

# Modelling the spatio-temporal dynamics of multi-species host–parasitoid interactions: Heterogeneous patterns and ecological implications

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## Abstract

A mathematical model of the spatio-temporal dynamics of a two host, two parasitoid system is presented. There is a coupling of the four species through parasitism of both hosts by one of the parasitoids. The model comprises a system of four reaction–diffusion equations. The underlying system of ordinary differential equations, modelling the host–parasitoid population dynamics, has a unique positive steady state and is shown to be capable of undergoing Hopf bifurcations, leading to limit cycle kinetics which give rise to oscillatory temporal dynamics. The stability of the positive steady state has a fundamental impact on the spatio-temporal dynamics: stable travelling waves of parasitoid invasion exhibit increasingly irregular periodic travelling wave behaviour when key parameter values are increased beyond their Hopf bifurcation point. These irregular periodic travelling waves give rise to heterogeneous spatio-temporal patterns of host and parasitoid abundance. The generation of heterogeneous patterns has ecological implications and the concepts of temporary host refuge and niche formation are considered.

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## 1. Introduction

Parasitoids are insects whose larvae develop by feeding on the bodies of their hosts, which are usually other arthropods, often insects in their juvenile life stages. Larval feeding almost always results in the death of the host. Parasitoids are of immense importance in natural and agricultural ecosystems, where they influence and occasionally regulate the density of their hosts. Much research on parasitoids has been stimulated by their success in

biological control programmes. Many parasitoid species have been used to combat agricultural pests, with huge savings in both financial and human terms resulting from successful programmes. A parasitoid is defined by the feeding habit of its larva. Only a single host is required for a parasitoid to complete development and often a number of parasitoids develop gregariously on the same host. Furthermore, many parasitoids will attack more than one host species.

Parasitoids can be considered intermediate between predators and parasites. Like predators, they kill the host they attack, but like many parasites they require just a single host on which to mature. In virtually all cases hosts are located by adult females, which lay their eggs directly on, or in the immediate vicinity of, the host. Parasitoids are almost all from the hymenopteran (sawflies, ants, bees and wasps) and dipteran (true flies) taxonomic groups. The

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coupling of host–parasitoid dynamics (each population directly impacts on the other) makes them ideal candidates for mathematical modelling. In this paper, we present a model which provides insight into the population dynamics of multi-species host–parasitoid interactions.

## 2. Multi-species host–parasitoid systems and mathematical modelling

We consider a mathematical model that focuses on the dynamics of a two-parasitoid, two-host system. Multi-species insect communities are the subject of significant interest in the ecological literature (Godfray, 1994; Hassell and Wilson, 1997), but have been largely neglected by mathematical modellers. The increased complexity of such systems and the difficulties associated with the solution and analysis of the corresponding models are partially responsible for this neglect. In particular, we wish to consider a multi-species system comprising of the parasitoids *Cotesia glomerata* and *C. rubecula* and the host species *Pieris brassicae* and *P. rapae*, the large and small white cabbage butterflies. These four species have a wide global range and there is a body of both field and laboratory evidence suggesting that all four species interact when in a shared niche (Geervliet et al., 1998; Vos et al., 1998; Harvey et al., 1999; Dicke et al., 2003). Both hosts of the *Pieris*–*Cotesia* system are common crop pests of brassica species, including commercial crops such as cabbage, cauliflower and kale and both parasitoids have been used as biological control agents against them (Barker et al., 1999; Cameron and Walker, 2002).

A key aspect of the *Cotesia*–*Pieris* interaction is the fact that *C. glomerata* can behave as a specialist, attacking only one host (*P. brassicae*, its primary host), or a generalist, attacking multiple host species (in this system, *P. rapae* and *P. brassicae*). Here, we model *C. glomerata* as a generalist that attacks both hosts. *C. rubecula*, on the other hand, is a specialist of *P. rapae* and is modelled accordingly. In this paper, we model the interactions of the species within a continuous-time framework because of observed overlap in population interactions (non-overlapping generations may be modelled within a discrete-time framework). Hence, the temporal dynamics of our host–parasitoid system are modelled by a coupled system of four ordinary differential equations. The multi-species interactions considered in our model exhibit oscillatory temporal dynamics and such population dynamics have long been a topic of interest in the literature (De Bach and Smith, 1941; Hochberg et al., 1990; Holt and Hassell, 1993; Rohani and Miramontes, 1996; Sherratt, 2001; Rohani et al., 2003). The presence of oscillatory dynamics in the system of ODEs provides motivation for extending our system spatially.

When spatial interactions are also taken into consideration via random motility of each of the four species, a system of four partial differential equations is obtained which models the spatio-temporal dynamics of our four species host–parasitoid community. In this paper, we

consider the interactions of the two hosts and two parasitoids in both one-dimensional and two-dimensional domains. A body of previous work has discussed the appearance of spatio-temporal heterogeneity when ODE systems with oscillatory dynamics are coupled with diffusion or random motility (Pascual, 1993; Sherratt, 1994, 2001; Sherratt et al., 1995, 1997), although this has generally been considered in two-equation frameworks and in one-dimensional domains. There have also been relatively few attempts to model multi-species host–parasitoid systems in a spatial setting, despite extensive bodies of work that consider modelling of invading and dispersing insect populations (Levin, 1974; Hamilton and May, 1977; Neubert et al., 1995; Kot et al., 1996; Rohani and Ruxton, 1999) and spatial modelling (Durrett and Levin, 1994; Holmes et al., 1994; Savill et al., 1997; Gurney et al., 1998; Hanski, 1998). We expand upon previous work by considering a reaction–diffusion model for a multi-species system interacting in a two-dimensional domain. Considering a system of more than two species allows explanation of the possible direct and indirect impacts species have on one another in a multi-species assemblage. In particular, the impact of parasitoid invasions and the role played by a generalist parasitoid are considered. The results of our computational investigations highlight a wide range of spatio-temporal dynamics, most significant of which are patterns of spatio-temporal heterogeneity. Critically, this observed spatio-temporal heterogeneity is due solely to the interplay of the species interactions in space and time and is not the result of either underlying environmental heterogeneity or stochasticity.

In the subsequent sections the model system and parameters are introduced and discussed. The system of equations is then non-dimensionalised to give insight into the relative magnitudes of the parameters required to produce biologically realistic behaviour. Subsequently, stability analysis and bifurcation analysis are carried out before the results of our numerical simulations are presented. Finally, the ecological implications of our results are discussed.

## 3. The mathematical model

The mathematical model is based on a system of partial differential equations. Reaction kinetics modelling the interactions of the hosts and parasitoids are coupled with spatial random motility, giving rise to a system of reaction–diffusion equations. Spatial random motility and species population interactions occur continuously. The underlying temporal dynamics are represented by a system of ordinary differential equations. Both host species (in the absence of parasitism) are modelled as having logistic, density-dependent growth, with intrinsic growth rates  $r_1$  and  $r_2$  and carrying capacities  $K_1$  and  $K_2$ , respectively. Parasitism by both parasitoids is modelled by an Ivlev functional response—a negative exponential function which accounts for a saturating maximum parasitism rate.

*C. glomerata* parasitises *P. brassicae* at the rate  $\alpha_1$  and *P. rapae* at rate  $\alpha_2$ . *C. rubecula* parasitises *P. rapae* at rate  $\alpha_3$ . The Ivlev functional response is similar to the Holling Type II functional response and is a standard function for modelling parasitism or predation (Sherratt et al., 1995; Savill et al., 1997). The efficiency of parasitoid discovery of hosts is denoted by  $a_1$ ,  $a_2$  and  $a_3$ , constants that determine host escape and the number of hosts parasitised. Each parasitised host gives rise to  $e_1$ ,  $e_2$  and  $e_3$  next generation parasitoids. In effect,  $e_1$ ,  $e_2$  and  $e_3$  are the parasitoid conversion efficiencies of hosts to parasitoids. Parasitoids are subject to intrinsic mortality rates  $d_1$  (*C. glomerata*) and  $d_2$  (*C. rubecula*). The addition of spatial motility terms model the parasitoids and hosts as moving randomly in a spatial domain. The motility coefficients  $D_1$ ,  $D_2$ ,  $D_3$  and  $D_4$  of the four species are constants and determine the rate at which each species disperses randomly through the domain. The full model system is thus as follows:

$$\begin{aligned} \frac{\partial N}{\partial t} &= \underbrace{D_1 \nabla^2 N}_{\text{random motility}} + \underbrace{r_1 N \left(1 - \frac{N}{K_1}\right)}_{\text{logistic growth}} \\ &\quad - \underbrace{\alpha_1 P (1 - e^{-a_1 N})}_{\text{mortality due to parasitism}}, \\ \frac{\partial M}{\partial t} &= D_2 \nabla^2 M + r_2 M \left(1 - \frac{M}{K_2}\right) - \alpha_2 P (1 - e^{-a_2 M}) \\ &\quad - \alpha_3 Q (1 - e^{-a_3 M}), \\ \frac{\partial P}{\partial t} &= D_3 \nabla^2 P + e_1 \alpha_1 P (1 - e^{-a_1 N}) \\ &\quad + e_2 \alpha_2 P (1 - e^{-a_2 M}) - d_1 P, \\ \frac{\partial Q}{\partial t} &= \underbrace{D_4 \nabla^2 Q}_{\text{random motility}} + \underbrace{e_3 \alpha_3 Q (1 - e^{-a_3 M})}_{\text{growth due to parasitism}} \\ &\quad - \underbrace{d_2 Q}_{\text{mortality}} \end{aligned} \tag{3.1}$$

where  $N$  and  $M$  represent the density of hosts *P. brassicae* and *P. rapae*, respectively and  $P$  and  $Q$  represent the density of parasitoids *C. glomerata* and *C. rubecula*.  $N = N(x, y, t)$  denotes local population density (organisms per area) at time  $t$  and spatial coordinates  $x, y$  (and likewise for  $M, P$ , and  $Q$ ). The system is posed on a given domain  $\Omega$  of length  $L$ , with smooth boundary  $\partial\Omega$ . Zero-flux Neumann boundary conditions are imposed on  $\partial\Omega$  to close the system. In one-dimension  $\Omega_1 = (0, L)$ , in two-dimensions  $\Omega_2 = (-L, L) \times (-L, L)$ .

Non-dimensionalising gives critical insight into the relative magnitudes of the parameters required to produce biologically reasonable behaviour. Using the following non-dimensional variables;  $t' = r_1 t$ ,  $x' = x/L$ ,  $N' = N/K_1$ ,  $M' = M/K_2$ ,  $P' = P/K_1$ ,  $Q' = Q/K_2$  and dropping primes gives the non-dimensionalised system:

$$\frac{\partial N}{\partial t} = D_N \nabla^2 N + N(1 - N) - s_1 P (1 - e^{-\rho_1 N}),$$

$$\begin{aligned} \frac{\partial M}{\partial t} &= D_M \nabla^2 M + \gamma M (1 - M) - s_2 P (1 - e^{-\rho_2 M}) \\ &\quad - s_3 Q (1 - e^{-\rho_3 M}), \\ \frac{\partial P}{\partial t} &= D_P \nabla^2 P + c_1 P (1 - e^{-\rho_1 N}) + c_2 P (1 - e^{-\rho_2 M}) - \eta_1 P, \\ \frac{\partial Q}{\partial t} &= D_Q \nabla^2 Q + c_3 Q (1 - e^{-\rho_3 M}) - \eta_2 Q, \end{aligned} \tag{3.2}$$

where  $D_N = D_1/r_1 L^2$ ,  $D_M = D_2/r_1 L^2$ ,  $D_P = D_3/r_1 L^2$ ,  $D_Q = D_4/r_1 L^2$ ,  $\rho_1 = a_1 K_1$ ,  $\rho_2 = a_2 K_2$ ,  $\rho_3 = a_3 K_2$ ,  $\gamma = r_1/r_2$ ,  $s_1 = \alpha_1/r_1$ ,  $s_2 = \alpha_2 K_1/\alpha_1 K_2$ ,  $s_3 = \alpha_3/r_1$ ,  $c_1 = e_1 \alpha_1/r_1$ ,  $c_2 = e_2 \alpha_2/r_1$ ,  $c_3 = e_3 \alpha_3/r_1$ ,  $\eta_1 = d_1/r_1$  and  $\eta_2 = d_2/r_1$ .

### 3.1. Parameter values

Realistic parasitoid dispersal ( $D_3, D_4$ ) has been documented of order  $10^{-3}$ – $10^{-4} \text{ m}^2 \text{ s}^{-1}$  (Corbett and Rosenheim, 1996; Barlow et al., 1998; Goldson et al., 1999) and is taken to be of order  $10^{-4} \text{ m}^2 \text{ s}^{-1}$  in our model. Host dispersal ( $D_1, D_2$ ) is considered to be small in comparison and is hence taken to be of order  $10^{-5} \text{ m}^2 \text{ s}^{-1}$ . The generational increase in population size of the host populations *P. brassicae* and *P. rapae* has been observed to be around 45% and 35%, respectively. *P. brassicae* has a higher reproductive rate due to laying a greater number of eggs (P.G. Schofield pers. comm.). Host growth rates are thus taken as  $r_1 = 0.45$  and  $r_2 = 0.35$ . Host carrying capacities are taken to be  $K_1 = 250$ ,  $K_2 = 250$ , which are realistic numbers observed in the field. Both parasitoids have similar parasitism efficiency rates on their primary host. *C. glomerata*, however, is considered less efficient at parasitising *P. rapae*, thus we take  $a_1 = 0.01$ ,  $a_2 = 0.001$  and  $a_3 = 0.01$ . Observed annual percentage parasitism rates of around 35% are reported in Cameron and Walker (2002). Also, as a secondary host, *P. rapae* is subject to less parasitism by *C. glomerata*, so we take parasitism rates  $\alpha_1 = 0.35$ ,  $\alpha_2 = 0.1$  and  $\alpha_3 = 0.35$ . *C. glomerata* has a higher conversion efficiency on its primary host, but significantly less on *P. rapae* so we take conversion efficiencies to be  $e_1 = 0.4$ ,  $e_2 = 0.02$ ,  $e_3 = 0.3$ . *C. glomerata* has been observed to suffer greater mortality, due to infections and other environmental factors than *C. rubecula*, thus we take  $d_1 = 0.08$  and  $d_2 = 0.06$ . Time is scaled with host intrinsic generational growth rate  $r_1 = 0.45$  (which has units  $t^{-1}$ ) and we consider domains of length  $L = O(10 - 10^2) \text{ m}$ , corresponding to the sizes of large laboratory-based experimental domains up to agricultural fields. Given the above parameter values, the baseline non-dimensional parameter set is thus:  $D_N = D_M = 0.0000008$ ,  $D_P = D_Q = 0.0000075$ ,  $\rho_1 = 2.5$ ,  $\rho_2 = 0.25$ ,  $\rho_3 = 2.5$ ,  $\gamma = 0.8$ ,  $s_1 = 0.8$ ,  $s_2 = 0.2$ ,  $s_3 = 0.8$ ,  $c_1 = 0.3$ ,  $c_2 = 0.004$ ,  $c_3 = 0.2$ ,  $\eta_1 = 0.2$  and  $\eta_2 = 0.1$ .

The one-dimensional domain ( $\Omega_1$ ) on which the system of equations is solved is a line of length one unit, with  $0 \leq x \leq 1$ . The system is solved with initial conditions  $N(0) = 0.75$ ,  $\forall x \in \Omega_1$ ,  $M(0) = 0.75$ ,  $\forall x \in \Omega_1$ ,  $P(0) = 0.075e^{-125x^2}$

and  $Q(0) = 0.075e^{-125x^2}$ . The two-dimensional domain ( $\Omega_2$ ) is a square of side length two units, centred at (0,0), with  $-1 < x < 1$  and  $-1 < y < 1$ . The system is solved with the initial conditions  $N(0) = 0.75, \forall x, y \in \Omega_2, M(0) = 0.75, \forall x, y \in \Omega_2, P(0) = 0.075e^{-125(x^2+y^2)}$  and  $Q(0) = 0.075e^{-125(x^2+y^2)}$ .

The one-dimensional system was solved numerically using two different numerical methods—the Fortran NAG routine DO3PCF and the Femlab finite element package. The Fortran NAG routine DO3PCF solves the system of PDEs using the method of lines to first obtain a system of ODEs and then uses a backward differentiation method to integrate the ODEs. For the finite element approach using Femlab, Lagrange quadratic elements were used as basis functions and the backward Euler time-stepping method was implemented to integrate the equations. The one-dimensional numerical results obtained using both the NAG routine and finite element method agree very closely. The two-dimensional system was solved by the finite element method on a square domain using triangular basis elements, Lagrange quadratic basis functions and a backward Euler time-stepping method was again used to integrate the system of equations.

#### 4. Steady states and stability analysis

We first of all examine the spatially homogeneous steady states of (3.2) and examine their stability. The steady states are solutions of the following algebraic equations:

$$\begin{aligned} 0 &= N^*(1 - N^*) - s_1 P^*(1 - e^{-\rho_1 N^*}), \\ 0 &= \gamma M^*(1 - M^*) - s_2 P^*(1 - e^{-\rho_2 M^*}) - s_3 Q^*(1 - e^{-\rho_3 M^*}), \\ 0 &= c_1 P^*(1 - e^{-\rho_1 N^*}) + c_2 P^*(1 - e^{-\rho_2 M^*}) - \eta_1 P^*, \\ 0 &= c_3 Q^*(1 - e^{-\rho_3 M^*}) - \eta_2 Q^*. \end{aligned}$$

There are a number of biologically relevant, non-negative, equilibrium states including the unstable trivial state (0,0,0,0), the unstable host only state (1,1,0,0) and the unstable states  $(N^*, M^*, P^*, 0)$  and  $(N^*, M^*, 0, Q^*)$  where only one parasitoid is present in the system. We are, however, primarily interested in the stability of the unique four species coexistent state  $(N^*, M^*, P^*, Q^*)$ . For the baseline parameter set (see Section 3.1), the four species equilibrium point is:

$$\begin{aligned} N^* &= 0.3379, & M^* &= 0.3389, \\ P^* &= 0.5043, & Q^* &= 0.3716. \end{aligned}$$

Linear stability analysis confirms that this equilibrium is stable.

In order to investigate the stability of this point more fully, we carried out a bifurcation analysis using the XPP auto package, which confirmed the presence of a Hopf bifurcation. Fig. 1 highlights the supercritical Hopf bifurcation point that occurs when parameter  $\rho_1$  is increased through a range of values against the steady

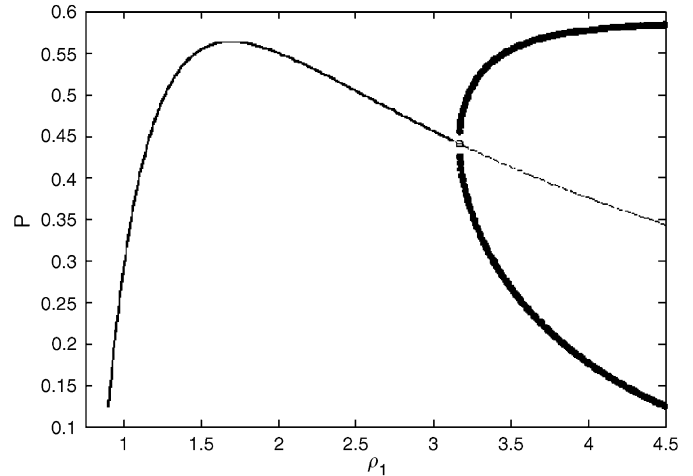


Fig. 1. Bifurcation diagram showing the steady-state value of  $P$ , plotted against  $\rho_1$  showing the supercritical Hopf bifurcation point at  $\rho_1 = 3.168$ .

state of  $P$  (parasitoid *C. glomerata*). Similar bifurcation plots are obtained for  $N$ ,  $M$  and  $Q$  (not shown).

The Hopf bifurcation occurring when  $\rho_1 = 3.168$  and  $\rho_3 = 3.276$  forms the basis of our numerical investigation of the spatio-temporal dynamics of the system. Varying  $\rho_1$  and  $\rho_3$  in the non-dimensional system is analogous to varying  $K_1$  and  $K_2$ , the host carrying capacities in the dimensional system. Due to the coupling of the system, varying parameters  $\rho_1$  or  $\rho_3$  independently gives rise to oscillatory dynamics of all four populations. Increasing  $\rho_1$  and  $\rho_3$  further into their unstable region gives rise to oscillations of increased amplitude. Throughout the remainder of this paper both  $\rho_1$  and  $\rho_3$  are increased simultaneously and set equal. This is analogous to setting the underlying dimensional parameters  $K_1 = K_2$ . The ecological plausibility of increasing the host carrying capacities can be supported. The carrying capacity represents the maximum sustainable population in a given domain. As the host larvae in our system feed exclusively on plants, an increase in plant size (through growth), or number (through seed germination), could give rise to higher maximum sustainable host population numbers. Furthermore, increasing  $\rho_1$  and  $\rho_3$  simultaneously has a more significant impact on the dynamics of the system than varying them independently. Oscillatory dynamics have long been shown to arise from difference equation and ODE models of host–parasitoid systems (Ives, 1992; Hassell, 2000). However, there have been few spatial models of such systems. The impact on the spatio-temporal dynamics of the oscillatory dynamics that arise by increasing  $\rho_1$  and  $\rho_3$  beyond their Hopf bifurcation point is dramatic and is highlighted and discussed in the following section.

#### 5. Spatio-temporal dynamics in one- and two-dimensional domains

In this section, we present the results of a numerical analysis of (3.2) in both one- and two-dimensional



domains. From the linear stability analysis of the steady states in the previous section, one might expect the appearance of some kind of travelling wave solutions to the system of equations (3.2). Given the results of the bifurcation analysis concerning the appearance of Hopf bifurcations, one may also expect a change in the nature of any travelling wave solutions as the stability of the unique fixed point  $(N^*, M^*, P^*, Q^*)$  changes from stable to unstable giving rise to a (stable) limit cycle.

Fig. 2 presents the results of numerical simulations on our one-dimensional domain while the analogous two-dimensional case is presented in Fig. 3. The parameter values are taken as the baseline set given in Section 3.1 i.e. the steady-state  $(N^*, M^*, P^*, Q^*)$  is stable. As is expected, we observe travelling waves of constant shape as the parasitoids invade the host domain. In the wake of the travelling waves of parasitoid invasion all the populations are at their stable steady states. Figs. 2 and 3 highlight that, for the baseline parameter set,  $P$  (*C. glomerata*) spreads through the domain ahead of  $Q$  (*C. rubecula*). An

examination of the non-dimensionalized system suggests that this difference is due to the differences in the parameter values in the terms describing how each parasitoid exploits its primary resource, since  $D_P = D_Q$ . The expected speed of a wave of invasion (where the state with the invader absent is unstable) is typically proportional to the square root of the product of the diffusion rate times the growth rate from zero density. In our system, since  $D_P = D_Q$ , for parasitoid  $P$  the growth rate from zero density based only on the utilization of the first host is given by  $r_1 = c_1(1 - \exp(-\rho_1)) - \eta_1 \approx 1.08$ . For parasitoid  $Q$ , the growth rate is given by  $r_2 = c_3(1 - \exp(-\rho_3)) - \eta_2 \approx 0.81$ . Thus, as  $r_1 > r_2$ , parasitoid  $P$  is expected to invade faster than parasitoid  $Q$ . This is the well-known “linear conjecture” of Mollison, which has been verified for many systems (Mollison, 1991; Owen and Lewis, 2001).

Figs. 4 highlights the dynamics of parasitoid  $P$  as  $\rho_1$  and  $\rho_3$  approach their respective Hopf bifurcation point. When  $\rho_1 = \rho_3 = 3.1$  the temporal dynamics indicate that convergence to the stable equilibrium state takes longer and

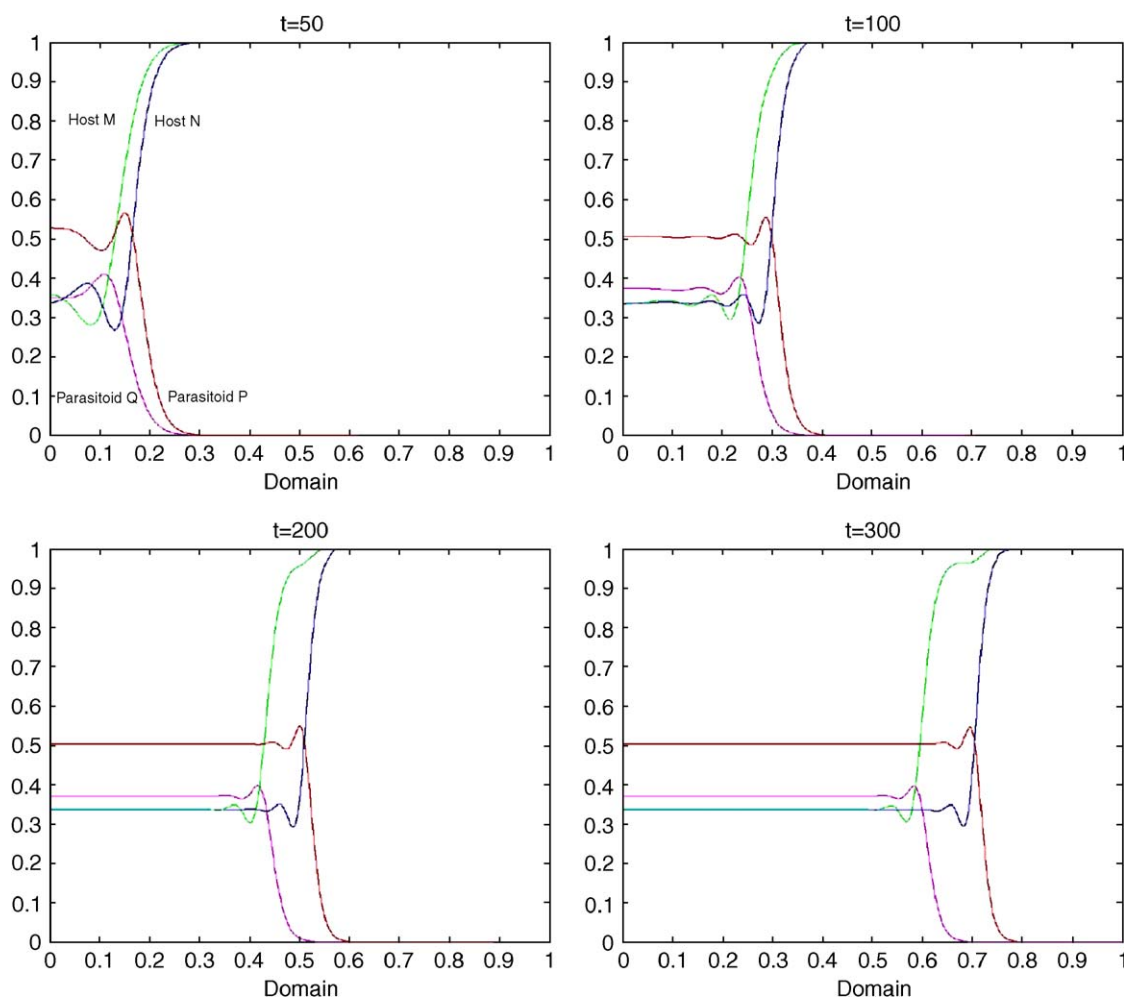


Fig. 2. Snapshots of the one-dimensional dynamics of  $N$ ,  $M$ ,  $P$  and  $Q$  at the generation times  $t = 50, 100, 200, 300$ . In all four sub-figures, host  $N$  is represented by a blue line, host  $M$  a green line, parasitoid  $P$  a red line and parasitoid  $Q$  a pink line. The four species interact in the domain  $\Omega_1 = (0, 1)$  with zero flux boundary conditions set up on  $\partial\Omega_1$ . For the initial conditions and parameter values discussed in the text, stable travelling waves of parasitoid invasion are observed when  $\rho_1 = \rho_3 = 2.5$  and  $\rho_2 = 0.25$ .

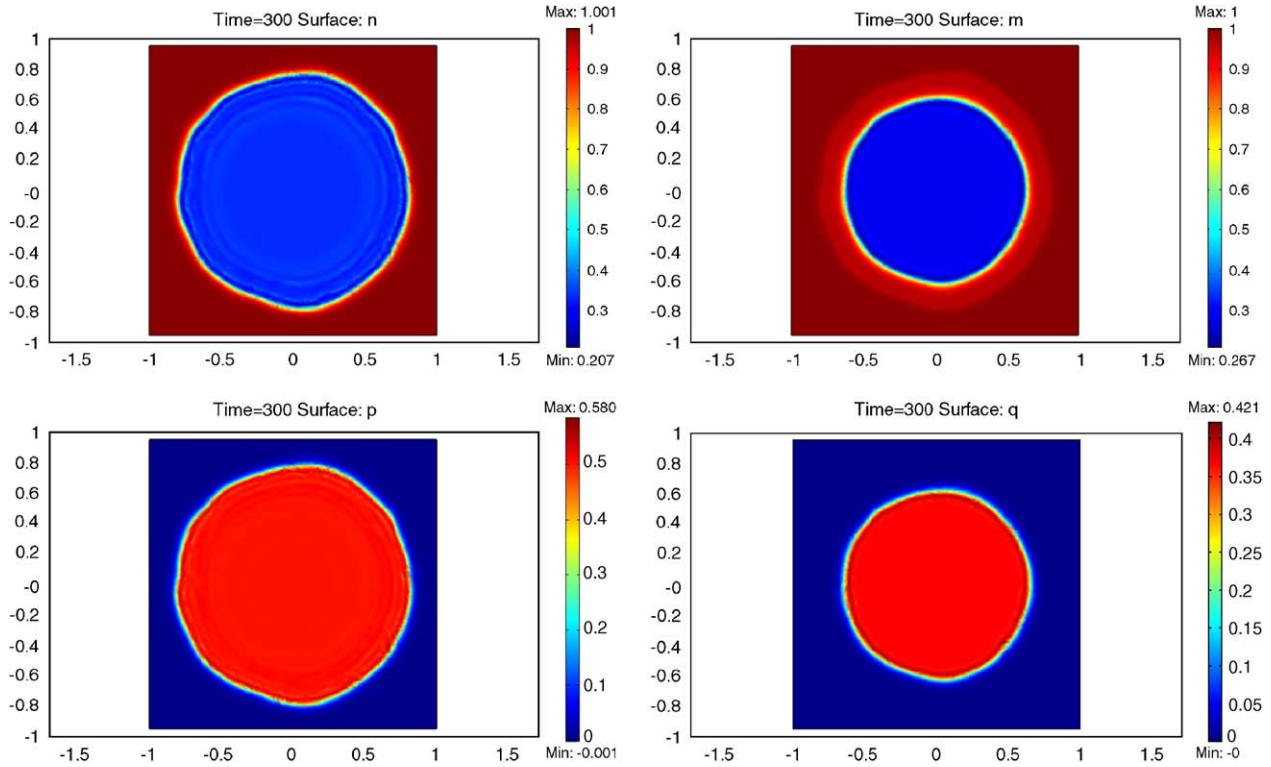


Fig. 3. Snapshots of the two-dimensional dynamics of  $N, M, P$  and  $Q$  at the generation time  $t = 300$ . Blue and green coloured regions represent areas of low species abundance, red and orange coloured regions represent areas of high species abundance. The four species interact in the domain  $\Omega_2 = (-1, 1) \times (-1, 1)$  with zero flux boundary conditions set up on  $\partial\Omega_2$ . For the initial conditions and parameter values discussed in the text, stable two-dimensional travelling waves of parasitoid invasion are observed when  $\rho_1 = \rho_3 = 2.5$  and  $\rho_2 = 0.25$ .

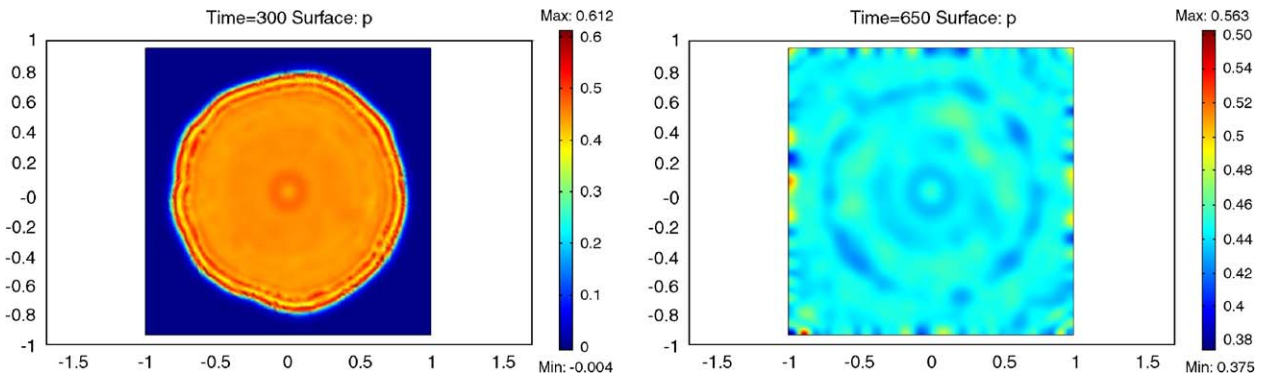


Fig. 4. Snapshots of the two-dimensional dynamics of parasitoid  $P$  at the generation times  $t = 300, 650$ . Blue and green coloured regions represent areas of low species abundance, red and orange coloured regions represent areas of high species abundance. Parasitoid  $P$  inhabits the domain  $\Omega_2 = (-1, 1) \times (-1, 1)$  with zero flux boundary conditions set up on  $\partial\Omega_2$ . For the initial conditions and parameter values discussed in the text, stable two-dimensional travelling waves of parasitoid invasion are observed when  $\rho_1 = \rho_3 = 3.1$  and  $\rho_2 = 0.31$ . A longer period of damped oscillations behind the invasion front are observed when comparing with Fig. 3. Spatio-temporal heterogeneity is temporarily observed ( $t = 650$ ), however, this does not persist at later times.

entails a longer period of damped oscillations. Furthermore, we see that the system does not immediately settle to its stable steady state. When  $P$  has spread throughout the domain there is a period of domain-wide dynamical heterogeneity (similar behaviour observed for the other three populations, results not shown). The system settles to its stable equilibrium state by around  $t = 800$ . However, the brief appearance of spatio-temporal heterogeneity hints

at the possibility of more interesting dynamics arising if we move into the unstable parameter space.

As discussed in Section 4, oscillatory temporal dynamics arise when  $\rho_1$  and  $\rho_3$  are increased beyond their Hopf bifurcation point. Fig. 5 presents the one-dimensional dynamics when  $\rho_1 = \rho_3 = 3.3$ . In the wake of the parasitoid travelling wave fronts we now observe oscillatory behaviour. These dynamics can be described as

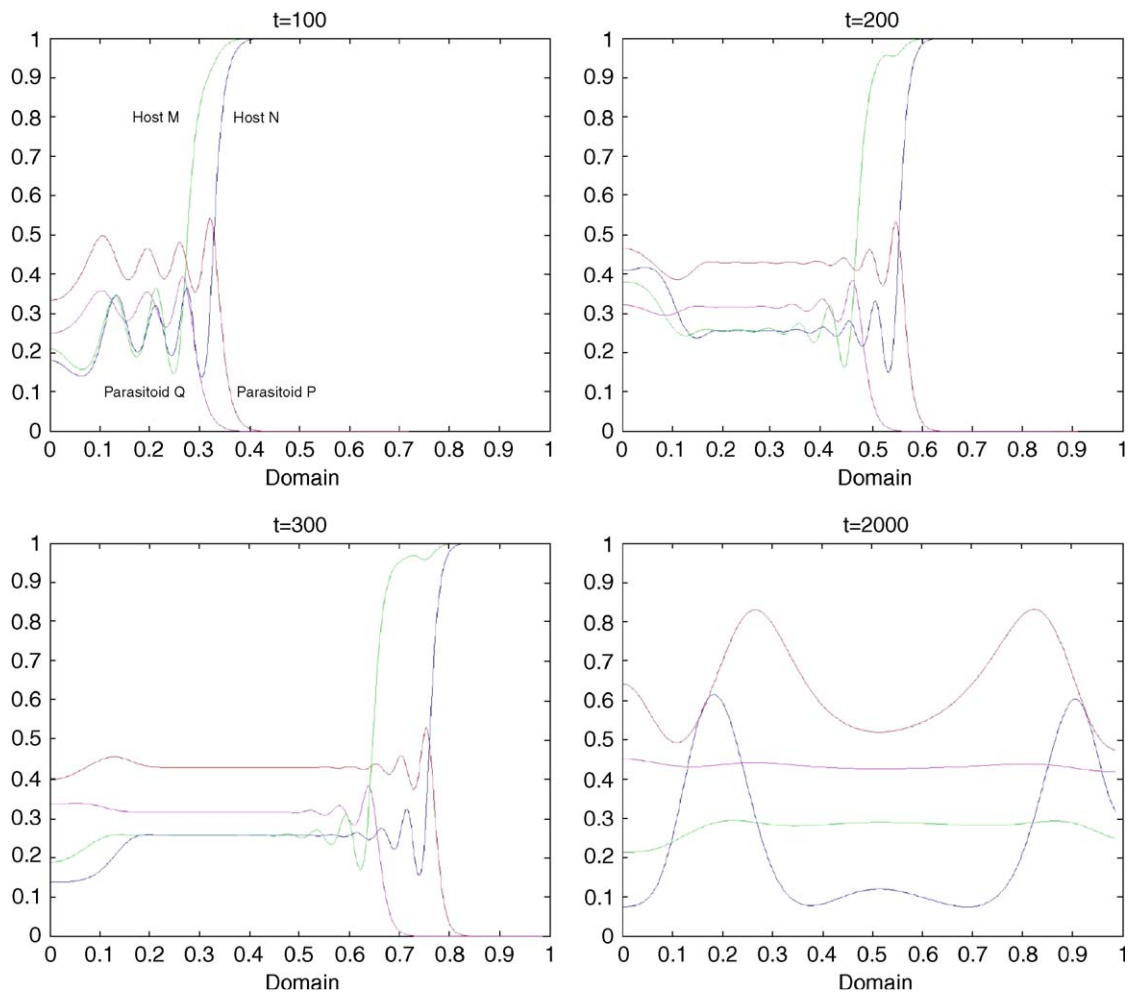


Fig. 5. Snapshots of the one-dimensional dynamics of  $N$ ,  $M$ ,  $P$  and  $Q$  at the generation times  $t = 100, 200, 300, 2000$ . In all four sub-figures, host  $N$  is represented by a blue line, host  $M$  a green line, parasitoid  $P$  a red line and parasitoid  $Q$  a pink line. The four species interact in the domain  $\Omega_1 = (0, 1)$  with zero flux boundary conditions set up on  $\partial\Omega_1$ . For the initial conditions and parameter values discussed in the text, disordered, quasi-periodic wave behaviour is observed in the wake of the parasitoid invasion fronts when  $\rho_1 = \rho_3 = 3.3$  and  $\rho_2 = 0.33$ . Persistent heterogeneous spatio-temporal dynamics are observed when the parasitoids have spread throughout the domain ( $t = 2000$ ).

quasi-periodic travelling waves. Periodic plane waves are waves of constant shape and speed that oscillate in both space and time (and correspond to limit cycle solutions of ODEs). However, the waves we observe are not of constant shape (they vary temporally) and their behaviour is hence described as quasi-periodic. The fourth sub-figure highlights the dynamics when the parasitoids have spread throughout the domain ( $t = 2000$ ). We see patterns of persistent spatio-temporal heterogeneity.

The corresponding two-dimensional dynamics of parasitoid  $P$  when  $\rho_1 = \rho_3 = 3.3$  are presented in Fig. 6. We observe persistent heterogeneous spatio-temporal dynamics in two-dimensional space. As the parasitoid  $P$  spreads through the domain, the dynamics behind the invasion front show evidence of quasi-periodic wave behaviour, but also, further behind the wave front, there are some signs of breakdown of the wave form into a quasi-chaotic state. This is most notable in the sub-figure for  $t = 300$ . When the parasitoid reaches the boundaries of the domain we observe the initial stages of domain-wide,

heterogeneity. The development of these heterogeneous patterns over time is highlighted. It is important to stress that there is a noticeable difference between the heterogeneous patterns exhibited by the species pairs  $N, P$  and  $M, Q$ . This can be partly attributed to the fact that the species  $M$  and  $Q$  are experiencing temporal oscillations of smaller amplitude than  $N$  and  $P$  (figures not shown). In other unpublished figures the impact of indirect interactions on the spatio-temporal dynamics is made clear. We observe distinct regions of low abundance of host  $M$  (coloured blue) which correspond with areas of low abundance of  $Q$ . Generally, areas of low host abundance correspond with regions of high parasitoid abundance (and vice versa). However, the low  $M$  regions correspond with regions of high  $P$  abundance (coloured red), offering explanation for the observed host distribution pattern.

As we increase  $\rho_1$  and  $\rho_3$  further into their unstable region we observe even more dramatic dynamic spatio-temporal behaviour. Fig. 1 shows that as  $\rho_1$  is increased the amplitude of the temporal oscillations experienced by

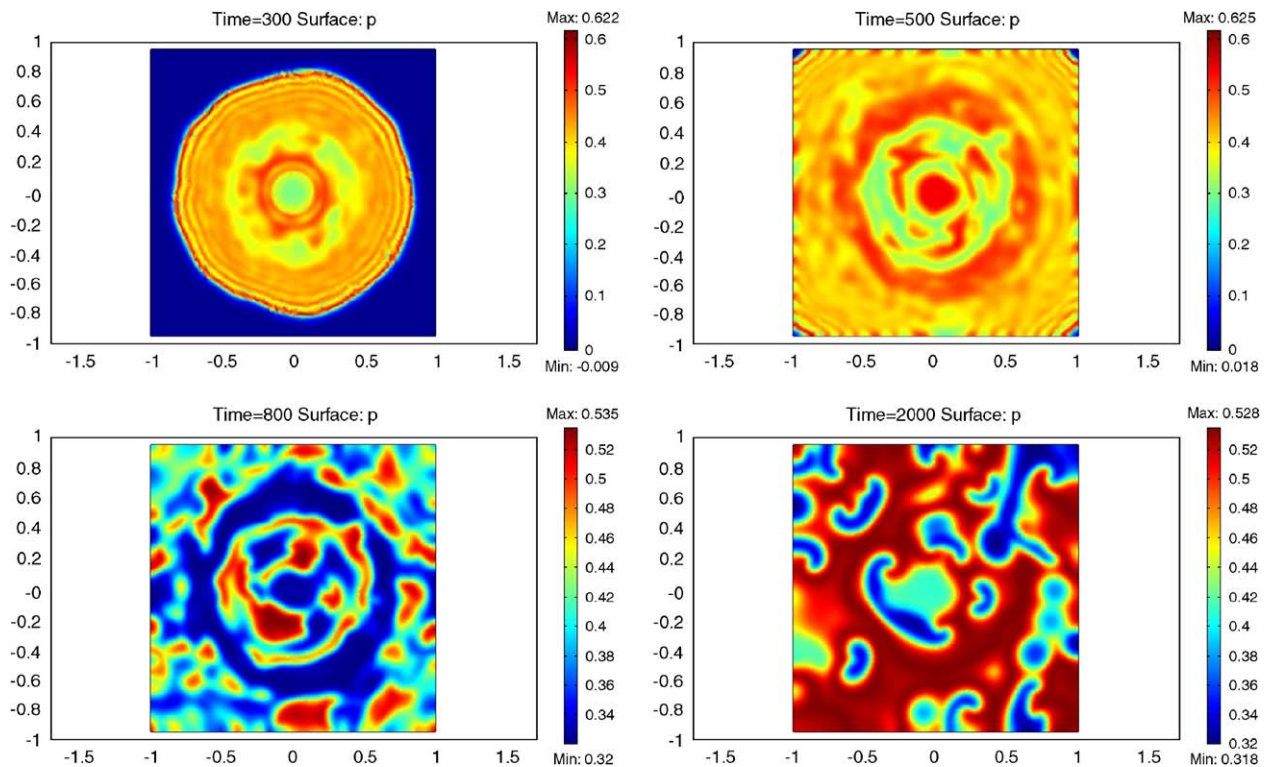


Fig. 6. Snapshots of the two-dimensional dynamics of parasitoid  $P$  at the generation times  $t = 300, 500, 800, 2000$ . Blue and green coloured regions represent areas of low species abundance, red and orange coloured regions represent areas of high species abundance. Parasitoid  $P$  interacts with the other three species in the domain  $\Omega_2 = (-1, 1) \times (-1, 1)$  with zero flux boundary conditions set up on  $\partial\Omega_2$ . For the initial conditions and parameter values discussed in the text, disordered, quasi-periodic wave behaviour is observed in the wake of the parasitoid invasion fronts when  $\rho_1 = \rho_3 = 3.3$  and  $\rho_2 = 0.33$ . At  $t = 800$  parasitoid  $P$  has spread through the domain and domain-wide heterogeneous spatio-temporal patterns are observed.

parasitoid  $P$  (and the other three species) increase. This increase in amplitude has a significant impact on the spatio-temporal dynamics. The two-dimensional dynamics of parasitoid  $P$  when  $\rho_1 = \rho_3 = 4$  are presented in Fig. 7. The most prominent development is the appearance of quasi-chaotic heterogeneous patterns in the wake of the travelling wave fronts (see sub-figure when  $t = 300$ ). This is most striking in the  $P$  population but similar behaviour is also observed for the  $N, M, Q$  populations (figures not shown). There is also a more pronounced ring-like pattern immediately behind the wave fronts, representing quasi-periodic waves of greater amplitude. The break-up of the quasi-periodic waves in the wake of the invasion front is of considerable interest, both mathematically and ecologically and corresponds with similar results discussed by Sherratt (2001) and Sherratt et al. (1995, 1997). These papers describe the appearance of chaos developing behind periodic waves, which are themselves behind the invasion front, in a two-equation reaction–diffusion system. It is suggested that a small instability in the periodic waves causes a small asymmetry to develop, which gives rise to chaotic dynamics. The dynamics observed in Fig. 7 also confirm that the observed heterogeneity is not a boundary effect as the heterogeneous break-up of the populations occurs before the parasitoids reach the boundaries of the domain.

Once the parasitoids have invaded the entire domain the distribution of the hosts and parasitoids becomes heterogeneous throughout. The labyrinthine patterns which we observe are striking and bear much similarity to quasi-chaotic, spiral-like patterns observed in other physical and biological systems. In ecology there has been some discussion of circular, spiral and heterogeneous patterns arising from population interactions (Nowak et al., 1994; Savill et al., 1997; Sherratt et al., 1997; Gurney et al., 1998). The paper of Schofield et al. (2002) considers an individual based model of a host–parasitoid system and similar patterns of spatio-temporal heterogeneity are also observed. Our patterns also bear considerable similarity with the signalling patterns of the slime mould *Dictyostelium discoideum* (Tyson et al., 1989; Palsson et al., 1997). Furthermore, spiral wave behaviour in cardiac tissue results in analogous patterning and has been the focus of considerable attention in the literature (Ito and Glass, 1991; Winfree, 1995; Panfilov, 1998). Finally, in a more general context, the dynamic heterogeneous patterns observed in Fig. 7 are reminiscent of the labyrinthine patterns observed in the work of Vasiev (2004) which examined the solutions of modified Fitz–Hugh–Nagumo equations. The ecological implications of our model dynamics are considered in the next section.



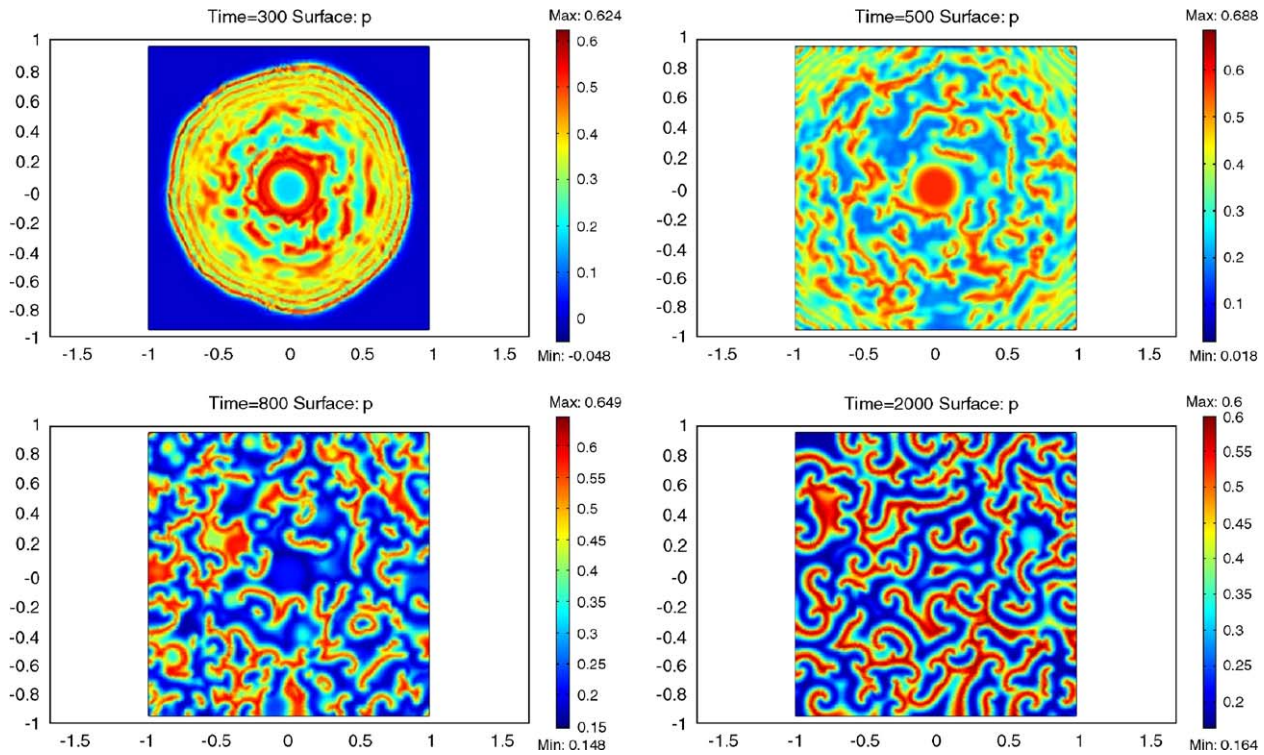


Fig. 7. Snapshots of the two-dimensional dynamics of parasitoid  $P$  at the generation times  $t = 300, 500, 800, 2000$ . Blue and green coloured regions represent areas of low species abundance, red and orange coloured regions represent areas of high species abundance. Parasitoid  $P$  interacts with the other three species in the domain  $\Omega_2 = (-1, 1) \times (-1, 1)$  with zero flux boundary conditions set up on  $\partial\Omega_2$ . For the initial conditions and parameter values discussed in the text, extremely pronounced and disordered, quasi-periodic wave behaviour is observed in the wake of the parasitoid invasion fronts when  $\rho_1 = \rho_3 = 4$  and  $\rho_2 = 0.4$ . The wave behaviour in the wake of the invasion front is observed to breakdown further from the front. At  $t = 800$ , parasitoid  $P$  has spread through the domain and domain-wide heterogeneous spatio-temporal patterns are observed.

## 6. Discussion

Reaction–diffusion equations have been identified as ideal tools for answering questions relating to invasions, interactions and spatial patterning. Our primary concern was assessing the possible impacts of parasitoid invasion in a multi-species community and we have observed the appearance of heterogeneous spatio-temporal patterns during the process of successful parasitoid invasion. Fundamentally, the appearance of spatio-temporal heterogeneity suggests that dispersive host–parasitoid interactions will exhibit spatial variation, a fact that has been reported in the literature (Hassell and Wilson, 1997; Sherratt et al., 1997). Our model highlights the wide range of dynamics that arise from the interplay of spatial random motility and oscillatory kinetics in a multi-species community and our results provide insights into multi-species host–parasitoid interactions.

The observed heterogeneous dynamics arise due to the coupling of random motility and limit cycle kinetics. Holmes et al. (1994) discuss the process of perturbations being amplified into spatial patterns, while the general theory of lambda–omega systems can also provide insight into the dynamics of our system. Lambda–omega systems are a class of simple two equation reaction–diffusion equations with limit cycle reaction kinetics. As the model system we have presented possesses limit cycle kinetics,

much of the underlying theory of lambda–omega systems can, to some extent, be applied to our model system. The seminal work of Kopell and Howard (1973) and Howard and Kopell (1977), was the first to consider such systems. The work of Dunbar (1983, 1986), discusses periodic wave trains in diffusive predator–prey systems, while Sherratt (1994) and Sherratt et al. (1995) have gone further, considering irregular (non-periodic) waves. The dynamical behaviour of our system appears to have much in common with Sherratt’s observations that, for certain parameter values, wave solutions of lambda–omega systems are unstable and that in these cases the periodic plane waves degenerate into more irregular oscillations that appear disordered. When the underlying cyclic dynamics of our system are coupled with spatial random motility, the resultant waves in the wake of the travelling invasion front appear to be always quasi-periodic and never periodic. As the parameters  $\rho_1$  and  $\rho_3$  are increased further into their unstable regions, the amplitude of the underlying oscillations increases. This causes the quasi-periodic wave dynamics to become increasingly erratic and fractured and results in more pronounced heterogeneous patterns.

The impact of the generalist parasitoid is of particular interest. The generalist has a significant impact on the dynamics of the system, influencing the dynamical behaviour in the host population  $M$  (directly) and thus parasitoid  $Q$  (indirectly). In Section 4, we showed that

when  $\rho_1$  is increased, oscillations are induced in all four species even though there is no direct connection between  $N$  and the host–parasitoid pair  $M, Q$ . Within the context of the *Pieris–Cotesia* system we are interested in whether the generalist and specialist parasitoids can coexist on shared resources and furthermore whether both parasitoids can successfully invade an initially host-only domain. The results of our model confirm that for a range of realistic parameter values, four species coexistence is indeed possible and that both parasitoids can invade successfully. There are, however, possible scenarios where species extinction can occur, which are not discussed here, but which merit further investigation. The results of our model also highlight the potential problems of an attempted biological control exercise using *C. glomerata* and *C. rubecula*. Biological control involves the use of parasitoids to suppress crop pests. The heterogeneous dynamics of our system highlight the inability of the parasitoids in our system to suppress uniformly the host populations and the constant appearance of regions of “boom-and-bust-type” dynamics. Despite this, it is possible to draw the general conclusion that if both host species are present they will most effectively be combatted by use of both parasitoids. More generally, it is important to know that quasi-chaotic, heterogeneous spatio-temporal dynamics can arise in our multi-species host–parasitoid system when the parasitoids are introduced into a domain containing both host species.

The appearance of heterogeneous patterns gives rise to temporary refuges for the hosts in regions of temporarily low parasitoid abundance. Refuges have been the subject of considerable attention in ecological literature (Hawkins et al., 1993; Hochberg et al., 1990; Holt and Hassell, 1993; Hochberg and Holt, 1995) and have been identified as being dynamically important since they generate variability in the intensity of parasitoid attacks on hosts within a given domain and allow hosts to benefit from enemy-free space (Krebs and Stephens, 1986; Holt and Lawton, 1994; Schmidt, 2004).

The heterogeneous patterns can also be considered in the context of niche formation. There is significant attention focussed on niche formation in recent literature (Vandermeer, 1972; Godfray, 1994; Leibold, 1995; Tilman and Kareiva, 1997). However, there remains uncertainty and debate as to what leads to niche creation. We can argue that the dynamical behaviour that exists in our model system has uncovered a mechanism of niche formation; that is, the formation of regions (niches) of high and low parasitoid and host abundance. The heterogeneous patterns continue to evolve over time and a fixed spatial distribution does not arise, however, suggesting that temporally and spatially fixed niches will not arise in dispersive host–parasitoid systems. Furthermore, it is important to stress that spatial dispersal of the parasitoids (of the realistic magnitudes considered) does not damp out population fluctuations when the hosts and parasitoids interact (which can occur in some situations). If anything, dispersal amplifies the impact of temporal oscillations on

the population dynamics leading to the quasi-chaotic heterogeneous spatio-temporal patterns observed.

The results of this paper make evident the value of further investigation of host–parasitoid interactions modelled by reaction–diffusion equations. There are many unanswered questions regarding multi-species host–parasitoid interactions in a spatial setting. The results do go some way to uncovering the behaviour of such systems, while also suggesting ways of testing our model against the ‘real’ *Pieris–Cotesia* system. Referring back to our dimensional parameters suggests that in a suitable domain size of say 50 m<sup>2</sup>, provided the conditions of the domain allow large populations of both hosts to be sustained (more than 350 individuals of each population say) heterogeneous patterns would be expected to develop over a period of several months. We suggest that field or laboratory-based experiments of the nature required to obtain spatio-temporal data would be challenging to implement and thus the results of the model can be used as a good approximation of the behaviour of this (and other) multi-species host–parasitoid systems. Future work will continue to focus on the current model system by incorporating more biological realism, including chemotaxis terms and considering a variety of domain shapes to assess the impact of habitat shape and fragmentation on the population dynamics. Furthermore, we intend to complement the current work by developing a system of discrete-time integro-difference equations to model non-overlapping generations and offer a comparison of two modelling frameworks of dispersive multi-species systems.

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