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Dynamic heterogeneous spatio-temporal pattern formation in host-parasitoid systems with synchronised generations

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Abstract. In this paper we develop a general mathematical model describing the spatio-temporal dynamics of host-parasitoid systems with forced generational synchronisation, for example seasonally induced diapause. The model itself may be described as an individual-based stochastic model with the individual movement rules derived from an underlying continuum PDE model. This approach permits direct comparison between the discrete model and the continuum model. The model includes both within-generation and between-generation mechanisms for population regulation and focuses on the interactions between immobile juvenile hosts, adult hosts and adult parasitoids in a two-dimensional domain. These interactions are mediated, as they are in many such host-parasitoid systems, by the presence of a volatile semio-chemical (kairomone) emitted by the hosts or the hosts' food plant. The model investigates the effects on population dynamics for different host versus parasitoid movement strategies as well as the transient dynamics leading to steady states. Despite some agreement between the individual and continuum models for certain motility parameter ranges, the model dynamics diverge when host and parasitoid motilities are unequal. The individual-based model maintains spatially heterogeneous oscillatory dynamics when the continuum model predicts a homogeneous steady state. We discuss the implications of these results for mechanistic models of phenotype evolution.

1. Introduction

Insect parasitoids are those insects which have in common a life cycle where the adults are free-living, but where the juvenile stages (larvae) are parasitic on other arthropods, usually the immature stages of other insects (11). Parasitoids have been a long-standing focus of research interest for both biologists and theoreticians for reasons which can be understood in terms either of their intrinsic biological

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importance or of their convenience as experimental systems with which to test mathematical models, or both. Their sheer diversity ($\sim 10\%$ of all multicellular animals), for example, means that they must play a significant role in the structure and dynamics of many natural ecological communities. Within this enormously diverse assemblage there exists a great variety of life history types, and it may be fair to say that, beyond what has been said above, there is no typical parasitoid.

There is, however, a sufficient degree of commonality for parasitoid-host associations to have become the favoured experimental metaphor for a much wider range of trophic interactions such as predator-prey, host-pathogen and plant-herbivore systems. Their generally small size and short lives make them easy to study in the laboratory, and most temperate species exhibit discrete, non-overlapping generations which gives them an additional utility in theoretical studies. Finally, the much more direct link between the numbers of eggs laid by a female parasitoid and the numbers of her offspring in the next generation, enables a much closer match between theory and experiment than is possible for, say, predator-prey systems. An excellent general introduction to host-parasitoid systems is given by (15).

Host-parasitoid systems therefore have proved fruitful models for many experimental and theoretical investigations in ecology and there is a rich literature on parasitoid population dynamics (see (15; 18; 21) and the references therein). In this paper we consider the spatio-temporal dynamics of interacting host-parasitoid systems. Although the area of host-parasitoid modelling has a fairly long history, there has been relatively little work done on systems which model spatial interactions explicitly. Much research has gone into investigating how models can produce realistic, stable solutions. Attention has focused on the lack of biological realism in the assumption that parasitoids search randomly. For example (19) suggested that foraging patterns of individuals resulted in the aggregation of parasitoids. (17; 29) introduced density-dependence in the rates of parasitism and (28) considered multi-trophic layers. There has also been increasing interest in the effects of spatial heterogeneity, particularly in meta-population models (see (9; 20; 22; 40; 44)). Modelling the dynamics of host-parasitoids in spatially-structured patchy environments requires a knowledge of the mechanisms used for patch selection, host location and other dispersal activity.

Although there has been much pioneering work carried out using discrete-generation nonlinear difference equation models (17; 19) one of the weaknesses with this approach to modelling the dynamics of a host-parasitoid system is that the structure of the model only gives the possibility of including phenomena such as density-dependence in a discrete manner. This may not actually reflect the underlying mechanism causing the density-dependence, which may in fact act in a continuous manner over the life-history stage of an organism, within the generation. If the basic rate of increase of parasitism is high, this can lead to over-compensation in the density-dependent alteration to the rates, leading to instability in the model and highly oscillatory dynamics. To avoid this, potentially unrealistically low intrinsic *per capita* rates of increase are needed for the organisms. The phenomenon of low increase rates is then accounted for by "other mortality" which is not included directly by the explicit mechanisms of the model.

If a density-dependent change in rate were caused by a mechanism that acted gradually during the generation, this extreme over-compensation is unlikely to happen. For example, a limitation on suitable egg-laying sites is more likely to build up gradually as eggs are laid. It may appear to be directly related to the number of searching hosts. However, the rate of oviposition of an adult host starts at the maximum rate, and as the environment fills up with eggs, the rate of laying will decrease. If parasitism is also acting to reduce the number of eggs then the rate of oviposition of the hosts will also be dependent on the number of searching parasitoids. One possible mechanism that might cause this gradual effect could be longer searching times required to find an available site for oviposition. This would act in a gradual manner through time rather than as a one-off event at the end of a generation.

Therefore accepting that the underlying mechanisms behind many phenomena act in continuous time, but still operate against a background of discrete, non-overlapping generations, a solution would seem to be to use a continuous model for within-generation dynamics, and at the end of the generation perform a discrete step to convert juveniles to adults, resetting the initial conditions for the next generation from the previous generation, and repeating the within-generation step. An alternative formulation is to use time-delayed ordinary differential equations (see (33; 39)). However, in this paper we consider simple synchronised host and parasitoid life stages, typical of many such associations in nature (15)

Simplifications are often made which allow *de facto* spatial ecological systems to be studied as ODE models or perhaps meta-population models (implicit spatial modelling). Some exceptions to this are the papers of (13; 14; 24; 25; 26; 44; 46; 47; 51). However, the work of (6; 10; 23; 35; 53) highlights areas where the continuum mean field assumption breaks down, and there has been increasing awareness that the continuum approximation of partial differential equations may not be the most appropriate way to model the movement of populations composed of discrete individuals distributed in space. A drawback with discrete meta-population or patch models is that between-patch dispersal is often modelled as a once in a life time event suited to passive or seed dispersal. However most parasitoids seldom have a nest or home range and dispersal can be as a continuous process and that process may be influenced by fine scale habitat or landscape features (52). A parasitoid that finds itself in a resource-poor or resource-depleted patch will move on.

Another common simplification made in many mathematical models of biological/ecological systems is to assume that a system is deterministic rather than stochastic in nature. This approximation is most valid when the system being modelled consists of large population sizes where stochastic processes can be assumed to have an effect on the population as a whole that is proportional to the mean effect of the stochastic processes. In this context partial differential equation models have been commonly used in mathematical modelling of biological and chemical systems and have a vast literature of their own. The use of such equations to model problems in ecology dates back to the work of (49) and many books, notably those by (16; 34; 36; 48), have focused on the biological and ecological application of reaction-diffusion equations. The diffusion equation itself can be viewed as a deterministic approximation to a random walk process. However a drawback of the

reaction-diffusion equation approach is that it permits unrealistically small populations to persist or disperse through very small non-zero population densities (cf. *ato foxes*, (31)). This is particularly a problem when considering organisms with a high birth rate (14), and many insects species including parasitoids are capable of producing hundreds if not thousands of offspring per individual if local resources permit.

It is possible, however to derive within-generation movement terms for a discrete stochastic individual-based model (interacting-particle system) from a deterministic continuum reaction-diffusion equation model. One way of achieving this is to consider that the spatial domain is composed of a number of grid-points which contain only discrete numbers of individuals and to use the standard five-point finite difference stencil (used to solve the PDE system numerically) to generate probabilities of movement of individuals to neighbouring grid-points. This was the approach taken by (2) in models of nematode movement and (3; 4) in models of blood vessel growth (angiogenesis), tumour growth and cancer invasion. Specific use of the technique with regard to host-parasitoid systems can be found in the work of (46). Indeed this current paper seeks to extend the work of (45).

Therefore, here we develop a detailed general model of host-parasitoid interactions based around a system of reaction-diffusion-taxis equations describing the interaction between adult hosts, adult parasitoids and juvenile parasitoids. We examine the role of diffusive chemicals (*kairomones*) in controlling these interactions. It is generally accepted that many foraging insects interact with the environment through an enhanced sense of smell and taste (see for example the book edited by (7)). Specifically, (50) showed that parasitoids make use of chemical cues (from chemicals such as *kairomones*), for the location of resource or host patches. Kairomones are also used to aid other decisions that must be made during foraging, such as assessing patch quality, and deciding when to stay in and when to move on from a patch. These kairomones can originate from various sources: those produced directly by the host, such as host frass, pheromones and other host semio-chemicals (1; 8), or those produced indirectly, for example chemicals produced by a herbivorous host's food plants.

2. Biological context

For a specific host-parasitoid system upon which our model can be based and to which our modelling results can be applied, we envisage a system involving a solitary endo-parasitoid such as *Venturia canescens* (Gravenhorst), (Hymenoptera; Ichneumonidae), interacting with a lepidopteran host such as one of the pests of stored grain products which occur within the family Pyralidae, such as *Plodia interpunctella* (Huber) or *Ephestia kuhniella* (Walker). These systems have been widely used as experimental models to test the within-generation descriptions of parasitoid-host behavioural interactions which underlie the non-linear difference equation approach to host-parasitoid population dynamics (17; 18). Characteristic of these systems, in both the laboratory and temperate field populations, is *synchrony* of host and parasitoid generations – *Venturia*, for example, is capable of speeding up or slowing down its development rate within a host so that the

developing parasitoid juvenile always has sufficient resources to sustain growth, but the population-level effect is to synchronise overall development rates of host and parasitoid populations. A similar degree of synchrony is imposed on many field populations by seasonal fluctuations in temperature.

Seasonal effects are manifest also in temperate field populations where juvenile hosts produced late in the season continue to feed and grow, albeit at a reduced rate related to temperature, and pupate the following spring, whereas juveniles which were able to feed to maturity in the previous generation pass the winter as pupae. Both cohorts, however, emerge from the pupal stage at the same time the following generation, as assumed by the models presented below. A similar argument applies to any parasitoids which these juveniles might contain, an example of such a system (on which the authors are presently working) is the braconid wasp *Cotesia glomerata* (L.) (Hymenoptera; Braconidae), attacking the larvae of the large white butterfly *Pieris brassicae* (L.) (Lepidoptera; Pieridae), and forest tent caterpillar *Malacosoma disstria* and its numerous dipteran and hymenopteran parasitoids.

The structure of this paper is, therefore, as follows. In the next section (section 3) we introduce and develop a new general mathematical model for an interacting host-parasitoid system which consists of a system of coupled, nonlinear PDEs and ODEs. From this system we develop an individual-based model which has the ability to track the motion of individual hosts and parasitoids in a 2-dimensional spatial domain. In section 4 we examine the spatio-temporal dynamics of the system both in the absence of the kairomone chemicals and also when the influence of kairomones is included. Comparisons between the spatio-temporal patterns are made and we also examine the resulting between-generation population levels. Finally, concluding remarks are made in the discussion section.

3. The Mathematical Model

The model developed in this paper is an individual-based stochastic model where the movement parameters are derived from an underlying continuum (PDE) model. This technique has been used to model nematode movement in soil (2; 5), endothelial cell migration (3) and cancer cell migration (4) and also host-parasitoid interactions (46). Indeed this paper is a development of the model of (46). This technique allows us to model populations of individual hosts and parasitoids moving on a discrete 2-dimensional grid (lattice) over a period of discrete time steps. Each individual host or parasitoid is restricted to move to one of its four orthogonal neighbouring grid-points or remain stationary at each time step. This is achieved by using the standard five-point finite difference stencil. It would be possible through the use of higher-order finite-difference schemes to enable movement to next-nearest neighbours to be incorporated (30). The movement of individuals is governed by movement probabilities derived from the continuum PDE system (1)–(5) and is therefore stochastic in the sense that no two simulation runs are the same. This technique enables the model to retain the same underlying movement parameters as the equivalent reaction-diffusion model and thus permits a direct comparison between the two modelling techniques.

The system we are considering models a solitary koinobiont endo-parasitoid searching for immobile concealed hosts within a 2-dimensional spatial domain. The concealed hosts are assumed to be in the juvenile stage and feed upon the substrate. The juveniles produce kairomones as a result of their feeding and these kairomones are assumed to diffuse and decay throughout the domain. The parasitoids are assumed to move randomly and also chemotactically in response to the gradients in kairomone concentration (see (37)), searching for juveniles at a vulnerable stage, for example first instars, to parasitise. If any juveniles are found by the parasitoids then there is a certain probability that the juvenile hosts will become parasitised and hatch as parasitoids. The adult hosts in the system move randomly throughout the domain, laying eggs which hatch into juveniles. There are therefore 5 variables in our model - unparasitised juvenile host density (j), parasitised juvenile host density (i), kairomone concentration (k), adult parasitoid density (p) and adult host density (h). The relevant equations describing the movement of individuals and the diffusion of kairomone are given below.

Adult parasitoids, p :

Adult parasitoids move throughout the domain in search of juvenile hosts. There is a random component to their movement as well as a directed component (in response to kairomone gradients). Therefore the equation governing the evolution of adult parasitoid density is given by:

$$\frac{\partial p}{\partial t} = \overbrace{D_p \nabla^2 p}^{\text{random motility}} - \overbrace{X \nabla \cdot (p \nabla k)}^{\text{chemotaxis}}, \quad (1)$$

where D_p is the (constant) random motility coefficient of the adult parasitoids and X is the (constant) chemotactic coefficient. This equation therefore consists of two parts, a random motility component and a directional bias in the parasitoid movement induced by a chemotactic attraction to the kairomone. X describes the strength of this attraction.

Adult hosts, h :

Adult hosts simply move through the domain randomly (while laying eggs and producing unparasitised juveniles). Therefore the equation governing the evolution of adult host density is given by:

$$\frac{\partial h}{\partial t} = \overbrace{D_h \nabla^2 h}^{\text{random motility}}, \quad (2)$$

where D_h is the (constant) host random motility coefficient.

Kairomone concentration, k :

Kairomones are produced by the juvenile hosts (both unparasitised and parasitised) as they feed. The kairomones then diffuse and decay throughout the domain.

Therefore the equation governing the evolution of kairomone concentration is given by:

$$\frac{\partial k}{\partial t} = \overbrace{D_k \nabla^2 k}^{\text{diffusion}} + \overbrace{N(j+i)}^{\text{production}} - \overbrace{Yk}^{\text{decay}}, \tag{3}$$

where D_k is the diffusion coefficient of the kairomone, N is the production rate (since the parasitoid is a koinobiont, both unparasitised juveniles j and parasitised juveniles i are assumed to produce kairomone), and Y is the decay rate of the kairomone. Details of the full PDE model are given in (45). However we note here that kairomone production is linked to the juvenile host and parasitoid equations.

Unparasitised juvenile hosts, j:

Unparasitised juvenile hosts are modelled as immobile. They are produced by adult hosts (i.e. hatch from eggs laid by the adults) and can be parasitised by adult parasitoids, thus converting them to parasitised juveniles. Therefore the equation governing the evolution of the unparasitised juvenile host density is given by:

$$\frac{\partial j}{\partial t} = \overbrace{Rh f(j, i)}^{\text{production}} - \overbrace{Sjp g(p, i)}^{\text{loss to parasitism}}.$$

Parasitised juvenile hosts, i:

Parasitised juvenile hosts are also immobile and are produced only when an unparasitised juvenile is parasitised by an adult parasitoid. Therefore the equation governing the evolution of the parasitised juvenile host density is given by:

$$\frac{\partial i}{\partial t} = \overbrace{Sjp g(p, i)}^{\text{production}}.$$

We assume a simple saturating function of the form $f(j, i) = (1 - (i + j)/J_c)$ where J_c is the local carrying capacity for juvenile hosts. Both unparasitised j and parasitised i juvenile hosts contribute to the carrying capacity since both continue to eat and develop. Juvenile hosts are parasitised at a rate Sjp , modified by the function which represents density-dependent parasitism. We assume parasitoid searching efficiency is reduced due to parasitoid interference and handling time for already-parasitised eggs giving $g(p, i) = e^{-A_p p} e^{-A_i i}$ (for constants A_p, A_i). The two constants R and S are conceptually simple parameters. R is the *per capita* lifetime number of eggs laid by adult hosts h in perfect conditions and S is the *per capita* lifetime number of hosts a parasitoid p would attack in perfect conditions. With these assumptions and the above functional forms for f and g the juvenile host equations become

$$\frac{\partial j}{\partial t} = Rh \left(1 - \frac{j+i}{J_c} \right) - Sjp e^{-A_p p} e^{-A_i i}. \tag{4}$$

The unparasitised juveniles j become parasitised upon encounter with adult parasitoids p at rate Sjp , modified by the function g , where S , $g(p, i)$ are as described above. Hence

$$\frac{\partial i}{\partial t} = Sjp e^{-A_p p} e^{-A_i i} . \quad (5)$$

The equations (1)–(5) are taken to hold on a two dimensional square domain of length L i.e. $[0, L] \times [0, L]$ with zero flux boundary conditions. Appropriate initial conditions $k(x, y, 0)$, $j(x, y, 0)$, $p(x, y, 0)$, $h(x, y, 0)$ are imposed to close the system. Before solving the system numerically, we non-dimensionalise the equations using appropriate scaling variables i.e. a length scale L (the size of the domain), time scale T_0 (related to the length of one generation, see below) and reference variables K_0 , J_0 , P_0 , H_0 for the kairomone concentration, juvenile host, adult parasitoid and adult host relative maximum densities respectively. Therefore, using the non-dimensionalisation:

$$\begin{aligned} x &= L\tilde{x}, & t &= T_0\tilde{t}, & j &= J_0\tilde{j}, & i &= J_0\tilde{i}, \\ p &= P_0\tilde{p}, & h &= H_0\tilde{h}, & k &= K_0\tilde{k}. \end{aligned}$$

Substituting these in equations (1)–(5) and dropping the tildes for clarity, we arrive at the following non-dimensional system:

$$\frac{\partial p}{\partial t} = \delta_p \nabla^2 p - \chi \nabla \cdot (p \nabla k), \quad (6)$$

$$\frac{\partial h}{\partial t} = \delta_h \nabla^2 h, \quad (7)$$

$$\frac{\partial k}{\partial t} = \delta_k \nabla^2 k + \nu(j + i) - \gamma k, \quad (8)$$

$$\frac{\partial j}{\partial t} = \rho h(1 - (j + i)) - \sigma j p e^{-\alpha_p p} e^{-\alpha_i i}, \quad (9)$$

$$\frac{\partial i}{\partial t} = \sigma j p e^{-\alpha_p p} e^{-\alpha_i i}, \quad (10)$$

where $\rho = RT_0 H_0 / J_0$, $\sigma = ST_0 P_0$, $\alpha_p = A_p P_0$, $\alpha_i = A_i J_0$, $\delta_h = D_h T_0 / L^2$, $\delta_p = D_p T_0 / L^2$, $\chi = X T_0 / k_0 L^2$, $\delta_k = D_k T_0 / L^2$, $\nu = N J_0 T_0 / K_0$ and $\gamma = Y T_0$ are all dimensionless parameters.

These equations now hold on the unit square $[0, 1] \times [0, 1]$ and zero flux boundary conditions are imposed. An estimated parasitoid life span is 20 days and it is estimated that there is an average of 10 active hours per day, thus giving a total searching time of 200 hours per parasitoid lifetime (i.e. one generation). Therefore, the reference time scale was taken as $T_0 = 200$ hours. The length scale was taken to be 10m. Finally, the kairomone diffusion coefficient D_k was taken to be $5 \times 10^{-4} \text{m}^2 \text{s}^{-1}$ (27) and the parasitoid random motility coefficient D_p was in the range $10^{-5} - 10^{-3} \text{m}^2 \text{s}^{-1}$ (46).

The system was solved numerically for one generation i.e. for a time $t_f = 1$ (equivalent to twenty days). This represents a period when the hosts are vulnerable

to attack, first and second instar, but not necessarily the whole juvenile development. A regeneration step was then performed and the initial conditions for the next generation, $g + 1$, were set from the conditions at the end of the previous generation g , using the following equations:

$$h_{g+1}(x, y, 0) = j_g(x, y, t_f), \quad (11)$$

$$p_{g+1}(x, y, 0) = i_g(x, y, t_f), \quad (12)$$

$$k_{g+1}(x, y, 0) = 0, \quad (13)$$

$$j_{g+1}(x, y, 0) = 0, \quad (14)$$

$$i_{g+1}(x, y, 0) = 0. \quad (15)$$

This generational step from generation g to $g + 1$ does not represent a real time continuous step but a discontinuous step when host juveniles are no longer vulnerable - for example certain hosts (e.g. *Pieris brassicae*) pupate over winter. This permits the assumption that all remaining kairomone in the environment at the end of generation g has time to decay away before the start of generation $g + 1$.

The continuum model (6)–(10) was solved numerically using a standard central-time finite difference method (see for example (30)) adapted to account for discrete generations in the following manner:

1. initial conditions at $t = 0$ were (i) a uniform density of adult hosts throughout the domain i.e. $h(x, y, 0) = 1$; (ii) adult parasitoids at a density of zero except in a square region \mathcal{D} in the centre of the domain where the density of parasitoids was 1, i.e.

$$p(x, y, 0) = \begin{cases} 0, & (x, y) \notin \mathcal{D}, \\ 1, & (x, y) \in \mathcal{D}. \end{cases} \quad (16)$$

(iii) unparasitised and parasitised juvenile densities at $t = 0$ were taken as zero throughout the domain i.e. $j(x, y, 0) = i(x, y, 0) = 0$; (iv) the kairomone concentration at $t = 0$ was taken to be zero throughout the domain (since there are no juveniles initially) i.e. $k(x, y, 0) = 0$;

2. within-generation dynamics were obtained by solving the system of equations (6)–(10) on a 100×100 2-dimensional grid with zero-flux boundary conditions;
3. equations (11) and (12) were used to calculate the next generation adult density initial conditions;
4. juvenile densities and kairomone concentrations were reset to zero throughout the domain at the start of each new generation;
5. steps 2–4 were iterated for 100 generations.

The results of the numerical simulations of the PDE model are presented in section 4. We also carried out simulations of the system using an individual-based model derived from the PDE model. Therefore before proceeding to the results section we discuss the derivation of the individual-based model from our system of equations (6)–(10).

3.1. The Individual-based model

Although the PDE model we have developed considers space explicitly, as noted in the introduction the PDE approach is concerned with interactions between population densities as a whole throughout the domain. It is very difficult to model local interactions with PDEs. However, it is possible to use the PDE model (6)–(10) as the basis to develop a discrete, individual-based model in which, in addition to individual movement it is possible to incorporate stochastic interactions and events taking place between the individual hosts and parasitoids e.g. egg-laying, occurrences of parasitism etc. It is possible with this interacting particle system to arrange for host-parasitoid interactions, (host reproduction, for example) to occur in one of two ways (45): (i) concurrent with movement, when a host may move and reproduce in the same time step, or (ii) exclusive to movement e.g. if the host moves it cannot reproduce. If movement is concurrent it must be decided if reproduction occurs before or after movement. The results presented in this paper are for concurrent movement and interaction, as this is equivalent to the continuum model.

Individual adult host and parasitoid movement probabilities are generated from the discretised form of equations (6) & (7). To illustrate this we present the discrete form of equation (6) for the adult parasitoids:

$$P_{x,y}^{\tau+\Delta t} = \mathcal{P}_0 P_{x,y}^{\tau} + \mathcal{P}_1 P_{x+1,y}^{\tau} + \mathcal{P}_2 P_{x-1,y}^{\tau} + \mathcal{P}_3 P_{x,y+1}^{\tau} + \mathcal{P}_4 P_{x,y-1}^{\tau} \quad (17)$$

where the subscript x, y specifies the location on the grid and the superscripts denote the time steps. The coefficients \mathcal{P}_0 to \mathcal{P}_4 are proportional to the probabilities of the individual parasitoid at grid point (x, y) being stationary (\mathcal{P}_0), or moving left (\mathcal{P}_1), right (\mathcal{P}_2), up (\mathcal{P}_3) or down (\mathcal{P}_4). These coefficients, obtained from the finite difference discretisation of equation (6) (cf. (2), (5), (46)) are as follows:

$$\begin{aligned} \mathcal{P}_0 &= 1 - \frac{\Delta t}{(\Delta x)^2} \left[4D_p - \chi_p(k_{x+1,y}^{\tau} + k_{x-1,y}^{\tau} + k_{x,y+1}^{\tau} + k_{x,y-1}^{\tau} - 4k_{x,y}^{\tau}) \right]; \\ \mathcal{P}_1 &= \frac{\Delta t}{4(\Delta x)^2} \left[D_p - \chi_p(k_{x+1,y}^{\tau} - k_{x-1,y}^{\tau}) \right]; \\ \mathcal{P}_2 &= \frac{\Delta t}{4(\Delta x)^2} \left[D_p + \chi_p(k_{x+1,y}^{\tau} - k_{x-1,y}^{\tau}) \right]; \\ \mathcal{P}_3 &= \frac{\Delta t}{4(\Delta x)^2} \left[D_p - \chi_p(k_{x,y+1}^{\tau} - k_{x,y-1}^{\tau}) \right]; \text{ and} \\ \mathcal{P}_4 &= \frac{\Delta t}{4(\Delta x)^2} \left[D_p + \chi_p(k_{x,y+1}^{\tau} - k_{x,y-1}^{\tau}) \right]. \end{aligned} \quad (18)$$

Each time step (Δt) of the simulation process involves solving the discrete form of the system numerically to generate the five coefficients \mathcal{P}_0 to \mathcal{P}_4 . Probability ranges are then computed by summing the coefficients to produce 5 ranges, $R_0 = 0$ to \mathcal{P}_0 and $R_j = \sum_{i=0}^{j-1} \mathcal{P}_i$ to $\sum_{i=0}^j \mathcal{P}_i$, where $j = 1$ to 4. We then generate a random number between 0 and 1, and depending on the range in which this number falls, the individual parasitoid currently under consideration will remain stationary (R_0) or move left (R_1), right (R_2), up (R_3) or down (R_4). The larger a particular range, the greater the probability that the corresponding coefficient will be selected. Each

parasitoid is therefore restricted to move to one of its four orthogonal neighbouring grid points or remain stationary at each time step. Individual hosts are moved in a similar manner (full details of this technique are given in (3)). At each time step there is a probability $\mathcal{J}_{x,y}$ for each individual adult host at a particular grid point (x, y) that the host will produce a new unparasitised juvenile host. This probability of host reproduction can be obtained from a discretisation of the reproduction part of the juvenile host equation (9):

$$j_{x,y}^{\tau+\Delta t} = \Delta t \left(\rho \left(1 - \frac{(j_{x,y}^* + i_{x,y}^\tau)}{\bar{j}_{x,y}} \right) h_{x,y}^\tau \right), \tag{19}$$

where $\bar{j}_{x,y}$ is the juvenile host carrying capacity for grid-point (x, y) and $j_{x,y}^*$ is the number of juvenile hosts including those already created during the current time step. Therefore we took $\mathcal{J}_{x,y} = \Delta t \rho \left(1 - \frac{(j_{x,y}^* + i_{x,y}^\tau)}{\bar{j}_{x,y}} \right)$. Since $\mathcal{J}_{x,y}$ is a probability its value must be between zero and one, and this can be assured by choosing $\Delta t < 1/\rho$. For the values of the parameter ρ used in the current paper, this condition was always satisfied due to the choice of Δt required by the stability condition for the finite difference scheme. The number of hosts that can reproduce is the number of adult hosts at grid-point (x, y) before any movement. This is less computationally expensive than using the number of hosts after movement, as all movement from the four neighbouring grid-points must be calculated first.

Similarly a probability $\mathcal{I}_{x,y}$ that a juvenile host at grid-point (x, y) will be converted to a juvenile parasitoid during a time step Δt can be obtained from the discretisation of the juvenile parasitoid equation (10):

$$i_{x,y}^{\tau+\Delta t} = \Delta t \left(\sigma f(p_{x,y}^\tau, i_{x,y}^\tau) j_{x,y}^\tau p_{x,y}^\tau \right). \tag{20}$$

Therefore, $\mathcal{I}_{x,y} = \Delta t \sigma f(p_{x,y}^\tau, i_{x,y}^\tau) p_{x,y}^\tau$ (in the concurrent case $p_{x,y}^\tau$ is the number of parasitoids at grid-point (x, y) before any movement).

After a given number of within-generation time steps the between-generation step is performed and all adult individuals on the grid are removed, juveniles hatch as adults and the kairomone concentration is reset to zero throughout the domain. This allows us to monitor the population levels from generation to generation. i.e. both within-generation dynamics and between-generation dynamics.

Although the model is a stochastic model, and therefore each individual simulation has unique dynamics, the results shown are representative of the most common dynamics for multiple runs of each configuration, and in fact the overall population dynamics were similar for simulations with the same parameter values even though the movement and fate of individuals varied.

In the following section we present both numerical solutions for the continuum model and simulation results for the individual-based model for the two parasitoid searching models i.e. (i) purely random searching (PRS) with random motility only, $\chi = 0$; (ii) kairomone-mediated searching (KMS) with chemotaxis $\chi > 0$ in addition to random motility.

The individual-based model was simulated on a 100×100 2-dimensional grid with both zero-flux and periodic boundary conditions. Two sets of different initial

conditions were used: (i) a small population of 100 adult parasitoids was placed at a few grid-points in the centre of the domain; and (ii) 1000 adult parasitoids were distributed randomly across the domain. In both instances 5000 adult hosts were distributed randomly across the domain. Each grid-point was given the same carrying capacity as 10 juvenile hosts.

4. Numerical Simulation Results

The models were used to investigate two different putative parasitoid search strategies, namely, Purely Random Searching (PRS) i.e. when $\chi = 0$, and Kairomone-Mediated Searching (KMS) i.e. when $\chi > 0$. Therefore for the KMS models in addition to their random motility the parasitoids respond chemotactically, influenced by the gradient of kairomone concentration. To give a specific biological example, *Venturia canescens* discovers its hosts through volatile chemicals emanating from the silk produced by the larvae during feeding (12). This affects their search strategy since areas of high concentrations of kairomone are likely to correspond to regions of high host number. Therefore in moving to regions of high kairomone concentration the parasitoids have a better chance of finding hosts. In all simulations presented in this section we took the chemotactic coefficient $\chi = 8 \times 10^{-3}$.

In each case three different dispersal scenarios comparing changes in the relative speed of movement of the hosts and parasitoids are considered: (i) when parasitoids disperse faster than the adult hosts i.e. $\delta_p > \delta_h$; (ii) when dispersal is equal i.e. $\delta_p = \delta_h$; and (iii) when parasitoids disperse more slowly than the adult hosts i.e. $\delta_p < \delta_h$. For all the results presented in this paper the (nondimensional) parameters values $\delta_k = 10^{-4}$, $\rho = 30$, $\sigma = 90$, $\alpha_p = 1$, $\alpha_i = 1$, $\nu = 1$ and $\gamma = 1$ were used.

4.1. Spatial Patterning

The key differences between the transient dynamics of the PRS and KRS models are highlighted in figure 1. These plots show the profiles of the host and parasitoid densities and the kairomone concentration as 1-dimensional radial cross sections of the 2d travelling wave as it advances across the domain (full 2d plots are given in figure 2). Figures 1(a)–(f) show the results of simulations of the continuum PRS model at an intermediate time and at steady state. As can be seen from the plots the travelling wave is characterized by some damped oscillations behind the wave front. However these oscillations are only sustained for a finite length of time in the case when the parasitoids are moving faster than the hosts. As can be seen from the profiles in figure 1(d)–(f) the parasitoid and host density and kairomone concentration all eventually settle to a spatially homogeneous equilibrium throughout the domain for all cases of the continuum model. These results are not dissimilar to the work of Dunbar on predator-prey interactions (13).

Figures 1(g)–(l) show the results of simulations of the continuum KMS model at an intermediate time and at steady state. Comparing figures 1(a)–(c) with (g)–(i) we note that there are distinct differences between the results from the KMS and PRS model evident in the initial travelling wave-like profiles of the invasion

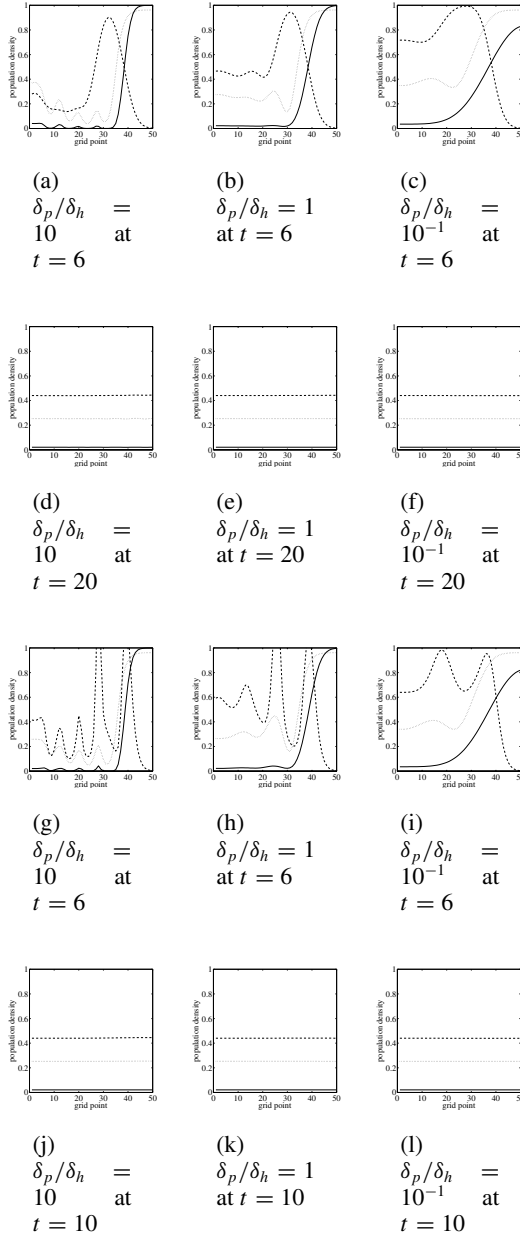


Fig. 1. Plots of parasitoid (dashed) and host (solid) density and kairomone (dotted) concentration with distance from the centre of the domain for the continuum model at $t = 6$ and $t = 20$ generations. $\delta_h = 5 \times 10^{-4}$, $\rho = 30$, $\sigma = 90$, plots (a)–(f) $\chi = 0$, plots (g)–(l) $\chi = 8 \times 10^{-3}$. These figures show the initial “travelling wave” profile which then settles down to a spatially homogeneous steady state.

of parasitoids into the unexploited host population i.e. the transient dynamics are different for the two search strategies. In the case of the continuum KMS model there is a distinct double crest to the initial wave of invasion in all three dispersal scenarios, followed by more marked, irregular, oscillations. These oscillations behind the wave front are more sustained and again marked in the case when $\delta_h < \delta_p$. However the distributions of parasitoids and hosts and kairomone throughout the domain eventually settle down to a steady state with a spatially homogeneous distribution of hosts and parasitoids as seen from figures 1(j)–(l). These final steady state distributions are the same as the distributions of hosts and parasitoids and kairomone when the parasitoid movement had no chemotactic term (as is to be expected from a straightforward analysis of equations (6)–(10)). Indeed, without the introduction of the seasonal forcing at the start of each new generation in theory it is possible to obtain closed form analytical solutions to the system (6)–(10) since the dynamics of the within-generation PDE system equations are relatively simple and only weakly nonlinear. In fact if equations (9) and (10) are added together we obtain a new equation for the variable $(i + j)$. Equation (7) can first of all be solved for h which in turn can be used to find the solution for $(i + j)$. This can then be used to solve (8) for the kairomone concentration k which can finally be used to solve (6). It is therefore the nonlinearity of the introduction of new hosts and parasitoids that occurs at the beginning of each new generation (equations (11), (12)) through the seasonal synchronising that is the source for the non-trivial dynamics and travelling waves.

Figure 2 compares spatial plots of the early time results of a typical numerical simulation for parasitoid density from the continuum model (equations (6)–(10)), with the results for parasitoid numbers from simulations of the individual-based model. Starting with an initial central distribution of parasitoids and a uniform (in the continuum model) or random (in the individual model) distribution of hosts, the plots show, despite some differences in the detail, an advancing travelling wave of parasitoids which invades the initial distribution of hosts.

Figures 2(c)–(d) show typical 2-dimensional plots of simulation results from the individual-based PRS model with an initial central distribution of parasitoids. The plots are for early times at generations 4 and 6. These plots show the numbers of hosts and parasitoids in the domain for the situation where $\delta_p = \delta_h$. Similar results were obtained in the case $\delta_p < \delta_h$. In the case $\delta_p > \delta_h$ the parasitoids found all the hosts and both populations went extinct within a few generations. The results presented in figure 2 show there is an initial travelling wave similar to that of the continuum results as the parasitoids invade the surrounding host population. For the individual-based KMS model, the spatial patterns and spatio-temporal dynamics are also different from those obtained using the PRS model. Figures 2(g)–(h) shows the spatial distributions of parasitoids from simulations of the individual-based KMS model when $\delta_p = \delta_h$ and parasitoids are initially centrally distributed in the domain. As can be seen, once again there is the familiar initial travelling wave-like advance in figure. However, there is then a second wave which emerges (figure 2 (g)) and then both waves break into small spotted regions (dark spots) of high parasitoid density. Although in some ways this is similar to the dynamics of the

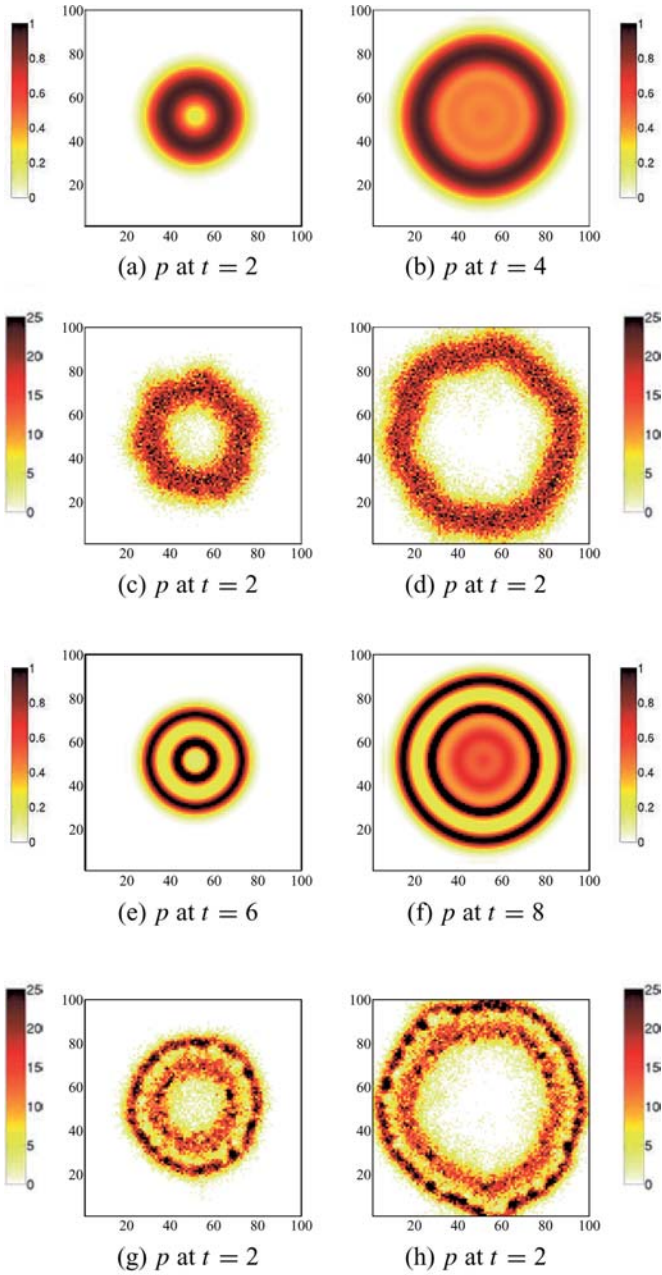


Fig. 2. Comparison of plots showing the spatial distributions of the parasitoid densities throughout the domain obtained from numerical simulation of the continuum model with plots for the parasitoid numbers obtained from simulation of the individual-based model at times $t = 2, 4$ generations. Plots (a)–(d) $\chi = 0$, plots (e)–(h) $\chi = 8 \times 10^{-3}$, for all plots $\delta_h = \delta_p = 5 \times 10^{-4}$, $\delta_k = 10^{-4}$, $\rho = 30$, $\sigma = 90$.

double-crested wave front in the continuum model (cf. figure 1), in the continuum case there is no break up.

A marked difference between the continuum model and the individual-based model occurs after the initial wave has crossed the domain. Whereas the density profiles of the continuum model settle down to a homogeneous steady state distribution of hosts and parasitoids, in the individual-based model, as can be seen from figure 3 (which shows later generations) neither the host nor the parasitoid populations reach a uniform spatially homogeneous equilibrium. Thus the long-time and steady-state dynamics of the continuum and discrete models are completely different. Indeed due to the stochastic nature of the simulations the underlying “symmetry” observed in the continuum results is not maintained and figure 3 shows persistent patterns of waves of patches of hosts and parasitoids moving across the domain. These appeared to persist indefinitely and were maintained in simulation runs for over 500 generations.

As figure 3 shows dynamic heterogeneous patches of organisms form in the domain. Figures 3(e)–(h) show a finer-grained heterogeneous, spotty pattern developing in the individual-based KMS model. This finer spotty pattern appears to persist and is in contrast to the more patchy pattern observed in the pure random search model results shown in figures 3(a)–(d). Although there is still larger scale heterogeneity with areas of high and low host numbers, the secondary pattern of spots of parasitoid density is maintained.

4.2. Population Dynamics

We now compare the between-generation dynamics of both types of model (continuum and individual-based) and Figure 4 contrasts the between-generation temporal-dynamics of the two models in more detail. Figures 4(a)–(c) and (g)–(i) show plots of the total population for the continuum PRS and continuum KMS models respectively (obtained by integrating the solution of PDE over domain at the end of each generation) and figures 4(d)–(f) and (j)–(l) show plots of the total population number for the individual-based PRS and individual-based KMS models respectively (obtained by calculating the total number of individuals at the end of each generation). For both continuum PRS and KMS models (stable) coexistence of hosts and parasitoid is seen in all three dispersal scenarios. This steady state shows that a very low density of hosts reproducing at a high rate birth rate, i.e. $\rho = 30$, can maintain a population of parasitoids at a constant higher density.

Comparing the results of the two modelling techniques, for the scenario when host and parasitoid motility are equal the overall dynamics appear to be qualitatively similar, with low densities of hosts increasing at high rates sustaining a larger population of hosts (with perhaps the stochastic nature of the individual-based model maintaining some spatial heterogeneity in the individual-based model results). However, this similarity is not maintained when host and parasitoid motility differ and for the individual-based model simulation there is a marked difference between the three dispersal cases. For all simulations of the individual-based model with parasitoid dispersal greater than adult host dispersal, an example of which is shown in Figure 4(d) & (j), the hosts were driven to extinction and consequently the

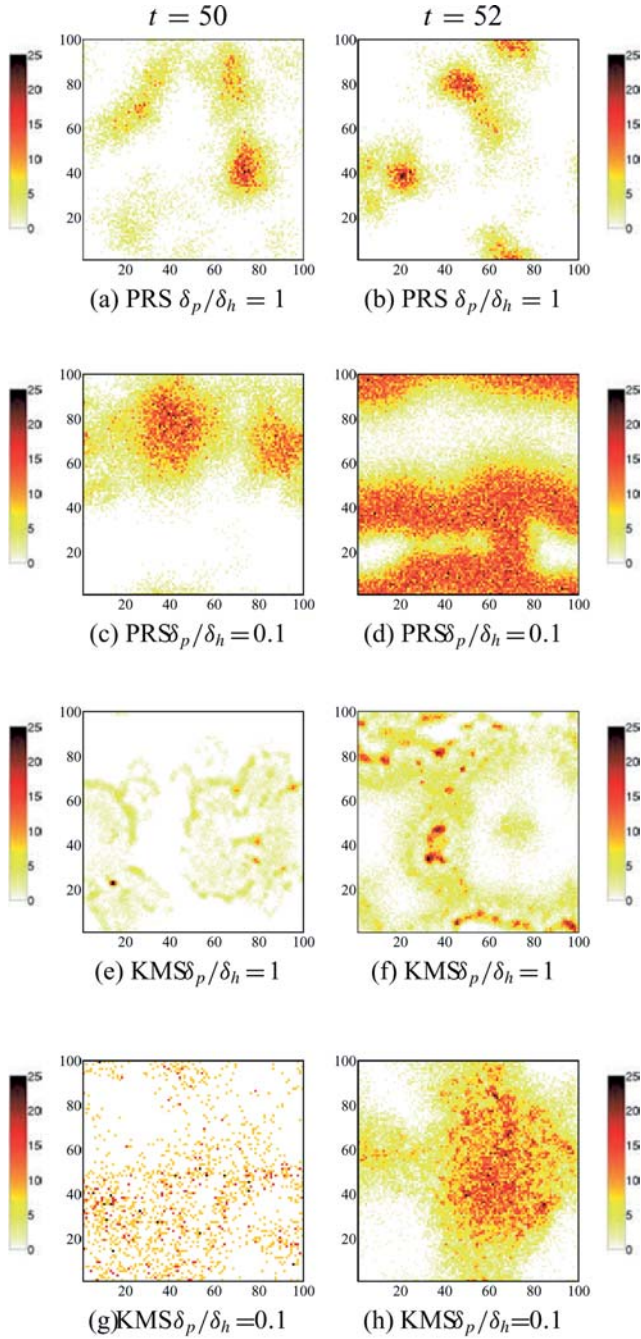


Fig. 3. Plots showing the spatial distributions of the populations of parasitoids obtained from simulation of the individual-based model at $t = 50, 52$ generations. $\delta_h = \delta_p = 5 \times 10^{-4}$, $\delta_k = 10^{-4}$, $\rho = 30$, $\sigma = 90$. plots (a)–(d) $\chi = 0$, plots (e)–(h) $\chi = 8 \times 10^{-3}$.

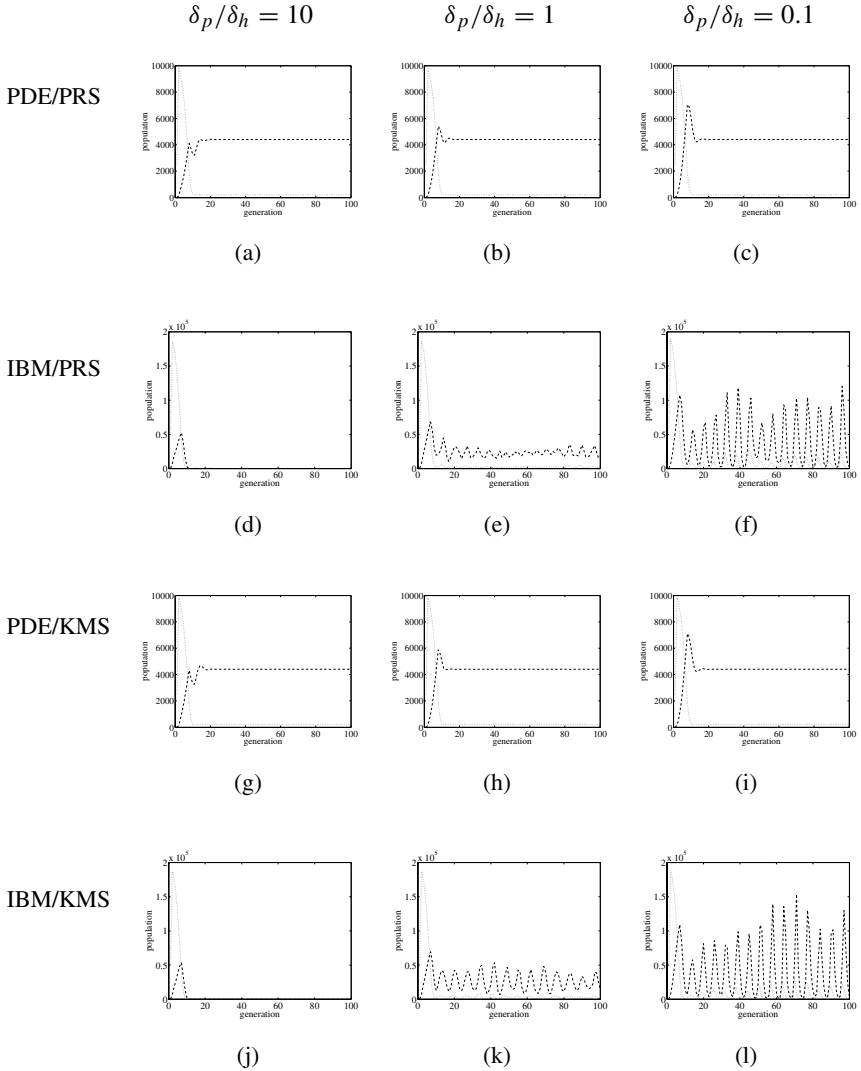


Fig. 4. Plots showing the population numbers of hosts (dotted) and parasitoids (dashed) over 100 generations. Figures (a)–(f) $\chi = 0$, (g)–(i) $\chi = 8 \times 10^{-3}$.

parasitoids became extinct also. When $\delta_p = \delta_h$, Figure 4(e) & (k), a quasi-equilibrium was achieved with the host population maintained at low numbers supporting a higher parasitoid population. This is comparable to the continuum model. When $\delta_p < \delta_h$, figure 4(f) & (l), the parasitoids were dispersing more slowly than the adult hosts and the amplitude of the sustained oscillations is increased. In figures 4(f) & (l) it can be seen that even small changes in host abundance can drive relatively large variation in parasitoid abundance.

4.3. Effects of the Initial and Boundary Conditions

The question may arise as to whether the oscillations seen in the individual-based model are artefacts resulting from the choice of boundary or initial conditions. For example, if a wave of hosts is pursued to the boundary of the domain by a wave of parasitoids and the hosts are trapped against the boundary by the advancing parasitoids and annihilated, perhaps the effect would disappear if the hosts were permitted to escape across the boundary and re-enter the domain from the opposite boundary. In order to investigate this we simulated the individual-based model using periodic boundary conditions.

Simulations of the individual-based PRS and KMS models were run with periodic (as opposed to zero-flux) boundary conditions and the temporal dynamics were very similar and the oscillations in population numbers are still present. However, upon deeper reflection these results may not be surprising since hosts escaping across one boundary are met at the opposite boundary by hosts fleeing in the other direction and then by the pursuing parasitoids. Thus, hosts at the boundaries are still experiencing being trapped by parasitoids i.e. the situation is not much different when the hosts are trapped between the boundary and the parasitoids or between two waves of parasitoids. The end result is the same i.e. annihilation of the hosts. It is possible that the periodic oscillations are set up due to the initially centrally distributed parasitoids spreading out across the domain with recovery of the host numbers in the centre generating a pulsing behaviour governed by the size of the domain the speed of individual movement and the rate of host increase. To further test if the oscillations are a real phenomenon rather than that due to the initial configuration of the model we imposed random initial conditions as opposed to a central initial distribution of parasitoids i.e. a population of 1000 adult parasitoids and 5000 adult hosts were spread randomly on the domain.

Figure 5 shows the spatial dynamics of the hosts and the parasitoids for the individual-based KMS model with periodic boundary conditions and random initial conditions for late time generations. These figures show that the patterns of waves of hosts and parasitoids forming within the domain using these random initial conditions and periodic boundary conditions are very similar to the patterns obtained in figures 3. There are waves forming from many moving centres in the domain that collide with each other and not just at the boundaries. These spatially heterogeneous patterns and temporal dynamics appear to persist indefinitely with simulations being carried out for over 500 generations, and a homogeneous pattern does not develop.

Figure 6 shows the between-generation temporal population dynamics of simulations of the individual-based model with random initial conditions and periodic boundary conditions. Figures 6(a) & (b) show the case when $\delta_h = \delta_p$ with $\chi = 0$ and $\chi > 0$ respectively and figures 6(c) & (d) show the case when $\delta_h > \delta_p$ with $\chi = 0$ and $\chi > 0$ respectively. As can be seen the oscillations are still present. This would indicate that the oscillations are not just an artefact of the initial or boundary conditions of the model, but are genuinely part of the dynamics. The waves also persisted when parasitoids were artificially removed from half of the domain after a few generations.

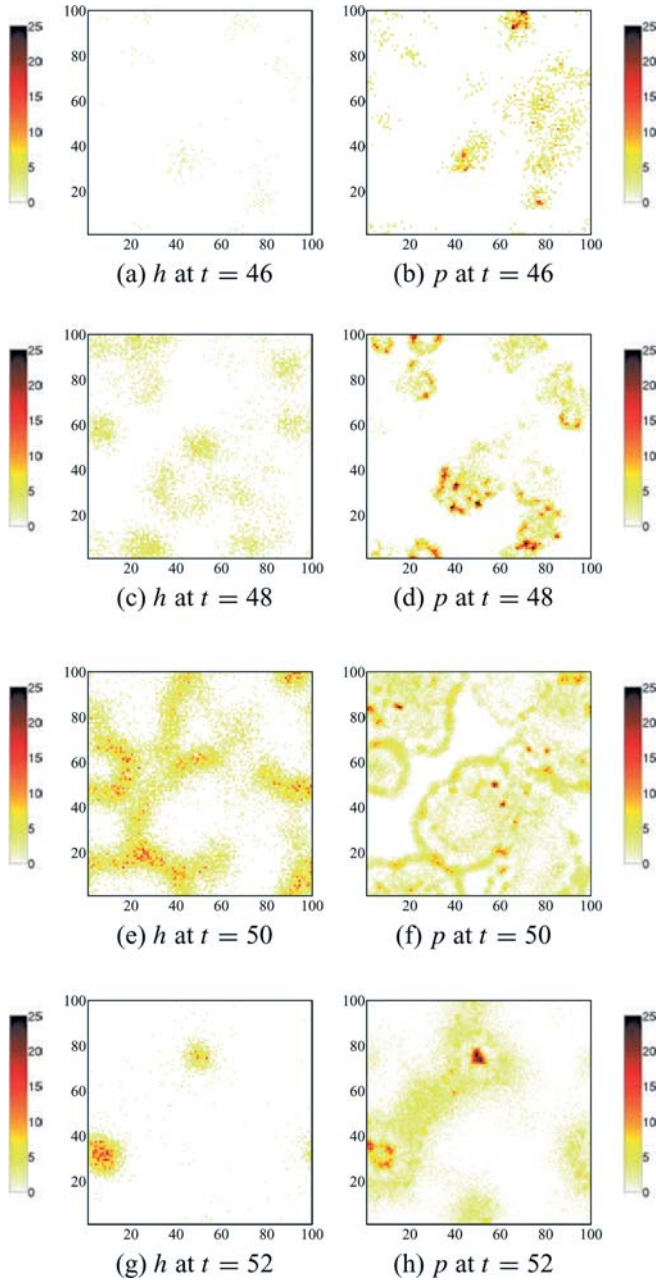


Fig. 5. Plots showing the spatial distributions of populations of hosts (a), (c), (e), (g) and parasitoids (b), (d), (f), (h) for the individual-based model with random initial conditions and periodic boundary conditions at $t = 46, 48, 50, 52$ generations. $\delta_h = \delta_p = 5 \times 10^{-4}$, $\delta_k = 10^{-4}$, $\rho = 30$, $\sigma = 90$, $\chi = 8 \times 10^{-3}$.

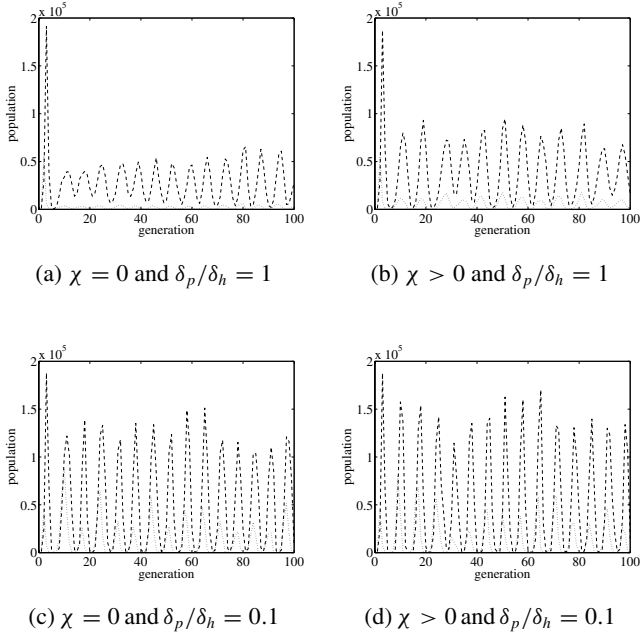


Fig. 6. Plots showing population numbers of hosts and parasitoids over 100 generations on a domain with periodic boundary conditions and random initial conditions. Figures (a) & (c) show between-generation dynamics from the PRS model while (b) & (d) are from the KMS model.

5. Discussion and Conclusions

Many temperate biological systems are subject to seasonal events that force the synchronicity of generations of univoltine organisms. In this paper we have developed and examined two different spatially-explicit discrete-generation models of interacting host-parasitoid systems. The models were constructed to incorporate both discrete (between-generation) and continuous (within-generation) population regulation mechanisms. This permits the use of realistic individual life-history parameters rather than mean-population parameters for potential rates of reproduction. The models developed were a deterministic continuum (PDE) model and an individual-based stochastic model. The models were used to investigate two different parasitoid searching strategies: (i) a purely random search (PRS), and (ii) a kairomone mediated search (KMS). Three different host and parasitoid relative dispersal scenarios were also investigated. These two models are linked by common movement parameters. However the results from the two models predict different spatial and temporal dynamics.

The models incorporate relatively high reproductive rates $\rho = 30$ for individuals in suitable environments, to reflect the high reproductive potential of many invertebrate species. Density dependence reduction on this rate acts continuously within-

generation rather than discretely at the end or beginning of a generation so that limits in local resources reduce immediate reproductive potential. The model realisations in this paper used spatially homogeneous environmental parameters with the only sources of heterogeneity being intrinsic in the interactions between host and parasitoid. As predicted the results from the continuum deterministic model showed a lack of long-term heterogeneity with both the host and parasitoid population densities across the domain settling to various homogeneous steady states for all the parameter values explored. Changes in both search strategy and relative host-parasitoid motility did not alter the long-term spatially homogeneous population patterns, although there were different patterns in the initial invasion. However, in the continuum model the dynamics are analogous to the situation of a virulent, fast-moving organism able to build up rapidly from low numbers (14), and it is perhaps questionable whether the levels of host density observed in the results represent a sustainable population and it is possible that what looks like the coexistence of the hosts and parasitoids is maintained purely by the existence of artificially small host densities (nano-hosts) which are able to rebuild the population density from these unrealistically low densities due to the high reproduction rate.

To investigate this further an individual-based model was developed that has a similar structure to the continuum model with the same within-generation density-dependence mechanisms and movement parameters. This was achieved using the technique developed by (2). The temporal dynamics of this individual-based model are very different from the continuum model dynamics. Although for the case when adult hosts and parasitoids have the same motility there is some agreement, there is extinction in the case when parasitoids are moving faster than the hosts, $\delta_h/\delta_p = 10^{-1}$ [Figure 4(a) & (j)], and sustained oscillations when the hosts move faster than the parasitoids, $\delta_h/\delta_p = 10$ [Figure 4(f) & (l)]. These oscillations were robust to changes in initial and boundary conditions

The results presented in this paper concentrated on an area of the parameter space, host increase $\rho = 30$ and parasitoid search-efficiency $\sigma = 90$, that lead consistently to extinction in the non-spatial versions of the continuum model (45). The explicit introduction of space in the continuum model, through use of partial differential equations, led to equilibrium, albeit at very low host levels. The results of simulations of the individual-based model show however that the equilibrium of the spatial continuum models may be misleading. Although other models for parasitoid searching efficiency could be used in equations (9) & (10) the within-generation dynamics of the complete system (6)–(10) would still ultimately lead to a steady state and the between-generation synchronising inter-generational step would still be the source of the heterogeneous dynamics and pattern formation.

When the parasitoids were moving faster than the hosts, the hosts were driven to extinction in all the simulations. This also proved the case for much lower values of the parameters ρ and σ . However, when the hosts and parasitoids move with the same motility coefficient there is indeed a form of quasi-equilibrium, although not the spatially homogeneous one that the continuum model predicted, but rather a constantly moving mosaic of patches of hosts pursued by parasitoids, despite spatial parameters being homogeneous. This is the type of dynamics seen in many forest defoliating lepidopteran pest species such as Forest Tent Caterpillar

Malacosoma disstria and Gypsy Moth *Lymantria dispar*, where the structure of extant forest can influence the dynamic spatial-temporal patterns of outbreak and scarcity occur, with large temporal oscillations in total population size (41; 42; 43; 38). In these systems pheromones are recognised as important for host aggregation and kairomones for parasitoid host location (32).

The addition of chemotaxis to the continuum model makes little or no qualitative difference to the long term population dynamics. This is perhaps not surprising as the parameters in the model are homogeneous across the domain. However, there was a qualitative difference in the early phase dynamics as the initial parasitoid population spread across the grid. The travelling wave-like invasion front had two distinct peaks rather than one and was followed by markedly irregular oscillations. These differences in transient dynamics may have an important effect on the population dynamics in environments that are heterogeneous and changing due to extrinsic factors such as human activity. This twin-peaked invasion front was also evident in the interacting particle system model, where again the inclusion of chemotaxis made little difference to the long term dynamics. As with the PRS models the KRS model did not show the spatial homogeneity of the continuum model and the population persistence in the continuum model proved to be unsustainable in the interacting particle system when parasitoids moved faster than hosts. An aspect of the models presented in this paper is the homogeneity of the spatial parameters, in particular, the host carrying capacity. Although non-stationary heterogeneous patterns appear in the simulations, hosts are often limited to explicit patches by environmental conditions. The inclusion of explicit patchiness may affect the KMS and PRS populations differently. This is an area of the model that requires further investigation.

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