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# The spatial dynamics of host–parasitoid systems

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## Summary

1. We consider models for host–parasitoid interactions in spatially patchy environments, where in each generation specified fractions of the host and parasitoid subpopulations in each patch move to adjacent patches. In most previous work of this general kind, the movement is not localized in this way, but involves ‘global’ mixing of the populations prior to dispersal.

2. A remarkable range of dynamical behaviour is exhibited by a mathematically explicit model with constant host reproductive rate, deterministically unstable local dynamics and dispersing hosts and parasitoids that only move to nearest-neighbour patches in a density-independent way. The density of the host and parasitoid subpopulations in a two-dimensional array of patches may exhibit complex patterns of spiral waves, spatial chaos, a so-called static ‘crystal lattice’ pattern, or they may become extinct. The probability of extinction rises rapidly when the number of patches present decreases below some characteristic arena size which varies with the scale of the spatial dynamics.

3. The different types of spatial dynamics that are observed depends critically on the fractions of hosts and adult parasitoids that disperse in each generation from the patches in which they emerged. Low rates of host dispersal tend to lead to chaotic patterns unless this rate is very low and parasitoid dispersal rates very high, in which case ‘crystal lattice’ patterns may occur. Intermediate to high rates of host dispersal tend to result in spiral patterns. The effect of varying host rates of increase, within-patch parasitism that is inherently stabilizing and random patch-to-patch variation are also discussed.

4. The results are relatively insensitive to the details of the interaction. Thus, a similar range of behaviour (spirals, chaos and crystal lattices) is discernible from a very general ‘cellular automaton’ model in which only qualitative categories of patch densities are specified together with a very simple set of ‘transition rules’. The diffusive dispersal of the explicit model is paralleled by making the new state in each generation depend, not only on the current state of the given ‘cell’, but also on the states of a specified set of neighbouring cells.

*Key-words:* heterogeneity, dispersal, host–parasitoid, spatial dynamics.

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## Introduction

There is now a large body of literature showing that spatially patchy environments can markedly influence the dynamics of species interactions. This is true whether one considers the dynamics of single species (e.g. DeJong 1979), of competing species in a patchy environment (e.g. Atkinson & Shorrocks 1981; DeJong 1981; Hanski 1981, 1983; Ives & May 1985; Comins & Hassell 1987), of plant–herbivore inter-

actions (e.g. Crawley 1983; Strong, Lawton & Southwood 1984) or of interactions with natural enemies and their hosts or prey (e.g. Crowley 1981; Reeve 1988; Taylor 1988; Hassell & Anderson 1989).

Recently, there has been particular interest in the relationship between the dynamics of populations at the local and regional (= metapopulation) scales (see Gilpin & Hanski (1991) for an excellent review). One suggestion to have emerged from models of predator–prey and insect host–parasitoid interactions is that migration *per se* between patches has ‘either no effect, or a detrimental one, on stability.

More specifically, a collection of unstable subpopulations cannot be stabilized by connecting them through migration' (Reeve 1990). In this paper we show, using simple host–parasitoid models, that connecting unstable subpopulations by *diffusive* dispersal to neighbouring 'patches' (in contrast to 'global' dispersal throughout the region) can readily lead to persistence of the combined metapopulation, even with no variability between patches and no explicit density dependences. Moreover, these models exhibit a remarkable range of dynamical behaviour: for example, host and parasitoid densities within subpopulations in a two-dimensional array of patches may exhibit complex patterns of spiral waves or spatially chaotic variation. The results are relatively insensitive to the details of the interactions and are demonstrated in the first place from mathematically explicit models. This is followed by a discussion of a very general 'cellular automaton' model in which only qualitative rules are specified. The work develops on that already reported by Hassell, Comins & May (1991).

### The model

Let us consider a habitat which is divided into discrete patches (e.g. food plants for a herbivorous insect) on which adult insects oviposit and the resulting larvae feed. The immature stages of these insects are hosts for a specialist parasitoid species whose life cycle is synchronized with that of its host. We model this patchy environment in a very simple way: as a two-dimensional arena in which host and parasitoid populations are distributed amongst a square grid of 'cells' or patches of arena width  $n$ . For each generation the dynamics consist of two phases: a dispersal phase and a reproduction-and-parasitism phase. In the dispersal phase, a certain fraction of adult hosts,  $\mu_N$ , and a fraction of adult female parasitoids,  $\mu_P$ , leave the patch from which they emerged, while the remainder stay behind to reproduce in their original patch. In most previous studies, these dispersing individuals are distributed over all other patches according to some specified rule. In this study, however, rather than entering a 'pool' for such global dispersal, the dispersing hosts and parasitoids diffuse outwards to colonize equally the eight nearest neighbours of the patch from which they emerge. Longer range dispersal can only occur through repetition of these single-patch movements over multiple generations. The equations for the dispersal stage in each patch are:

$$N'_{i,t} = (1 - \mu_N)N_{i,t} + \mu_N \bar{N}_{i,t} \quad \text{eqn 1a}$$

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

Here  $N_{i,t}$  and  $P_{i,t}$  are the pre-dispersal host and parasitoid population densities in patch  $i$  at time  $t$ ,  $N'_{i,t}$  and  $P'_{i,t}$  are densities after dispersal, and  $\bar{N}_{i,t}$  and

$\bar{P}_{i,t}$  are the average host and parasitoid populations over the eight nearest neighbouring patches. Thus,

$$\bar{N}_{i,t} = \sum_j N_{j,t}/8 \quad \text{eqn 2a}$$

$$\bar{P}_{i,t} = \sum_j P_{j,t}/8 \quad \text{eqn 2b}$$

in which  $j$  runs over the eight nearest neighbours of patch  $i$ . Henceforth we suppress the index  $i$ , since the dynamics are the same for all patches.

For patches along the boundary of the arena the definitions of  $\bar{N}_t$  and  $\bar{P}_t$  are slightly different. We consider three cases.

*Cyclic boundary conditions.* In this obviously unrealistic case, opposite edges of the arena are effectively joined together. This has the advantage that all patches are dynamically equivalent, with no edge effects (the arena size affects the dynamics of all patches equally). The nearest neighbours on the outside of edge patches are defined to be patches on the opposing edges.

*Absorbing boundary conditions.* Individuals dispersing across the boundary are lost. The normal definitions of  $\bar{N}_t$  and  $\bar{P}_t$  may be used if the arena is considered to be bordered by a ring of permanently empty patches.

*Reflective boundary conditions.* Dispersing individuals are prevented from crossing the boundary, and remain in an edge patch. This effect applies separately to the horizontal and vertical components of the attempted movement. Thus, a dispersing individual attempting to move south-east on the east boundary of the arena will actually move south. If it were at the south-east corner, it would remain in its starting patch.

In the examples discussed in this paper, we use only reflective boundaries. Using cyclic or absorptive boundary conditions is observed to have little effect, except that simulations with cyclic boundaries tend to produce symmetrical patterns (because of their more symmetrical mathematical properties).

To lay bare the effect of this diffusive dispersal alone, we commence by letting all patches be identical in 'quality' and assume that parasitism is random in each patch. The reproduction-and-parasitism phase thus follows the usual Nicholson & Bailey (1935) formulation:

$$N_{t+1} = \lambda N_t \exp(-aP_t) \quad \text{eqn 3a}$$

$$P_{t+1} = cH_t[1 - \exp(-aP_t)] \quad \text{eqn 3b}$$

in which  $\lambda$  is the finite rate of increase of the host population,  $a$  is the per capita parasitoid attack rate and  $c$  is the conversion efficiency of parasitized hosts into adult female parasitoids of the next generation. Because of the uniform environment, all three parameters are spatially homogeneous. It is well known that the parameters  $a$  and  $c$  of the Nicholson-Bailey

model can be set to one by suitably scaling the population densities (Hassell 1978), and this process can equally be applied to our spatially homogeneous dispersal model. The assumption of random parasitism within patches can easily be changed to one of aggregated attacks by replacing the zero term of the Poisson distribution in equation 3a,b to that of the negative binomial distribution (May 1978). In this case, aggregation increases as the clumping parameter,  $k$ , tends to zero, while random parasitism is recovered as  $k \rightarrow \infty$ . Parasitism is assumed to be random within patches in all the numerical examples below unless specifically stated otherwise.

## Results

The model with the parameters  $a$  and  $c$  scaled depends on four parameters: the host rate of increase,  $\lambda$ , the dispersal fractions  $\mu_N$  and  $\mu_P$ , and the width of the square grid of patches,  $n$ . Also, the boundary conditions may be reflective, absorptive or cyclic, as described above. Simulations are started with random host and parasitoid populations in a single patch, with all other patches empty.

Simulations with small arenas ( $n \leq 10$ ) are almost always observed to become extinct in less than a few hundred generations (except for the 'crystal lattice' cases described below). The mechanics of extinction in the computer simulations generally involves numeric underflows (i.e. the setting to zero of numbers less than  $10^{-38}$  due to restrictions on the computer's representation of small numbers). This can be made more explicit by imposing minimum and maximum host densities, as described in Appendix A. With a reasonably large range of densities the result is unchanged; both the metapopulation, as well as its constituent patches, show divergent oscillations of both populations leading to global extinction.

Markedly different results are obtained when the arena width is increased to between 15 and 30 patches. Three general types of behaviour are found, which we describe as 'spirals', 'spatial chaos' and 'crystal lattices' (see Fig. 1). All three behaviours permit long-term persistence of the host and parasitoid populations, with a relatively narrow range of population densities (see Fig. 2). The behaviours may be characterized as follows.

*Spatial chaos.* The host and parasitoid populations fluctuate from patch to patch with no long-term spatial organization. Randomly oriented wave-fronts are observed, but each persists only briefly. The total metapopulations generally remain within narrow bounds, but occasional large excursions are observed. Despite the lack of recognizable structure, the populations appear to coexist indefinitely if the arena is sufficiently large.

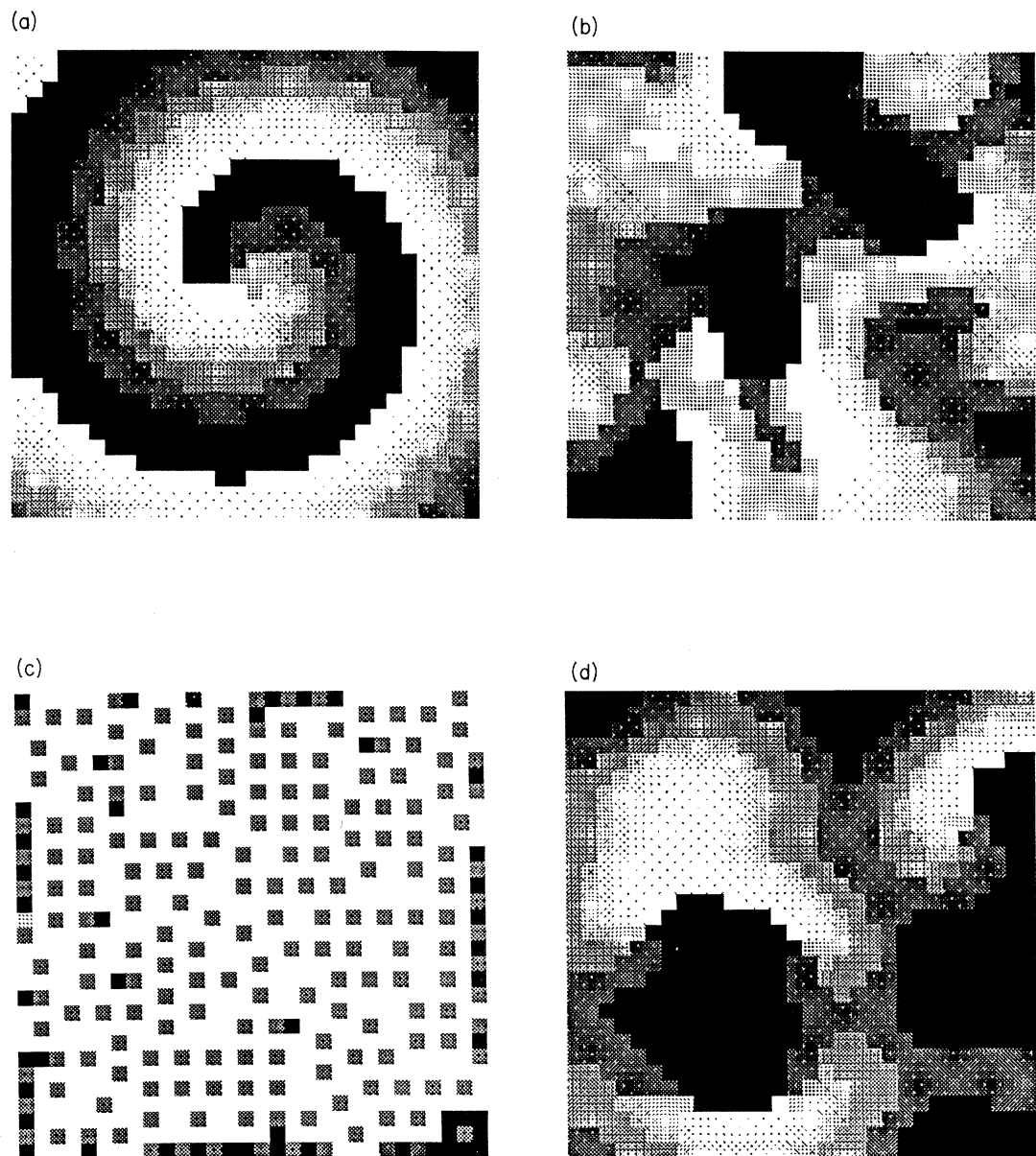
*Spiral structure.* In this case the local population densities form spiral waves which rotate in either direction around almost immobile focal points. The phase-space dynamics of each patch are almost as docile as a discrete-generation approximation to a limit cycle (i.e. a close approximation to a fixed track, even though no exact repetition occurs). However, strictly speaking, it is still chaotic, since the position and number of focal points varies slowly with time in non-repeating patterns.

*Crystalline structures.* Some extreme combinations of dispersal fractions give persistent 'crystal lattice-like' structures in which relatively high density patches occur at a spacing of two grid units. These patterns are statistically stable, and may give stable coexistence even when  $n = 2$ . The current model should be regarded as predicting the general possibility of fairly evenly arranged stable patterns of characteristically high and low density patches, rather than predicting the precise form of these lattice-like patterns (which depend heavily on the artificially imposed square grid).

Examples of these different behaviours are shown in Fig. 3 for the cases  $\lambda = 2$  and  $\lambda = 10$ . Note that the boundaries are imprecise as one behaviour shades into another. Thus, the apparently chaotic fluctuations near the chaos-spiral boundary exhibit features which appear subjectively to be short-lived spirals. Similarly, there are intermediate cases between crystal lattices and chaos; these exhibit relatively constant patches with crystalline spacing, in a matrix of spatial chaos.

Non-persistence for  $n = 30$  may occur for two reasons. First and less importantly, the starting conditions for the simulation may not be suitable (this is discussed further in the next section). The areas in Fig. 3 described as 'hard to start spirals' do not persist when started in a particular manner from a single non-empty cell. However, once spirals have been initiated, they permit persistence in all cases. The second reason for non-persistence is intrinsic dynamic instability. This is restricted to parameter combinations in which either  $\mu_N$  or  $\mu_P$  is very low. It is difficult to delineate the non-persistence area exactly, but in the two cases shown it is contained within the parameter space area where  $\mu_N < 0.02$  or  $\mu_P < 0.02$ .

The large area of parameter space over which populations persist in this model runs counter to the view that dispersal or migration cannot be stabilizing in the absence of density dependence or extrinsic spatial variation. This view is based largely on the intuition that dispersal should tend to make all subpopulations equal in the absence of any external differences between patches (once the populations are equal it is easily shown that the dynamics are not stabilized by dispersal). The equalizing effect of



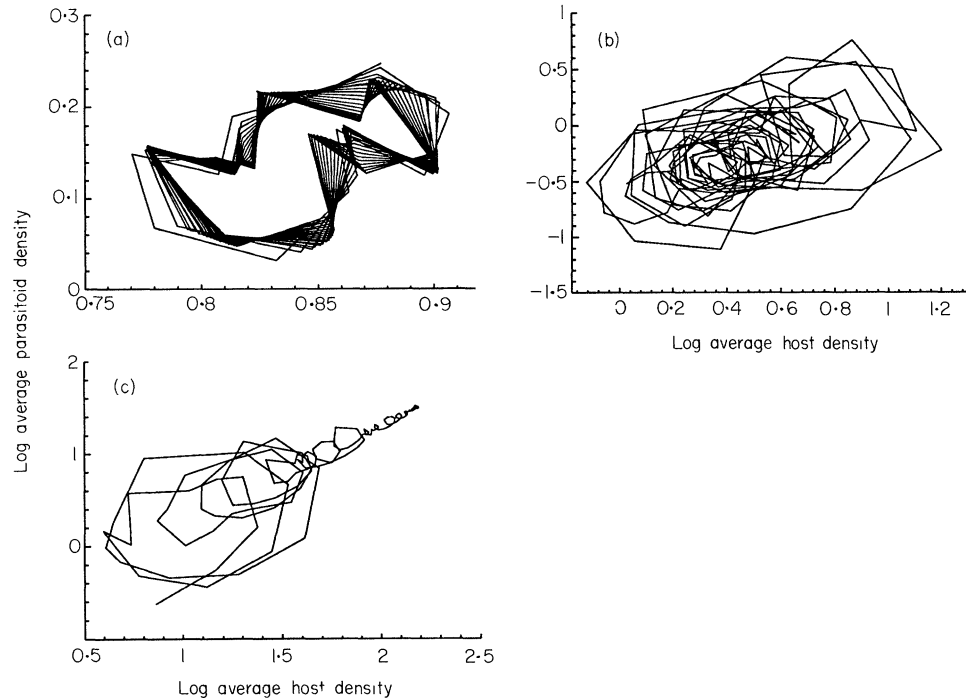
**Fig. 1.** Instantaneous maps of population density for simulations of the dispersal model with Nicholson-Bailey local dynamics, with  $\lambda = 2$  and arena width of 30 patches. Different levels of shading represent different densities of hosts and parasitoids. Black squares represent empty patches; dark shades becoming paler represent patches with increasing host densities; light shades to white represent patches with hosts and increasing parasitoid densities. (a) spirals:  $\mu_N = 1$ ,  $\mu_P = 0.89$ ; (b) spatial chaos:  $\mu_N = 0.2$ ,  $\mu_P = 0.89$ ; (c) crystalline structures:  $\mu_N = 0.05$ ,  $\mu_P = 1$ . Case (d) is a similar map obtained with Lotka-Volterra local dynamics (May 1973), using  $\lambda = 1.4$ , the parasitoid death rate,  $d = 0.9$ ,  $\mu_N = 0.8$ ,  $\mu_P = 0.8$ ; it exhibits highly variable spirals. (The maps are single frames from simulations over many generations, which take about 0.2 s per generation on a 33 MHz 80486 personal computer.)

dispersal may be demonstrated analytically for the continuous-time Lotka-Volterra model with diffusion (Britton 1986, p. 21), and can be generalized to other two-population continuous-time diffusion models with either point-stable or neutrally stable local dynamics.

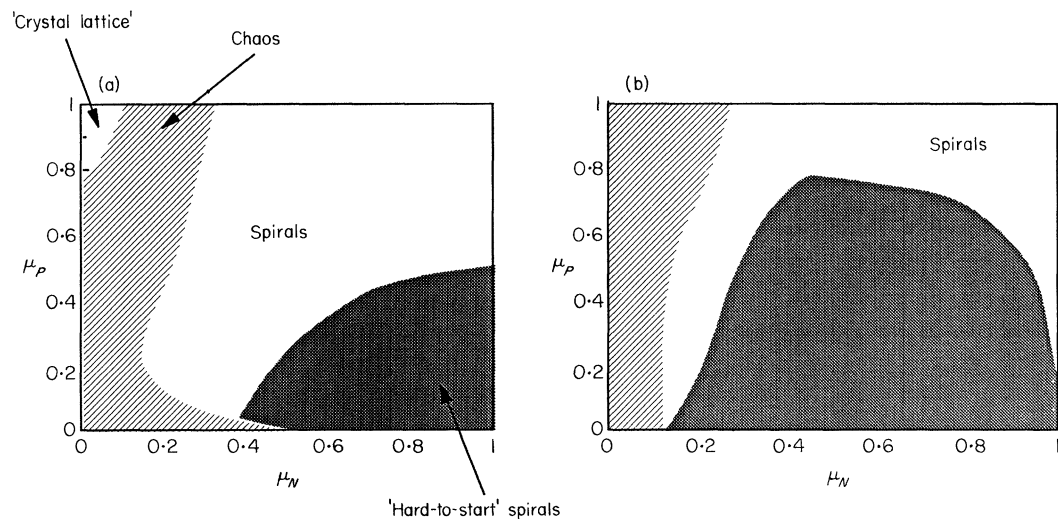
The present model shows that the intuitive view of dispersal as an equalizing force may be inadequate for models where the within-patch dynamics are oscillatorily unstable. In this case, self-maintaining spatial patterns may arise, which intrinsically maintain differences between adjacent patches and thus

invalidate the usual conclusions based on equal populations at equilibrium. This result is particularly interesting for predator-prey population dynamics, since the simplest discrete-generation, predator-prey models are oscillatorily unstable. This applies not only to the Nicholson-Bailey model, but also to the discrete-generation Lotka-Volterra model (May 1973) which similarly produces self-maintaining patterns leading to persistence (see Fig. 1d).

The possibility that diffusion may create self-organizing structures is well recognized in other fields. The Belousov-Zhabotinskii reaction (Roux



**Fig. 2.** Phase-space plots of mean population densities for the same parameters as in Fig. 1a–c: (a) spirals, (b) spatial chaos, (c) crystalline structures. Cases (a) and (b) are typical phase-space plots during long-term persistence; whereas (c) shows the damping of initial variation as crystalline structures are formed, leading to a static equilibrium (limit point at top right).



**Fig. 3.** Dependence of the observed persistent spatial pattern on  $\mu_N$  and  $\mu_P$  for arena width 30: (a)  $\lambda = 2$ , (b)  $\lambda = 10$ . The boundaries are obtained by simulation, and are approximate (and partly subjective). The hatched areas indicate the regions in which the spatial pattern is chaotic. The shaded areas represent parameter combinations for which the persistent spatial pattern is unlikely to be established by starting the simulation with a single non-empty patch. Spirals may be established in these cases by starting with a lower  $\mu_N$  and increasing it after 50–100 generations. Non-persistence occurs for some combinations with very small  $\mu_N$  or  $\mu_P$ ; this area is imperceptible in the figures.

*et al.* 1981) is a well-known chemical system in which reactions and diffusion interact to generate visible spiral patterns. Other reaction–diffusion differential equations have applications in physics, epidemiology, developmental biology and biochemistry (Murray 1989). Finite-state cellular automata are only broadly analogous to reaction–diffusion models,

but are also observed to evolve self-maintaining spiral patterns (see below) (Leichleiter *et al.* 1991).

Our use of the term ‘persistent’ in describing the spiral structures requires some caution. Phase-space portraits of the *average* population sizes for simulations with persisting spirals may yield graphs reminiscent of a discrete-generation approximation

to a limit cycle (see Fig. 2a and Fig. 5 below). Furthermore, the same qualitative pattern of spirals may be observed over thousands of simulated generations. Nevertheless, the location of spiral foci is usually variable (with apparently chaotic variations) and, if two foci come close enough together, they may annihilate each other. It is thus conceivable that the populations might become extinct if a spiral is broken up and not replaced, and hence the observed coexistence may be transitory on a very long time scale.

Empirically, it appears that there are weak forces which govern the relative spacing (and hence spatial density) of spirals. Characterizing these forces fully would require a detailed analytical treatment, or extensive simulations in large arenas, both of which are currently unfeasible.

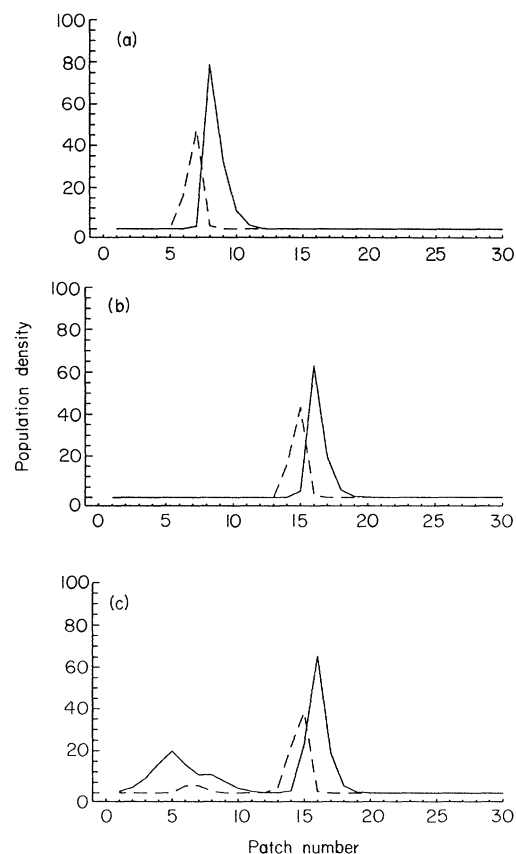
### Analysis

#### BASIS OF PERSISTENCE

The dynamical behaviour of the model (in either spatially chaotic or spiral realms) is founded on the propagation of a wave, in which a front of hosts invades (almost) unoccupied space, and is then consumed by a wave of parasitoids, which then die out. Figure 4a and b illustrate the propagation of a plane wave-front in our diffusion model. Note that host and parasitoid densities are reduced once more to very low densities following the passage of the wave front. In the case of stable or neutrally stable single-patch dynamics (illustrated in Fig. 4c by introducing negative binomial parasitoid attacks with  $k = 1$ ) the wave does not maintain the distance of  $N_t$ ,  $P_t$  from the equilibrium point in phase space, and spatial variations eventually die out.

Suppose then that we have dynamics within a patch that are oscillatorily unstable, so that the passage of a wave-front tends to produce lower host and parasitoid densities in the train of the wave than those in front of it. If the wave is expanding on a circular front, then the interior space is left with relatively low population densities. Since the host population grows much faster than the parasitoid population when both are rare, a second wave-front can be generated within the circle. This reduces the densities even further, and the passage of repeated circular fronts leads to extinction in a way that mirrors the diverging cycles of the single-patch, Nicholson-Bailey model.

Suppose, however, that there are gaps in the circular wave-front. Then patches which were not in the path of the wave will be adjacent to those in its train. Dispersal from the unaffected patches can recolonize those in the wave train, thus limiting the extremes of low density which the wave can produce. Preventing the occurrence of very low densities prevents the Nicholson-Bailey cycles from attaining



**Fig. 4.** Propagation of a predator–prey wave-front in the dispersal model with Nicholson-Bailey dynamics ( $\mu_N = 0.6$ ,  $\mu_P = 0.02$ ). The initial conditions are specially contrived so that the wave-front is linear (and horizontal). (a) Initial conditions, (b) after 10 generations, (c) after 10 generations with negative binomial parasitoid attacks ( $k = 1$ ). Solid lines are hosts; dashed lines are parasitoids.

large amplitudes, and so prevents extinction. We can thus explain the persistence afforded by the two major forms of spatial pattern which are observed.

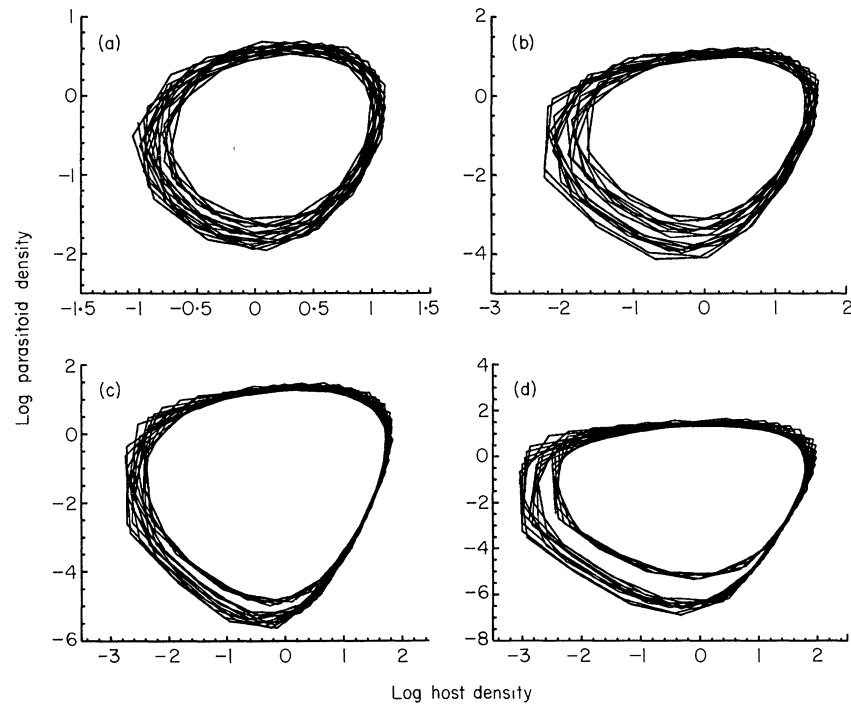
*Spatial chaos.* A sufficiently complex set of intersecting wave fronts is established so that patches in the train of any wave are likely to contact those near the peak of other wave-fronts.

*Spirals.* The spiral is an organized structure which ensures that patches in the train of a wave are in contact with undepleted patches. In continuous reaction–diffusion equations the population densities do not vary at the focus of a spiral wave (since it is at the intersection of the lines of phase of the cyclic variations in the surrounding area (Murray 1989, p. 347)). Spiral foci in our spatially discrete model approximate this condition, so population densities at the foci are roughly constant. Populations may diffuse from the focus into the areas nearby which have been depleted by a passing wave-front (i.e. the spiral arm). Note that the topology of the spiral makes this possible. This diffusion tends to

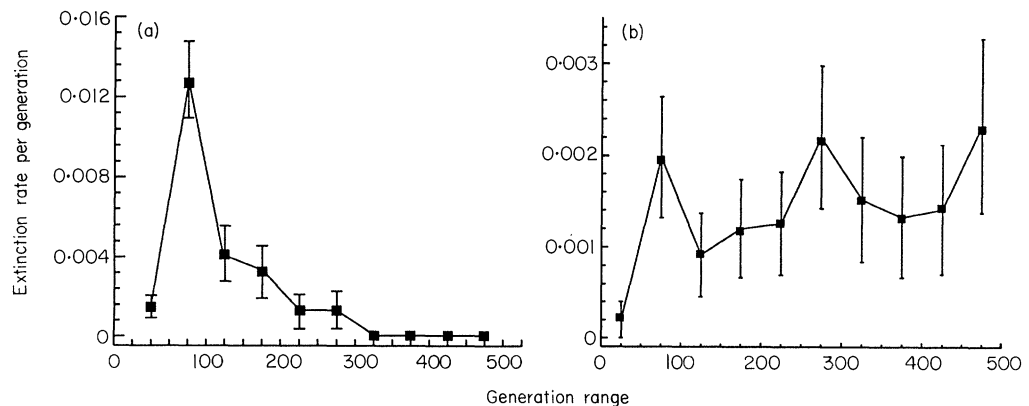
limit variation in areas close to the focus. Similarly, populations may diffuse from these variation-limited patches into depleted patches even further out. The result is a progression from little-changing to violently oscillating population densities as we move out from focus (see Fig. 5). The progression is ultimately limited by the proximity of a neighbouring spiral or the edge of the arena.

Provided the arena is sufficiently large, we find that systems with established spatial chaos or spirals are very much more likely to persist than arbitrarily

selected population density patterns. We have never been able to establish coexistence from an initial uncorrelated, uniformly random pattern (this approximates a constant initial density when averaged over the wavelength of the host–parasitoid wave-fronts). Simulations started from a single non-empty patch establish to the extent that they develop spatial chaos or spirals. Figure 6a dramatically illustrates how, with a sufficiently large arena size, the extinction of single-starting-patch simulations is associated with their maturation into self-maintaining



**Fig. 5.** Phase-space traces for patches at increasing distances from a spiral focus, with arena size 30,  $\lambda = 2$ ,  $\mu_N = 0.5$ ,  $\mu_P = 0.5$ . In order to obtain reliable results, the focus is pinned in the manner described in Appendix B, using  $r = 0.9$ .



**Fig. 6.** Extinction probability per generation (with error bars from the Poisson approximation), as a function of time after starting a simulation with a single non-empty patch (third from left in top row). 100 simulations were performed, in which the initial patch had independent uniformly distributed host and parasitoid densities. Extinction probability is assumed equal for each generation in a block of 50. (a)  $\mu_N = 0.8$ ,  $\mu_P = 0.89$ ,  $\lambda = 2$ ,  $n = 15$ ; 31 of the simulations persisted to the 500th generation (all showing spiral patterns). (b)  $\mu_N = 0.2$ ,  $\mu_P = 0.5$ ,  $\lambda = 2$ ,  $n = 10$ ; 49 of the simulations persisted to the 500th generation (showing chaotic spirals).



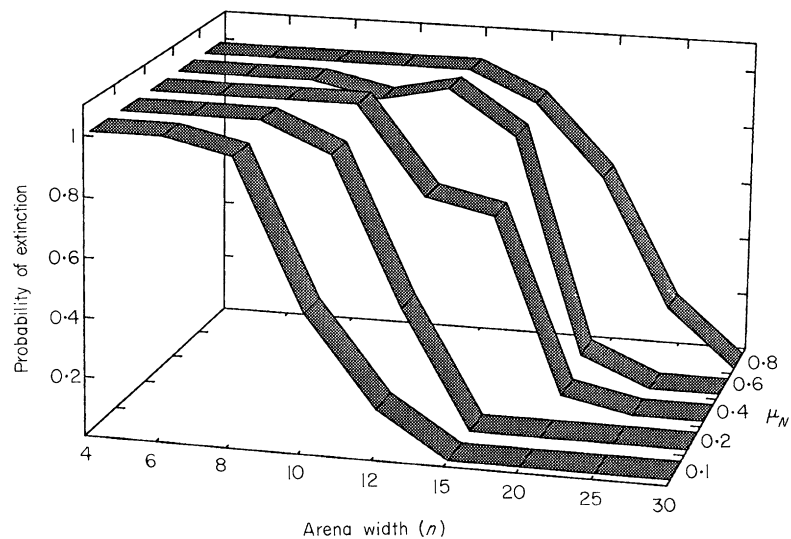
patterns. No extinctions were observed after the first 300 generations.

On the other hand, simulations in sufficiently small arenas go extinct even when spirals have evolved. Figure 6b illustrates the non-declining extinction probability observed in such a case. This indicates that no long-term persistent patterns are possible.

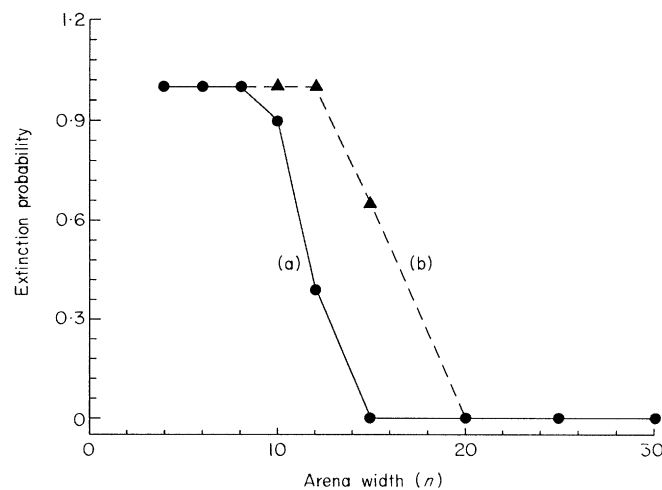
Figure 7 shows how the probability of long-term persistence varies with arena width, for various parameter combinations. Intuitively, it appears that failure to persist in small arenas is due to the insufficient space to fit a self-maintaining pattern. We expect the pattern to scale with the individual dispersal distance; thus we can test this 'minimal pattern space' hypothesis by increasing individual dispersal distance. We use a variant of the model in which

equal fractions of dispersal occur to the 12 nearest neighbours of each patch (rather than the eight nearest in the standard model). This is observed to produce somewhat wider spirals. Figure 8 shows how the probability of persistence varies with arena size for two cases which differ only in the dispersal pattern. The critical arena size (50% survival) is increased by a factor of about 1.3. This lies between the ratio of average dispersal distances, 1.22, and the ratio of maximum dispersal distances, 1.414 [the ratio of average distances is calculated by dividing  $1.471 = (4 \times 1 + 4 \times 1.414 + 4 \times 2)/12$  by  $1.207 = (4 \times 1 + 4 \times 1.414)/8$ ].

Since simulations of greater dispersal distances require more calculations per patch and also larger arena sizes for stability, we are currently prevented from using larger dispersal patterns by problems of



**Fig. 7.** Extinction probabilities for simulations started in various sizes of arena of width,  $n$ , by setting non-zero population densities in only the third patch from the left in the top row ( $\mu_p = 0.89$ ,  $\lambda = 2$ , arena width 30). The host and parasitoid densities in the initial patch are independently uniformly distributed.



**Fig. 8.** Extinction probabilities as a function of arena size for  $\lambda = 2$ ,  $\mu_N = 0.2$ ,  $\mu_p = 0.89$ : (a) equal dispersal to eight nearest neighbour patches, (b) equal dispersal to 12 nearest neighbour patches (eight orthogonal, four diagonal).

computational convenience. However, one further variant of the model has been tried, with additional global parasitoid dispersal (equal dispersal to all patches). The model is quite sensitive to the fraction of parasitoids performing global dispersal. For example, in the case shown in Fig. 1a, 2% of parasitoids dispersing globally causes a different spiral pattern to evolve, while 10% causes extinction. A detailed examination of mixed local and global dispersal is beyond the scope of this paper.

#### SENSITIVITY ANALYSIS

##### *Host rate of increase*

Varying the host rate of increase ( $\lambda$ ) has complex effects on the model. Persistence is possible, however, for  $\lambda$  ranging from close to unity to very large. We have noted the following effects.

1. For large  $\lambda > 10$  it becomes difficult to establish self-maintaining patterns from a single non-empty cell. This is because any circular wavefronts which are generated initially cause more violent oscillations and more rapid extinction than they do with small  $\lambda$ . Once established, spirals may be stable for very large  $\lambda$  (up to about 200).
2. Increasing  $\lambda$  reduces the number of generations which are required by a patch to complete a cycle in phase-space. This means that wave-fronts are thinner, and hence persistent patterns such as spirals have a reduced spatial scale. Conversely, the spatial scale is increased for small  $\lambda$ . There is thus a minimum value of  $\lambda$  for which a persistent pattern will fit into a given sized arena (for  $n = 30$  spirals can be established for  $\lambda > 1.2$ ).
3. Increasing  $\lambda$  appears to favour the formation of spirals (rather than spatial chaos) at low host dispersal rates (compare Fig. 3a and 3b). This may be because large  $\lambda$  increase the effectiveness of host dispersal (diffusion over several generations from occupied patches is effectively faster if aided by rapid reproduction in newly infected patches).

##### *Within-patch stability*

Parasitism within patches in equations 3a,b is random and therefore inherently destabilizing. To explore the effects of stabilizing parasitism, we use May's (1978) negative binomial distribution of attacks within patches, which gives

$$S = \left(1 + \frac{aP_t'}{k}\right) \quad \text{eqn 4a}$$

$$N_{t+1} = \lambda N_t S \quad \text{eqn 4b}$$

$$P_{t+1} = cN_t(1 - S) \quad \text{eqn 4c}$$

Here  $k$  expresses the degree of contagion in the distribution of parasitoid attacks (random when  $k \rightarrow \infty$  and increasingly clumped as  $k \rightarrow 0$ ). With  $k < 1$ , the

single-patch dynamics are stable, as is the total population over all patches. Only if the within-patch dynamics are oscillatorily unstable, do we obtain the range of patterns shown in Fig. 1. For example, in the case  $\mu_N = 0.8$ ,  $\mu_P = 0.89$ ,  $\lambda = 2$  and  $n = 30$ ,  $k \geq 1.2$  is needed in order to establish persisting metapopulation dynamics starting from a single non-empty patch. Reducing  $k$  has the same effect as reducing  $\lambda$ , by increasing the scale size of self-maintaining patterns. Thus, with  $k \leq 1.2$  in the above example it is impossible to fit a self-maintaining pattern in an arena of width 30 patches. In general, therefore, almost-stable dynamics within patches make it difficult to achieve coexistence through the effects of dispersal.

##### *Random noise*

The models described so far reveal underlying patterns that can occur in a patchy environment with diffusive dispersal. We now consider to what extent these are resistant to superimposed random variation from patch to patch. Such random patch-to-patch variation has been introduced as a random multiplier for the host rate of increase,  $\lambda$ . In this case there is a distinction between two possible models, depending on the stage of the host life-cycle which is affected by parasitism. By applying the same patch-dependent multiplier to  $\lambda$  and  $c$  in equations 3a,b, we are considering the case in which parasitism follows egg-to-pupal survival within a patch (i.e. pupal parasitism). Interestingly, with the exception of the crystal lattice pattern which is quite easily disrupted, the different spatial patterns remain clearly evident even with quite appreciable levels of random variation. We also find that random multipliers with no patch-to-patch covariance increase the probability that self-maintaining patterns will be established. For example, in simulations with  $\lambda = 2$ ,  $n = 30$ , spatial chaos and spirals may be generated from completely uniform initial population densities if the growth-factor multiplier is chosen uniformly from the range 0.25–3.

It is arguable that the interaction of dispersal with patch-to-patch variability would by itself permit persistence. Thus, it probably aids establishment by preventing extinction before a persistent pattern is established. Once spirals are established the random noise has little effect on their evolution, since the patch-to-patch scale of variation is much smaller than the spatial scale of spirals. This would also appear to be true of spatial chaos, although only a subjective opinion can be offered.

It is also possible to consider spatially correlated random noise, with a scale of variation much larger than the distance between neighbouring patches. This question is outside the scope of the present paper, and is explored elsewhere (Hassell, Godfray & Comins 1992).

**Cellular automata as an alternative model structure**

In the models described so far we have used explicit expressions for the dynamics in each patch and the movement to neighbouring patches. We now show that a similar range of behaviour is obtained when we explore a cellular automaton approach, in which we acknowledge only qualitative categories of patch densities and a very simple set of ‘transition rules’. These rules are only qualitative embodiments of the biology described above. The value of this approach is in emphasizing those general properties of mathematically explicit models that are detail-independent and as such have been rather neglected as tools for exploring the robustness of conclusions about population dynamics (but see Crawley & May 1987).

We commence by denoting the possible states of single cells in a cellular automaton model by letters ‘*ABC...I*’. There are only a finite number of possible cell states, as opposed to the continuous set of host and parasitoid population densities in a patch in the host–parasitoid models. In each generation the state of every cell in a square arena may change to a new state. Diffusive effects are paralleled by the fact that the new state depends not only on the current state of the given cell, but on the states of a specified set of neighbour cells. We consider simple isotropic automata, in which the nearest four or eight cells have equal effects, and no other neighbours have any effect.

We write the transition rules of the automaton in the following form: ‘*[ABC]*’ means ‘a state *A* cell becomes a state *B* cell if there is at least one neighbour in state *C*’; ‘*[AB]*’ means ‘a state *A* cell becomes a state *B* cell regardless of neighbours’. If no rules apply then the cell remains in its current state. Simulations are started with an uncorrelated random distribution of states.

The following 10-state automaton attempts to mimic a predator–prey system (*A* = empty patch; *B, C, D* = prey only; *E, F, G, H, I* = prey and predators; *J* = predators only).

Prey invade: *[AB]B*

Prey multiply: *[BC], [CD]*

Predators invade: *[DEF]*

Predators multiply: *[EF], [FG], [GH], [HI], [IJ]*

Predators die: *[JA]*

With four neighbours this model produces persistent wave-fronts in non-repeating patterns (Fig. 9b). The results are qualitatively similar to the spatial chaos in the Nicholson-Bailey model with diffusive dispersal.

The automaton may be generalized by using different numbers of ‘prey-only’ and ‘prey-plus-predator’ states. This has only a weak effect on the results. The model is much more sensitive to changes in the invasion rules, such as changing *[AB]B* to *[AB]C* or

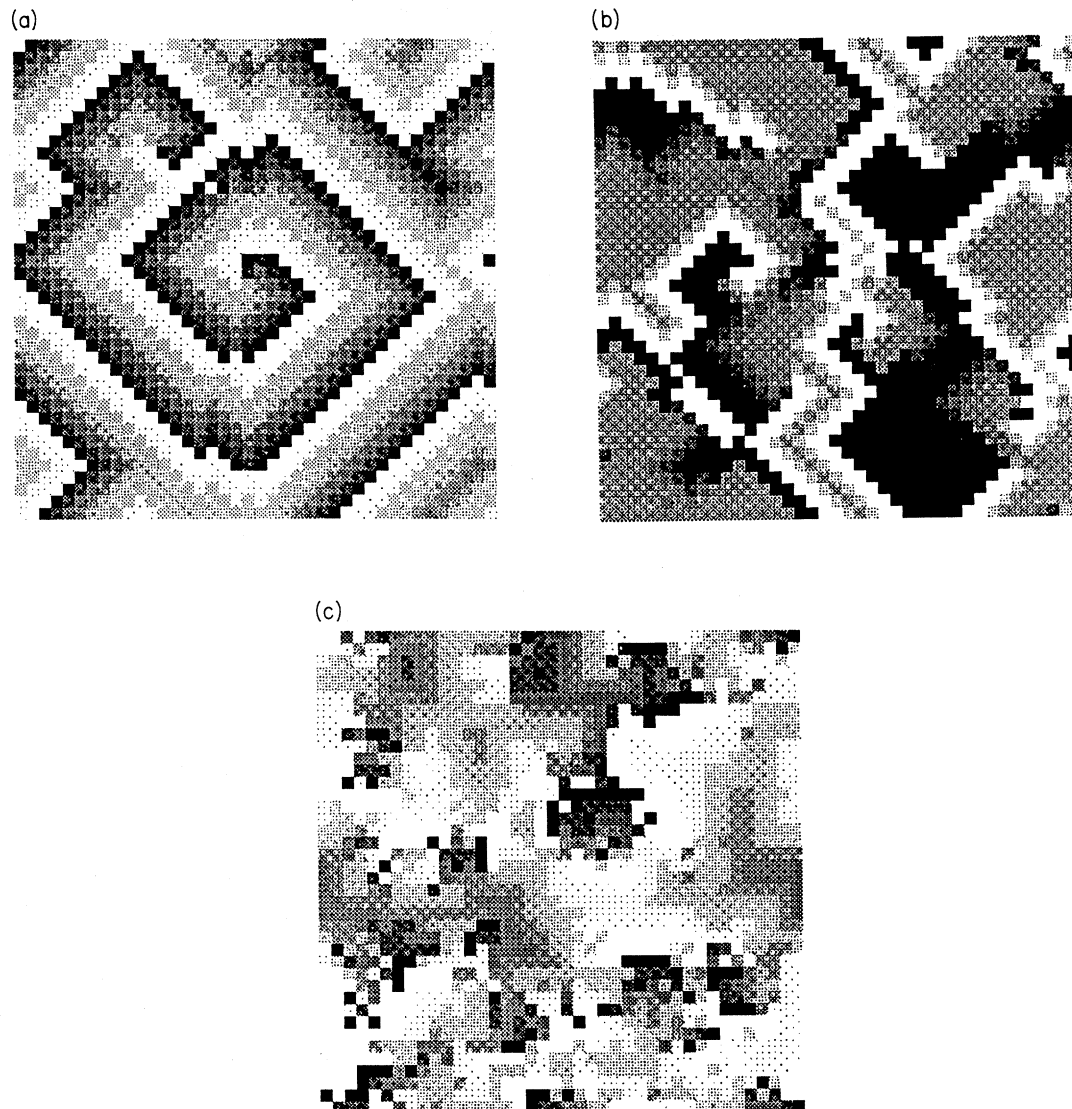
*[AB]D*, and changing *[DE]F* to *[DE]E*, *[DE]G* or *[DE]H*. These particular rule changes alter the speed of the invading wave-fronts (prey invading empty cells and predators invading prey-only cells, respectively) and are analogous to  $\mu_N$  and  $\mu_P$  in the diffusion model. The wave-front speeds may also be modified by using eight nearest neighbours rather than four. This class of models yields examples of spiral and crystal lattice behaviour as well as chaos (Fig. 9). A fuller treatment of such cellular automata will be given elsewhere (H.N. Comins, M.P. Hassell & R.M. May, unpublished).

Caution must be exercised in regarding cellular automata as highly simplified versions of biological models with diffusion, since the information flow between neighbouring cells is only an analogy to diffusion. In ordinary diffusion, the speed of wave-fronts is determined by easily understood parameters such as  $\mu_N$ . In the case of cellular automata, it may be determined by rather subtle properties of the transition rules. These effects must be correctly understood before any conclusions are drawn.

**Conclusions**

In a homogeneous environment, host–parasitoid interactions with discrete generations will not persist unless the parasitoids attack hosts non-randomly, or unless host or parasitoid populations exhibit some form of density-dependent effect. In a subdivided environment, previous work has shown that such associations can persist with parasitoids searching randomly within patches, provided that the hosts in each generation are sufficiently aggregated in their distribution among patches and that there is sufficient variability in the density of searching parasitoids in the vicinity of individual hosts (e.g. Pacala, Hassell & May 1990; Hassell *et al.* 1991; see also Appendix C). In this paper, we show that a purely deterministic process, namely local dispersal in which constant fractions of hosts and parasitoids ( $\mu_N$  and  $\mu_P$ , respectively) move to immediately neighbouring patches in each generation, can also lead to meta-population persistence, even when parasitoids search randomly within patches and no explicit density-dependent mechanisms are present. The densities of host and parasitoid subpopulations in a two-dimensional ( $n \times n$ ) array of patches can exhibit spiral waves, or spatial chaos, or ‘crystal lattice’ patterns, depending on the magnitude of the parameters,  $\mu_N$  and  $\mu_P$ , and provided  $n$  is big enough.

These complex patterns of spatial variation in population density arise even though the environment in all the patches is the same; the patterning is thus intrinsically generated by the interplay of local dispersal and local dynamics. The complex patterns in the densities of host and parasitoid subpopulations in individual patches (as shown in Fig. 1) are produced by strictly deterministic rules or equations.



**Fig. 9.** Typical cell-state maps for cellular automata (shading as in Fig. 1). (a) Spirals: four neighbours, with invasion rules  $[AB]B$  and  $[DE]E$ ; (b) spatial chaos, with separate prey and predator wave-fronts: four neighbours, with invasion rules  $[AB]B$  and  $[DE]F$ ; (c) crystalline structures: eight neighbours, invasion rules  $[AB]B$  and  $[DE]E$ . These crystals are unchanging, and do not show long-wavelength features. However, they differ from those observed in the Nicholson-Bailey model, in that each cell cycles regularly through the states  $A-J$ , rather than having a constant state (the same map is seen after 10 generations).

These results seem robust, being true for both an explicit mathematical model, and for a cellular automaton model based on qualitatively similar rules.

Habitat size is critical for the persistence of the above patterns. With the exception of the 'crystal lattice' patterns, the probability of extinction rises rapidly as the arena width becomes small. The failure to persist in small arenas appears related to there not being enough space in which to fit the characteristic pattern of the spatial dynamics. For example, the large spiral in Fig. 1a is much more sensitive to reduction in arena size than is the more irregular chaotic pattern in Fig. 1b, while the 'crystal lattice' can even persist in arenas of width two.

These underlying deterministic patterns are rela-

tively insensitive to superimposed random variation at the patch-to-patch level. Hence, random variation in the host growth rate,  $\lambda$ , or in the parasitoid 'survival' parameter,  $c$ , does little to disrupt the pronounced spiral patterns, even with quite appreciable levels of random variation. Only if the scale of random variation approaches, or is greater than, the characteristic scale of the spatial dynamics does it have an important disruptive effect (Hassell, Godfray & Comins 1992). On the other hand, the 'crystal lattice' in Fig. 1c can easily be destroyed by patch-to-patch variation, while the large spiral pattern in Fig. 1a is only obliterated by variation on a much coarser scale.

Pacala, Hassell & May (1990) and Hassell *et al.*

(1991) derived a general criterion for the regulation of host–parasitoid associations in models where the populations have discrete generations and interact in a patchy environment with random exploitation within patches (see also Hassell & Pacala (1990)). The interactions are locally stable if the coefficient of variation squared ( $CV^2$ ) of the density of searching parasitoids in the vicinity of each host exceeds approximately unity (see Appendix C for non-random parasitism within patches). This approximate criterion only depends on the degree of heterogeneity in the risk of parasitism between individual hosts; thus spatial patterns of parasitism that are directly or inversely related to host abundance per patch, or that show no such covariance, can all contribute to population persistence in the same way. In all the simulations carried out in this study, histograms have been produced of the value of  $CV^2$  for each generation. These show the  $CV^2 > 1$  rule to be supported in a qualified way: the associations which persist by virtue of spatial chaos or spirals consistently have  $CV^2$  slightly greater than one; on the other hand, static crystal lattices have  $CV \ll 1$ .

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### Appendix A (local extinction and carrying capacity)

The Nicholson-Bailey model can be made somewhat more realistic by introducing local extinction thresholds and local host carrying capacities. We replace  $N'_i$  in equations 3a,b by the minimum of  $N'_i$  and  $N_{\max}/\lambda$ . If  $N_{t+1}$  is less than  $N_{\min}$  then it is set to zero. Obviously setting a narrow range between the extinction threshold,  $N_{\min}$ , and the host carrying capacity,  $N_{\max}$ , will make persistence difficult. Since we are not interested in this specialized model, but rather wish to make explicit the mechanism of local extinction (rather than relying on numeric underflow), we permit a broad range of host densities, typically from  $N_{\min}$  equal to 0.0001 of the Nicholson-Bailey (unstable) equilibrium to equal to 1000 times the equilibrium.

### Appendix B (pinning spiral foci)

In cases exhibiting stable spirals, the spiral foci move very slowly around the arena, and do not show a preference for being centred at any particular point. For the purpose of analysing the dynamics, it would be more convenient if spirals could be pinned in one place.

This effect can be achieved by endowing one of the patches with a greater than normal tendency to have stable population densities. We replace eqns (3a,b) in this patch by:

$$N_{t+1} = rN_t + (1-r)\lambda N'_t \exp(-aP_t) \quad \text{eqn B1a}$$

$$P_{t+1} = rP_t + (1-r)cN'_t[1 - \exp(-aP_t)] \quad \text{eqn B1b}$$

where the 'retarding factor'  $r$  varies between zero and one (there is no effect when  $r=0$ , whereas the populations in the patch remain constant if  $r=1$ ).

A retarded patch (with say  $r=0.5$ ) is able to attract and pin a spiral focus from a distance of one or two patches. It has negligible effect on the spiral dynamics, as judged by the visual appearance of the spiral when pinned and not pinned.

### Appendix C (effective $CV^2$ )

Hassell *et al.* (1991) show that the ' $CV^2 > 1$  rule' is either exactly or approximately true as a local stability condition for a number of examples of host-parasitoid associations in patchy environments where the only stabilizing process is the heterogeneity in the distribution of parasitoids from patch to patch. In this appendix we give an example of the extent to which this rule is affected by the additional stabilizing effect of non-random parasitism within patches, in this case achieved by using the zero term of the negative binomial distribution for host survival within patches (May 1978). It is to be expected that lower levels of  $CV^2$  are needed for persistence as the

parameter,  $k$ , of the negative binomial distribution decreases.

Consider the following patchy model with complete mixing of the populations once in each generation:

$$N_{t+1} = \lambda \sum_j \alpha_j N_t S(\beta_j P_t) \quad \text{eqn C1a}$$

$$P_{t+1} = \sum_j \alpha_j N_t [1 - S(\beta_j P_t)] \quad \text{eqn C1b}$$

$$S(\beta_j P_t) = \left(1 + \frac{\beta_j P_t}{k}\right)^{-k} \quad \text{eqn C1c}$$

where the  $\alpha_j$  and  $\beta_j$  are the fractions of total hosts and total adult parasitoids, respectively, in the  $j$ th patch and thus sum to unity, and  $S(\beta_j P_t) = (1 + \beta_j P_t/k)^{-k}$ .

Using linearized stability analysis, one can show that the equilibrium is stable if the following criterion is satisfied:

$$\left(\frac{1}{\lambda}\right) - \left(\frac{1}{\lambda}\right)^2 > P^* \sum_j \alpha_j \beta_j \left(1 + \frac{\beta_j P_t}{k}\right)^{-(k-1)} \quad \text{eqn C2}$$

where  $P^*$  is the equilibrium parasitoid density.

In the limit  $\lambda \rightarrow 1$ , we have  $P^* \rightarrow 0$ . Regarding  $P^*$  as the independent variable, and using the equilibrium condition:

$$\frac{1}{\lambda} = \sum_j \alpha_j S(\beta_j P^*) \quad \text{eqn C3}$$

we can expand equation C2 in powers of  $P^*$ . Keeping only terms of order larger than  $(P^*)^3$ , we derive

$$\left[ \sum_j \alpha_j \beta_j^2 / \left( \sum_j \alpha_j \beta_j \right)^2 \right] \left(1 + \frac{1}{k}\right) > 2. \quad \text{eqn C4}$$

The term in the square bracket is  $1 + CV^2$ . Thus, the  $CV^2$  criterion is generalized to

$$(1 + CV^2) \left(1 + \frac{1}{k}\right) > 2. \quad \text{eqn C5}$$

Thus, no between-patch heterogeneity is needed for stability if the within-patch parasitism is sufficiently non-random ( $k \leq 1$  in this example), and only modest levels of  $CV^2$  are required for intermediate levels of  $k$  (e.g. for  $k=2$ ,  $CV^2 \geq 0.33$  is needed for stability).

### Appendix D ('crystalline' structures)

We consider the limiting cases of equations (1-3) where  $\mu_P = 1$  and  $\mu_N$  is very small. Consider a very small arena in which a single patch with very high host and parasitoid densities,  $N_1$  and  $P_1$ , respectively, is surrounded by  $r \leq 8$  patches containing no hosts and a low density of parasitoids. In the dispersal step the parasitoids in the high-density patch all move to the other patches, along with a small proportion of the hosts. To a good approximation, all of these emigrant hosts are parasitized, leaving no hosts and equal parasitoid populations in the other patches. Thus in subsequent generations, all the surrounding patches have the same parasitoid density. We denote

the current parasitoid density in surrounding patches by  $P_2$ . The population dynamics is thus represented by the following equations:

$$N_{1,t+1} = \lambda(1 - \mu_N)N_{1,t}\exp(-aP'_t) \quad \text{eqn D1a}$$

$$P_{1,t+1} = c(1 - \mu_N)N_{1,t}[1 - \exp(-aP'_t)] \quad \text{eqn D1b}$$

$$P_{2,t+1} = c(\mu_N/8)N_{1,t} \quad \text{eqn D1c}$$

$$P'_t = (r/8)P_{2,t} \quad \text{eqn D1d}$$

It is apparent that  $P_1$  does not occur on the right-hand side of the equations, and it may thus be ignored. The equilibrium values of  $N_1$  and  $P_2$  are found to be:

$$N_1^* = [8/c\mu_N]P_2^* \quad \text{eqn D2a}$$

$$P_2^* = (8/r)\ln[\lambda(1 - \mu_N)] \quad \text{eqn D2b}$$

and linear stability analysis shows that this is stable if

$$\ln(\lambda(1 - \mu_N)) < 1. \quad \text{eqn D3}$$

Since  $\mu_N$  is small, this condition is approximately  $\lambda < e = 2.718\dots$ . Simulations show further that values of  $\lambda$  in the approximate range 2.7–3.4 lead to stable limit cycles.