of Canadian lynx populations in space and time. *Ecography*, **20**, 454–460.
- Ranta, E., Lindstrom, J., Kaitala, V., Kokko, H., Linden, H. & Helle, E. (1997b) Solar activity and hare dynamics: a cross-continental comparison. *American Naturalist*, **149**, 765–775.
- Rohani, P., Lewis, T.J., Grunbaum, D. & Ruxton, G.D. (1997) Spatial self-organization in ecology: pretty patterns or robust reality? *Trends in Ecology and Evolution*, **12**, 70–73.
- Royama, T. (1992) *Analytical Population Dynamics*. Chapman & Hall, London, UK.
- Snyder, R.E. & Nisbet, R.M. (2000) Spatial structure and fluctuations in the contact process and related models. *Bulletin of Mathematical Biology*, **62**, 959–975.
- Solé, R.V., Valls, J. & Bascompte, J. (1992) Spiral waves, chaos and multiple attractors in lattice models of interacting. *Physical Letters A*, **166**, 123–128.
- Wilson, H.B. & Hassell, M.P. (1997) Host–parasitoid spatial models: the interplay of demographic stochasticity and dynamics. *Proceedings of the Royal Society of London Series B*, **264**, 1189–1195.
- Wood, S.N. & Thomas, M.B. (1996) Space, time and persistence of virulent pathogens. *Proceedings of the Royal Society of London Series B*, **263**, 673–680.

Received 6 February 2001; revision received 1 June 2001