Emergence of global behaviour in a host–parasitoid model with density-dependent dispersal in a chain of patches

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ABSTRACT

We present a time discrete spatial host–parasitoid model. The environment is a chain of patches connected by dispersal events. Dispersal of parasitoids is host-density dependent. When the host density is small (resp. high), the proportion of migrant parasitoids is close to unity (resp. to zero). We assume fast patch to patch dispersal with respect to local interactions. Local host–parasitoid interactions are described by the classical Nicholson–Bailey model. By using time scales separation methods (or aggregation methods), we obtain a reduced model that governs the total host and parasitoid densities (obtained by addition over all patches). The aggregated model describes the time evolution of the total number of hosts and parasitoids of the system of patches. This global model is useful to make predictions of emerging behaviour regarding the dynamics of the complete system. We study the effects of number of patches and host density-dependent parasitoid dispersal on the overall stability of the host–parasitoid system. We finally compare our stability results with the $CV^2 > 1$ rule.

1. Introduction

The study of spatial dynamics of host–parasitoid associations has received a lot of attention (see the review by Briggs and Hoopes, 2004). Most models consider a set of spatial patches connected by dispersal events. These models usually combine two sub-models, one describing local host–parasitoid interactions on each patch and the other describing dispersal among patches. In early works, Hassell et al. (1991a) and Comins et al. (1992) considered a spatial environment which is a two-dimensional network of patches connected by dispersal. The local dynamics was represented by the classical Nicholson–Bailey model which is unstable. Regarding the dispersal

sub-model, they defined host (resp. parasitoid) mobility as the proportion of hosts (resp. parasitoids) moving from one patch to its eight closest neighbouring patches between two time steps. In this model, it was assumed that dispersal is "constant", i.e. proportions of migrants do not depend on local host and parasitoid densities and are simply constant parameters. Furthermore, dispersal was considered as isotropic, i.e. migrant individuals were uniformly distributed on neighbouring patches. These models were mostly developed to study the dynamics and the persistence of the host–parasitoid system (Adler and Nuernberger, 1994; Allen, 1975; Reeve, 1988; Rohani et al., 1994; Rohani and Ruxton, 1999) and the spatial structures that may emerge such as spiral waves,

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chaotic dynamics, or crystal structures, hence providing models where the global system is persistent while the local sub-model predicts unstability. Numerical simulations have shown that the type of spatial structure that emerges depends on the value of the host and parasitoid mobilities. Stability and persistence also disappear as radius and speed of dispersal increases (Nguyen Huu et al., 2006a).

Some other works considered host-density dependent dispersal of parasitoids. In reality, individual organisms move on a large range of time and space scales. At the landscape level, hosts and parasitoids can frequently move from a favourable patch to another one. French and Travis (2001) suggested that parasitoids are able to disperse more than once during the dispersal period, and can therefore "compare" host densities of several patches. Our knowledge about the effect of these repeated dispersal events between favourable patches on the overall host–parasitoid dynamics is still limited. Parasitoid dispersal is mainly connected to host availability. When the density of host is high on a given patch, parasitoids should rather remain on that patch than move to another one. Most parasitoids and hosts are sensitive to chemical products (pheromones) whose detectability depends on the density of organisms that are locally present (Travis and Dytham, 1999; Wiskerke et al., 1993). It is thus important to incorporate density dependent dispersal of organisms into models. Rohani and Miramontes (1995) and French and Travis (2001) showed that density dependent dispersal of parasitoids promoted the self-organization of spiral waves. This model therefore showed the interplay between the type of dispersal (density-dependent or not) and the emergent spatial pattern.

Another family of models considers a set of patches with local host–parasitoid interactions. However, in these models, the dispersal process is not explicit. It is assumed that after some dispersal process that is not described, hosts and parasitoids are distributed among spatial patches according to some given distribution (Hassell and May, 1973, 1974; Hassell et al., 1991b). These models are mostly dedicated to studying the effects of particular spatial host and parasitoid distributions on the stability of the host–parasitoid system, i.e. on the existence and stability of a non-trivial positive equilibrium point. A condition, called the 'CV^2 > 1 rule', has been proposed as an approximate criterion for stability (Pacala et al., 1990; Hassell et al., 1991b; Taylor, 1993). It states that if the square of the coefficient of variation of the parasitoid spatial distribution for each host is larger than unity, then the host–parasitoid system should be stable. These models clearly demonstrated the importance of the spatial distribution of host and parasitoid individuals on the stability of a host parasitoid system.

When some conditions on dispersal are met, persistence and stability can be analysed through a reduced model built using approximation methods (or aggregation methods). This reduced model (aggregated model) allows predicting the asymptotic behaviour of the system for fast dispersal. Differences between the local sub-model and the aggregated model correspond to the emergence of properties. When the mathematical expressions of the complete and the aggregated model are not the same, there is functional emergence. When the dynamics of the complete and the aggregated models are qualitatively not the same, there is dynamical emergence

(Auger et al., in press). In the case of density-independent dispersal, aggregation methods have been used to study the global behaviour of a model using unstable local dynamics (Nguyen Huu et al., 2006a) and persistent local dynamics (Nguyen Huu et al., 2006b). In both models, there was no functional emergence as local and aggregated models are of the same type, but there was dynamical emergence. In the present work, we show that density-dependent dispersal promote both functional and dynamical emergence.

In this work, we consider a chain of spatial patches connected by a series of dispersal events. In Lett et al. (2005), we show that when a radial symmetry condition is met, a 2D network of patches can be perfectly aggregated into a 1D chain of patches. For perfect aggregation, we refer to Iwasa et al. (1987). We also refer to the case of a 1D chain (Ruxton, 1996). Approximate aggregation methods have been presented in Iwasa et al. (1989), see also Auger and Bravo de la Parra for time scale separation methods (2000). Aggregation methods in linear and discrete time models have been described in Bravo de la Parra et al. (1999) and Auger and Bravo de la Parra (2000). In this work, we use an extension of those methods to a nonlinear situation, to appear in Sanz et al. (submitted), because the present model includes a dispersal sub-model that is not linear.

Local host–parasitoid interactions are described by the classical Nicholson–Bailey model. The patches are assumed to be close enough to support the assumption of frequent patch to patch dispersal with respect to local interactions. Spatial distributions of hosts and parasitoids are calculated explicitly from the dispersal sub-model. In the next step, by using aggregation methods, we obtain a global model that governs the total host and parasitoid densities (obtained by addition over all patches). We assume host-density dependent dispersal of parasitoids. When the host density is small (resp. high), the proportion of migrant parasitoids is close to unity (resp. to zero). We study the effects of number of patches and density dependent dispersal on the overall stability of the host–parasitoid system. We finally compare our stability results with the CV^2 > 1 rule and discuss emergence in this model.

2. The model

We consider a host–parasitoid system in a spatial environment which is a chain of A patches (Fig. 1). Let $n_{i,t}$ and $p_{i,t}$ be, respectively, the host and parasitoid density on patch i,
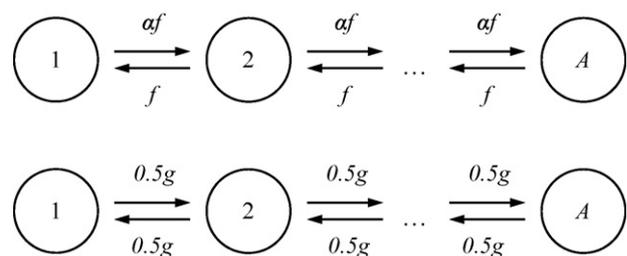
Fig. 1 – The chain of patches with the migration parameters used in the model for the hosts (top) and the parasitoids (bottom).
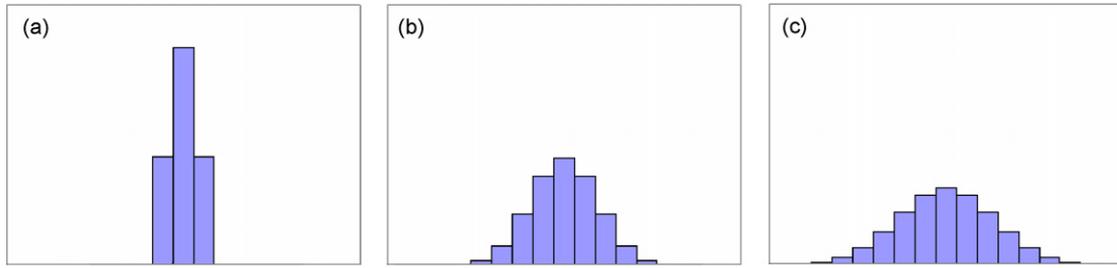
Fig. 2 – Distribution of a population of insects after a dispersal event composed of random walk. The insects are first located on the central patch. For each elementary dispersal event and for each patch, a constant proportion of insects move to an adjacent patch, leading to a diffusion-like distribution. The final distribution is shown after (a) 1, (b) 5 and (c) 10 elementary dispersal events.

$i \in \{1, \ldots, A\}$ at each generation t. We define the population vector as follows

$$X_t = (n_{1,t}, n_{2,t}, \ldots, n_{A,t}, p_{1,t}, p_{2,t}, \ldots, p_{A,t})^T$$

where the upper index T denotes the transposition.

The complete model is composed of two sub-models, one for dispersal between patches and one for host–parasitoids interactions on each patch.

2.1. Host and parasitoid dispersal sub-model

We assume that insects can move over a distance of k patches at each generation, in a diffusion-like dispersal process. In the case of a pure random walk, insects starting on a patch would be distributed according to a Gaussian distribution centred on this particular patch after dispersal. In the present model, hosts move according to an asymmetrical dispersal process (a biased random walk) while parasitoids dispersal is host density-dependent. In order to compute the distribution obtained for hosts and parasitoids, we discretize this process in time and decompose it into k elementary dispersal events consisting in movements from one patch to one of its nearest neighbours. Fig. 2 shows the effects of the number k of elementary symmetrical dispersal events on the host spatial distribution after a series of k symmetrical dispersal events with hosts initially located at the central patch.

Hosts' movements correspond to an asymmetric random walk: probabilities to go to the left or to the right patch are not the same. Let, f be the proportion of hosts moving from any patch to the neighbouring patch situated on its left between two time steps of dispersal. We define parameter $\alpha > 0$ and assume that the proportion of migrants from any patch to the neighbouring patch on its right is αf at each elementary dispersal event. When $\alpha > 1$, the proportion of hosts moving to the right is larger than in the opposite direction. Thus, after several elementary dispersal events, one expects to end up with a spatial host distribution shifted towards the right hand side of the chain. On the contrary, when $\alpha < 1$, the proportion of hosts moving to the left is larger than in the opposite direction and one expects a spatial host distribution shifted towards the left. To be biologically relevant, the proportion of hosts leaving a patch to go to left and right ones must be smaller than 1, and thus, we assume that $(1 + \alpha)f < 1$.

For parasitoids we assume a host density-dependent dispersal process. Dispersal corresponds to a random walk, but the probability of leaving the patch (and thus the proportion of migrants) depends on the density of hosts on that patch. Parasitoids may use chemical stimuli from their hosts (Vinson, 1976). Host stimuli are highly reliable but not very detectable (Vet and Dicke, 1992). In this model, if the parasitoid is unable to detect the presence of hosts thanks to the pheromones left by hosts, it will leave the patch. Thus, the density of hosts on a patch directly affects the proportion of migrants that will stay on that patch, as this proportion is related to the probability to find hosts pheromones which increases with density of hosts. Let, $g(n_{i,t})$ be the proportion of parasitoids leaving any patch i to go to the two neighbouring patches at each elementary dispersal event, which only depends on the density of hosts on patch i at timestep t. In this study, $g(n_{i,t})$ is given by a general classical type of function of the following form:

$$g(n_{i,t}) = \frac{1}{1 + \tau n_{i,t}^{\beta}} \tag{1}$$

where τ and β are positive parameters. A similar host density dependent dispersal process for parasitoids was used in the case of two spatial patches in Lett et al. (2003). Here, we extend the model to a chain of any number of patches.

Curves obtained for different values of β intersect at ($n = (1/\tau)^{1/\beta}$, $g = 0.5$). Fig. 3 shows function $g(n_{i,t})$ for $\tau = 1$ and different values of β. As modifying parameter corresponds to changing scale for hosts, we will assume that $\tau = 1$ in all this study. The main idea in Eq. (1) is that when many hosts are available on patch i, parasitoids remain on this patch. On the contrary, when few hosts are present there, parasitoids leave the patch. This shift in the parasitoid behaviour (stay or leave) is all the more "brutal" than β is large. We will later study the influence of β on the model.

We assume that parasitoids leaving patch i go in equal proportions to the two neighbouring patches. Then for any patch $1 < i < A$, the elementary dispersal process reads as follows:

$$n_{i,t+1} = [1 - (1 + \alpha)f]n_{i,t} + \alpha f n_{i-1,t} + f n_{i+1,t},$$
$$p_{i,t+1} = [1 - g(n_{i,t})]p_{i,t} + (1/2)g(n_{i-1,t})p_{i-1,t} + (1/2)g(n_{i+1,t})p_{i+1,t}$$
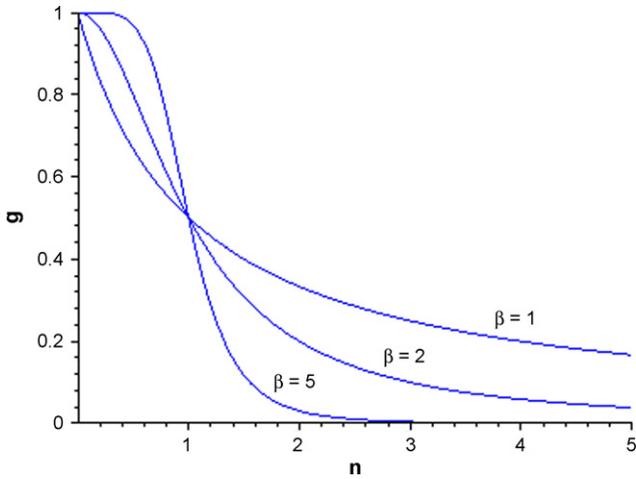
Fig. 3 – The proportion g of migrant parasitoids as a function of host density n, for $\tau = 1$ and different values of parameter β.

and for patches at both ends of the chain

$$
\begin{aligned}
n_{1,t+1} &= [1 - \alpha f]n_{1,t} + fn_{2,t}, \\
p_{1,t+1} &= [1 - (1/2)g(n_{1,t})]p_{1,t} + (1/2)g(n_{2,t})p_{2,t}, \\
n_{A,t+1} &= [1 - f]n_{A,t} + \alpha f n_{A-1,t}, \\
p_{A,t+1} &= [1 - (1/2)g(n_{A,t})]p_{A,t} + (1/2)g(n_{A-1,t})p_{A-1,t}
\end{aligned}
\tag{2}
$$

The elementary dispersal process can be therefore described by the following system

$$
X_{t+1} = M(X_t)X_t
\tag{3}
$$

where the time unit corresponds to a single elementary dispersal event. $M(X_t)$ is the following block matrix:

$$
M(X_t) = \begin{pmatrix} M_h & 0 \\ 0 & M_p(X_t) \end{pmatrix}
\tag{4}
$$

M_h is a $A \times A$ matrix for host dispersal and $M_p(N_t)$ a matrix for parasitoid dispersal:

$$
M_h = \begin{pmatrix}
1 - \alpha f & f & 0 & \cdots & & \cdots & 0 \\
\alpha f & 1 - (1+\alpha)f & f & \ddots & & \ddots & \vdots \\
0 & \ddots & \ddots & \ddots & & \ddots & \vdots \\
\vdots & \ddots & \ddots & \ddots & & \ddots & 0 \\
\vdots & \ddots & & \ddots & \alpha f & 1 - (1+\alpha)f & f \\
0 & \cdots & & \cdots & 0 & \alpha f & 1 - f
\end{pmatrix}
\tag{5}
$$

The full dispersal sub-model is given by the elementary dispersal process composed k times. For simplicity in notation, it is written as follows:

$$
X_{t+1} = M(k, X_t)X_t
\tag{7}
$$

The whole dispersal process is a slow process, thus one step corresponds to one time step at slow time scale. For each generation, k elementary dispersal events occur. In Eq. (7), the index k means that the elementary dispersal process is repeated k times, i.e. $M(k, X_t)$ is recursively defined by: $M(1, X_t) = M(X_t)$ and for $k > 1$,

$$
M(k, X_t) = M(M(k-1, X_t)X_t)M(k-1, X_t).
\tag{8}
$$

2.2. Host–parasitoid interactions sub-model

On each patch i of the chain, we assume that hosts and parasitoids interact according to the Nicholson–Bailey model

$$
\begin{aligned}
n_{i,t+1} &= \lambda_i n_{i,t}\, e^{-a_i p_{i,t}} = h_i(n_{i,t}, p_{i,t}), \\
p_{i,t+1} &= c_i n_{i,t}(1 - e^{-a_i p_{i,t}}) = k_i(n_{i,t}, p_{i,t})
\end{aligned}
\tag{9}
$$

where λ_i is the host growth rate on patch i, a_i the searching efficiency of parasitoids and c_i the average number of viable parasitoids that emerge from an host parasitized at the previous generation.

We define a map $S : \mathbb{R}^{2A} \to \mathbb{R}^{2A}$ as follows:

$$
S = (h_1, h_2, \ldots, h_A, k_1, k_2, \ldots, k_A)^T
\tag{10}
$$

in which functions h_i and k_i, $i \in [1, \ldots, A]$, are defined by Eq. (9) and describe the local host–parasitoid interactions.

2.3. The complete model

The complete model combines the two previous sub-models as follows:

$$
X_{t+1} = S(M(k, X_t)X_t)
\tag{11}
$$

We consider the slow time scale for this model: one time step corresponds to a single event of reproduction, and thus one generation. Therefore, it is assumed that between time t and $t + 1$ hosts and parasitoids first explore the environment by performing k elementary dispersal events before settling down, then they enter a phase where they have local demographic and parasitism interactions. Local interactions occur at the same time on every patch. Thus, all patches are

$$
M_p(X_t) = \begin{pmatrix}
1 - (1/2)g(n_{1,t}) & (1/2)g(n_{2,t}) & 0 & \cdots & & \cdots & 0 \\
(1/2)g(n_{1,t}) & 1 - g(n_{2,t}) & (1/2)g(n_{3,t}) & \ddots & & \ddots & \vdots \\
0 & \ddots & \ddots & \ddots & & \ddots & \vdots \\
\vdots & \ddots & \ddots & \ddots & & \ddots & 0 \\
\vdots & \ddots & & (1/2)g(n_{A-2,t}) & 1 - g(n_{A-1,t}) & \ddots & (1/2)g(n_{A,t}) \\
0 & \cdots & & \cdots & 0 & (1/2)g(n_{A-1,t}) & 1 - (1/2)g(n_{A,t})
\end{pmatrix}
\tag{6}
$$

synchronized. As previously stated, the model can then be seen as coupling a diffusion model (close to continuous diffusion) with regular demography events.

2.4. The aggregated model

When parameter k becomes large, the elementary dispersal process is repeated a large number of times with respect to local interactions (which occur only once per generation). In this case, the dispersal process is "fast" in comparison to local interactions. It is then possible to build up a reduced model, also called aggregated model (see Appendix A). This aggregated model governs the total host and parasitoid densities:

$$n_t = \sum_{i=1}^{A} n_{i,t} \text{ and } p_t = \sum_{i=1}^{A} p_{i,t} \qquad (12)$$

To obtain the aggregated model, one has to study first the fast dispersal process and to look for the existence of a fast stable equilibrium. First, one can note that dispersal is conservative, i.e. total host and parasitoid densities remain constant during dispersal. Indeed, individuals leaving a patch go to another patch, making the global balance equal to zero along the chain. In other words, total densities n and p are invariant at the fast time scale. In Appendix A, for each value of the "constant" n at the fast time scale, we obtain the coordinates, n_i^*, of the unique host fast equilibrium point, which is stable. Also, for each pair of values of the "constant" n and p at the fast time scale, we obtain the coordinates, p_i^*, of a unique parasitoid fast equilibrium point.

$$n_i^* = \nu_i^* n, \qquad p_i^* = \mu_i^*(\nu^* n) p \qquad (13)$$

where $\nu^* = (\nu_1^*, \ldots, \nu_A^*)$. The host fast equilibrium depends linearly on total host density and the parasitoids patch proportions at the fast equilibrium depend on total host density. The proportion of hosts on patch i at the fast equilibrium are

$$\nu_i^* = \frac{1-\alpha}{1-\alpha^A} \alpha^{i-1} \qquad (14)$$

and the proportion of parasitoids are

$$\mu_i^*(\nu^* n) = \frac{1 + (\nu_i^* n)^\beta}{A + \sum_{j=1}^{A} (\nu_j^* n)^\beta} \qquad (15)$$

According to expression (15), if the proportion of hosts is high on patch i, the proportion of parasitoids on this patch will also be large. In other words, the parasitoids are spatially distributed like the hosts. Parameter β makes this effect more or less important. If β is large, the parasitoids will be mostly found on the few patches having larger host densities. The parasitoid distribution also depends on total host density n: when it is low, parasitoids tend to distribute uniformly among the patches ($\mu_i^* \to 1/A$ when $n \to 0$), whereas when it is high they tend to distribute according to the host distribution ($\mu_i^* \propto \nu_i^{*\beta}$). When $\beta = 1$, expression (15) is similar to the distribution proposed by Comins and Hassell (1979), which was based on the optimal foraging theory.

When parameter k is large, we assume that dispersal dynamics is fast in comparison with local interactions. Then, we can make an approximation by assuming that at any generation t, the system reaches the fast equilibrium (14) and (15) corresponding to the equilibrium of the dispersal sub-model. We then replace values of densities of hosts and parasitoids after dispersal by values at fast equilibrium. Thus, adding host and parasitoid densities of model (9) and substituting the fast equilibrium Eqs. (14) and (15) leads to a reduced model governing the total host and parasitoid densities:

$$n_{t+1} = n_t \sum_{i=1}^{A} \lambda_i \nu_i^* \, e^{-a_i \mu_i^*(\nu^* n_t) p_t},$$

$$p_{t+1} = n_t \sum_{i=1}^{A} c_i \nu_i^* (1 - e^{-a_i \mu_i^*(\nu^* n_t) p_t}) \qquad (16)$$

Model (16) is obtained from model (9) by making an approximation that is valid when k is large enough. In Appendix A, we show that when k is becoming large, $k \gg 1$, the aggregated model can be used to study the asymptotic behaviour of the complete model.

Setting $p_t = 1$ in the second Eq. (16) shows that, from one generation to the next, parasitoids emerging from a single individual emerge from a series of patches belonging to the spatial equilibrium distribution:

$$n_t \sum_{i=1}^{A} c_i \nu_i^* (1 - e^{-a_i \mu_i^*(\nu^* n_t)}) \qquad (17)$$

This equation means that parasitoids emerging at the next generation from a single parasitoid come from different patches which were visited during the dispersal process by this insect at the previous generation according to the fast equilibrium distribution.

3. Results

In this section, we summarize the analytical results obtained in Appendices A and B regarding aggregation, existence and stability of the fixed points.

Moreover, we illustrate our results with two examples of systems with different asymptotic behaviour. We present systems with an aggregated model dynamics tending to an equilibrium point, then tending to an attracting closed invariant curve.

The origin is a trivial fixed point of model (16) and it is asymptotically stable if, and only if $\sum_{i=1}^{A} \lambda_i a_i < 1$. Under certain conditions (see Appendix B) the points $(n,0)$ (for certain values of $n > 0$) are semi-trivial fixed points of model (16). These points are unstable.

In Appendix B, we show the existence of at least a positive fixed point (n^*, p^*) which verifies Eq. (16) when $\lambda_i = \lambda$, $c_i = c$ and $a_i = a$ for $i = 1, \ldots, A$. In more general cases, existence and uniqueness of a non-trivial positive equilibrium has to be found numerically solving:

$$1 = \sum_{i=1}^{A} \lambda_i \nu_i^* \, e^{-a_i \mu_i^*(\nu^* n^*) p^*}, \qquad p^* = n^* \sum_{i=1}^{A} c_i \nu_i^* (1 - e^{-a_i \mu_i^*(\nu^* n^*) p^*}) \qquad (18)$$

Thanks to the results in Appendix A, the existence of a fixed point to the aggregated system (16) implies the existence of a fixed point for the general system (11) for large enough values of k. The local stability of the positive equilibrium (n^*, p^*) of Eq. (16) must be determined numerically by calculating the trace and the determinant of its Jacobian matrix. Moreover, let (n^*, p^*) be hyperbolic. If it is an asymptotically stable (resp. unstable) equilibrium of the aggregated system (16), then $X^* = E(n^*, p^*)$ is an asymptotically stable (resp. unstable) equilibrium of the complete model (11).

3.1. Aggregated model with an equilibrium point

Numerical simulations were run in order to illustrate theoretical results. We use a chain of $A = 5$ patches, with the set of parameters $\alpha = 2.3$, $\beta = 4$, $f = 0.2$, $\lambda_i = 2$, $a_i = 0.5$ and $c_i = 1$, $i \in \{1, \ldots, A\}$. The trajectories of the aggregated model tend toward an equilibrium point of coordinates $(n^*, p^*) = (7.666, 3.833)$, which is stable. For low values of k ($k \leq 2$), the behaviour of the complete model differs from the behaviour of the aggregated model. For $k = 1$, the system is unstable, and the parasitoid population eventually goes extinct (observe that this is not the case in which the semi-trivial fixed points are unstable, because $\sum_{i=1}^{A} \lambda_i a_i \neq 1$). For $k = 2$, the system is not unstable anymore, but the trajectory of the complete model asymptotically seems to tend to a chaotic attractor. For larger values of k ($k > 2$), the complete model has an equilibrium point like the aggregated one, but their values differ from the equilibrium (Ruxton (1996) obtained a similar result). We reported in Table 1 the value of the equilibrium obtained for the complete model using different values of the number of dispersal events k. Results show that when k increases, the equilibrium point of the complete model tends to the one of the aggregated model. Fig. 4 shows the distance between equilibriums for the complete and the aggregated models using different values of k. For $k > 8$, relative error is less than 5%. The trajectories of the aggregated model and the complete model are shown in Fig. 5 for different values of k.

3.2. Aggregated model with an attractor

With the set of parameters $A = 5$, $\alpha = 2.3$, $\beta = 3$, $f = 0.2$, $\lambda_i = 1.5$, $a_i = 0.5$ and $c_i = 1$, $i \in \{1, \ldots, A\}$, the trajectory of the aggregated
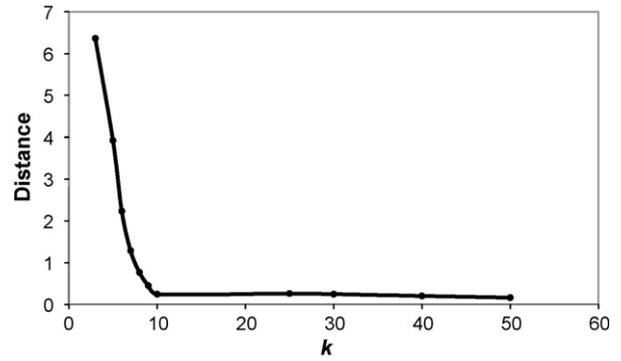
Fig. 4 – Distance between equilibrium for the complete model and equilibrium for the aggregated model for different values of k. For $k \geq 9$, this distance is lower than 5% of $||(n^*;p^*)||$, where $||.||$ is Euclidian norm.

model tends to an attracting closed invariant curve shown in Fig. 6. For $k = 1$, the dynamics of the complete model seem to be chaotic, but for $k \geq 2$, it tends toward an equilibrium point. For $k \geq 17$, it tends toward an attracting invariant curve which becomes closer to the attractor of the aggregated model as k increases. Those dynamics are represented of Fig. 6. Unfortunately, theoretical results relating attracting closed invariant curves for both the general and the aggregated system are not yet available.

3.3. Effects of the number of patches on the system stability

Fig. 7 presents the local stability regions in black of a positive fixed point of model (16) as a function of parameters α and β for different number of patches in the chain. The white area corresponds to non-stable regions in the sense that the stability condition is not verified. Two symmetrical areas are found. The upper one corresponds to a value of parameter $\alpha > 1$, i.e. a spatial distribution of hosts shifted to the right hand side of the chain of patches. The lower stability area corresponds to the same spatial distribution of hosts but shifted to the left. When the number of patches increases, the stability area increases in size. This is rather a general result in ecological dynamics that the persistence of a system is favoured when its size is large. It is interesting to note that there is a critical value for parameter β in order to obtain stability. For a two-patch chain, this critical value is about 3, for 3 patches, it is about 2 and for 5 patches about 1.5. When few patches are available, parasitoids should go therefore to the most favourable patches (those where the hosts are) to ensure global stability. When the number of patches increases, parasitoids still have to be spatially distributed by choosing patches where hosts are abundant, but smaller values of β are required, i.e. parasitoids can have less sensitivity to detect host abundance.

3.4. Effects of the "ac" product on stability

The domains of stability of the fixed point of the aggregated model in terms of parameters α and β are shown for a chain of

Table 1 – Coordinates of the equilibrium of the complete model for different values of dispersal frequency k		
k	n	p
3	13.359	6.679
5	11.177	5.588
6	9.663	4.831
7	8.816	4.408
8	8.352	4.176
9	8.070	4.035
10	7.887	3.943
25	7.432	3.716
30	7.445	3.722
40	7.483	3.741
50	7.5204	3.7602
500	7.666	3.833
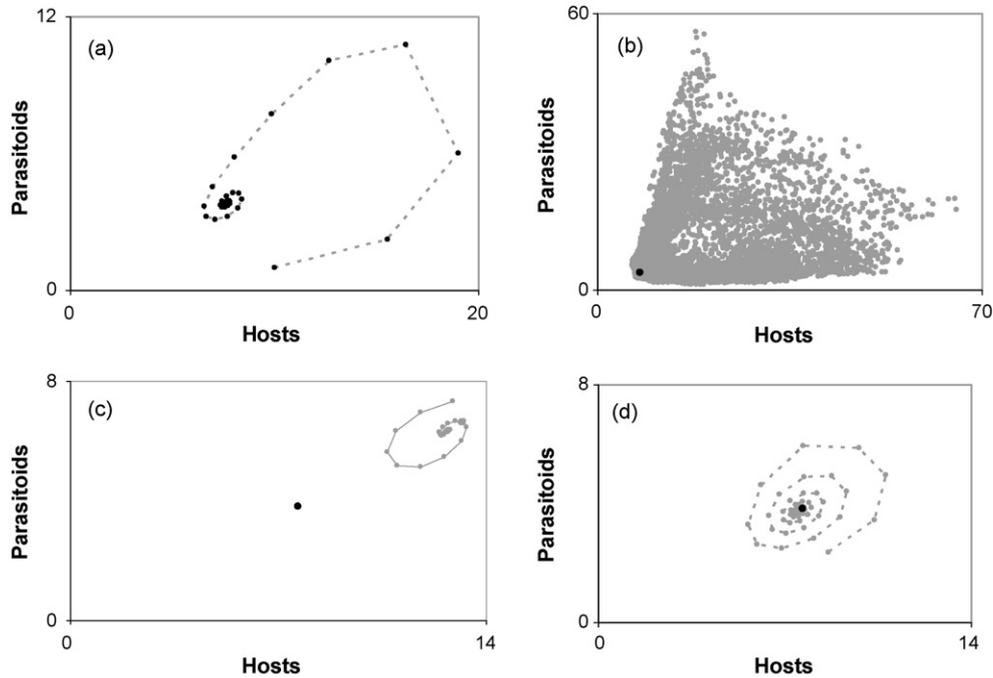
Fig. 5 – (a) Trajectory of the aggregated model. **(b, c and d)** Trajectory of the complete models with the set of parameters $A = 5$, $\alpha = 2.3$, $\beta = 4$, $f = 0.2$, $\lambda_i = 2$, $a_i = 0.5$ and $c_i = 1$, $i \in [1, \ldots, A]$ for different values of k. Trajectories of the complete model are represented in grey, and the black circle represents the equilibrium found with the aggregated model.**(b)** For $k = 2$, the dynamics of the complete model is chaotic. **(c)** For $k = 4$, host and parasitoid populations tends toward an equilibrium point which is not the equilibrium point found in the aggregated model. **(d)** For $k = 50$, the equilibrium point of the complete model is nearer to the one of the aggregated model.
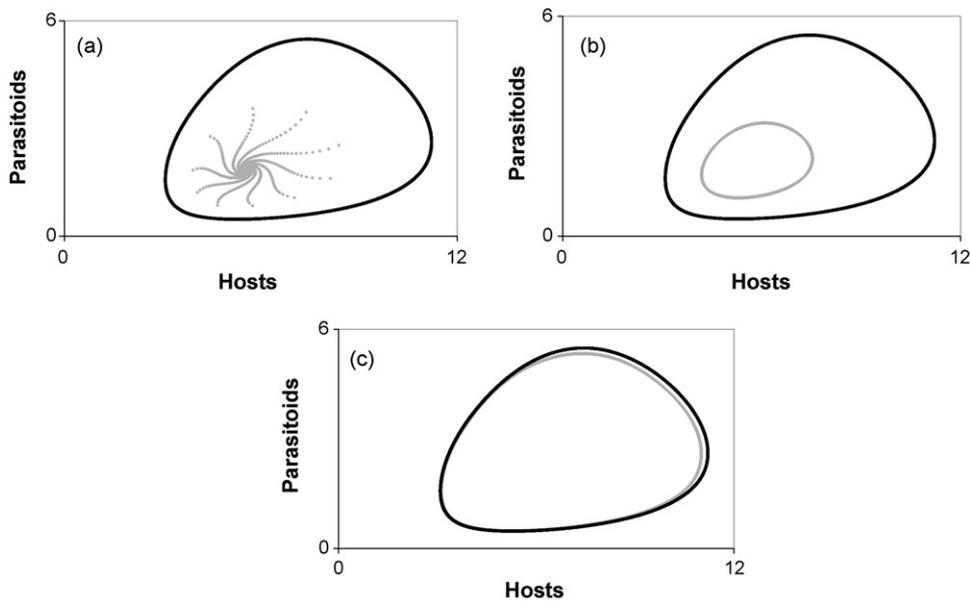
Fig. 6 – Trajectories of the complete (grey) and aggregated (black) models with the set of parameters $\alpha = 2.3$, $\beta = 3$, $f = 0.2$, 1.5, $a_i = 0.5$ and $c_i = 1$, $i \in \{1, \ldots, A\}$ for different values of k. A part of transient dynamics has not been represented. (a) For $k = 15$, the attractor of the complete model is an equilibrium point. (b) For $k = 20$, the attractor of the complete model is of the same type as the attractor of the aggregated model. (c) For $k = 50$, the attractor of the complete model almost matches the one of the aggregated model.
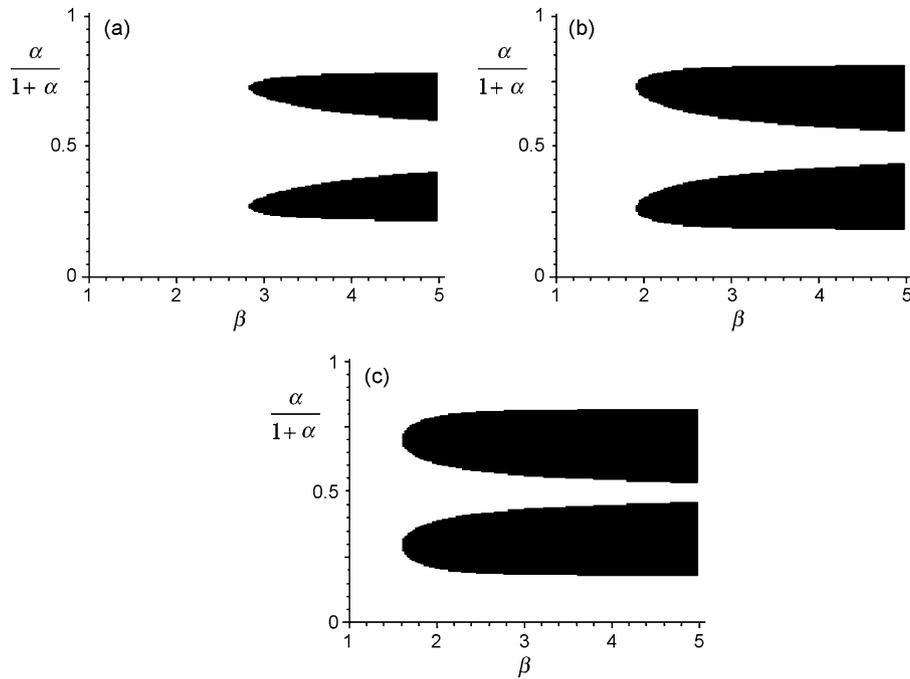
Fig. 7 – Domain of stability (in black) of the positive fixed point of the aggregated model for different values of parasitoid aggregation parameter β and host migration asymmetry parameter α for a chain with (a) A = 2 patches, (b) A = 3 and (c) A = 5. Parameter values: $\lambda_i = 3$, $a_i = 0.05$ and $c_i = 1$, $i \in \{1, \ldots, A\}$.

A = 5 patches, with $\lambda_i = 2$ and $a_i c_i = 0.05$ (Fig. 8a), 0.5 (Fig. 8b), or 1 (Fig. 8c), $i \in [1, \ldots, A]$. This figure shows that an increase of ac product, i.e., of either the parasitoid searching efficiency a or the number of parasitoids emerging from one parasitized host c, leads to a decrease of the domain of stability. Higher values

of one or the other parameter correspond to parasitoid populations that are more efficient in killing hosts, and therefore more likely to lead to unstable interactions. The fact that an increase in one parameter can be counter-balanced by a similar decrease in the other parameter (i.e., only the value of
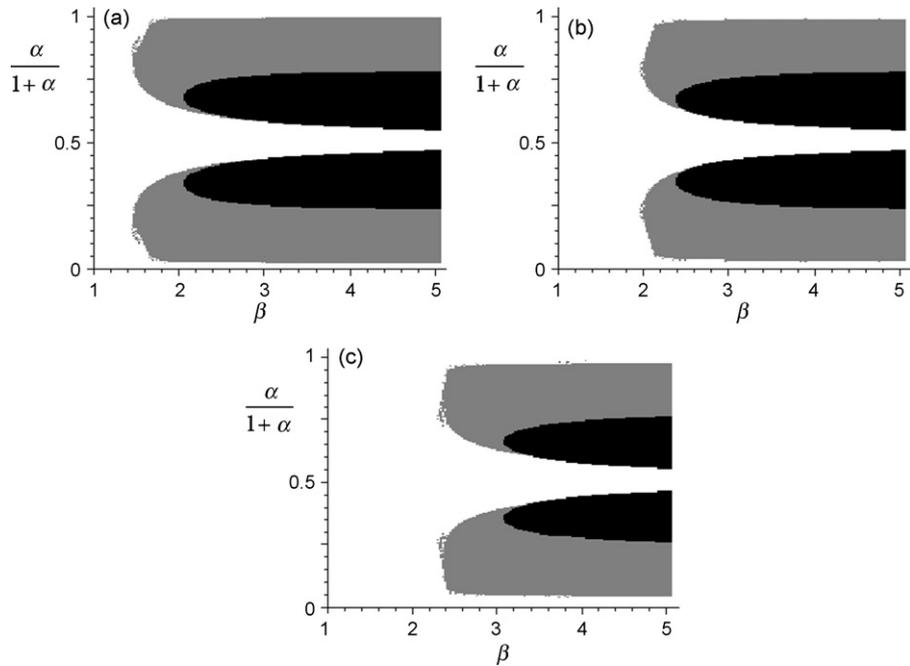
Fig. 8 – Domain of stability (in black) and of persistence (in grey) of the positive fixed point of the aggregated model for different values of parasitoid aggregation parameter β and host migration asymmetry parameter α for a chain with A = 5 patches, $\lambda_i = 2$ and (a) $a_i c_i = 0.05$, (b) $a_i c_i = 0.5$ and (c) $a_i c_i = 1$, $i \in \{1, \ldots, A\}$.
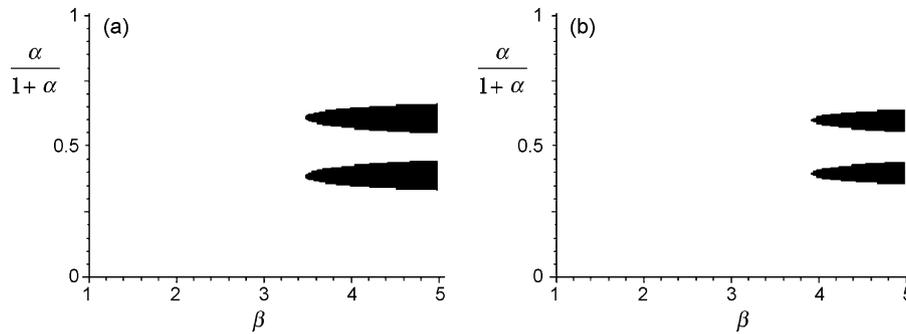
Fig. 9 – Domain of stability of the positive fixed point of the aggregated model using (a) the usual stability condition and (b) the CV^2 > 1 rule. Parameter values: A = 5 patches, λ_{1-5} = 1.1, a_{1-5} = 0.05 and c_{1-5} = 1.

the ac product counts) only comes true when all patches are identical.

Domains of persistence also have been represented in grey in Fig. 8. They are qualitatively the same than stability domains; domains of persistence are however larger than the corresponding stability domains. Increasing product ac also leads to enlarging domains of non-persistent interactions.

3.5. Comparison with the CV^2 > 1 rule

Using the aggregated model (17), it is assumed that at any generation, the spatial fast dispersal equilibrium is achieved. This spatial equilibrium distribution is represented by host and parasitoid patch frequencies given by Eqs. (15) and (16). Models using global dispersal (Hassell and May, 1973, 1974; Hassell et al., 1991b) are based on similar assumptions. For these models, stability is linked to heterogeneity, and more precisely to the frequency distribution of parasitoid density between patches (Pacala et al., 1990). The 'CV^2 > 1 rule', where CV is the coefficient of variation of parasitoid density in the vicinity of each host, has been shown to be an approximate criterion for stability (Pacala et al., 1990; Hassell et al., 1991b; Taylor, 1993). This criterion states that interactions are stable if CV^2 is greater than unity. For more details on the calculation of CV, we refer to Hassell (2000). In our case, it can be shown that the CV^2 > 1 condition is equivalent to inequality (19) (see Appendix C for details):

$$\sum_{i=1}^{A} v_i^* [\mu_i^*(n^*)]^2 > 2 \left[\sum_{i=1}^{A} v_i^* \mu_i^*(n^*) \right]^2 \tag{19}$$

Fig. 9 shows the stability area with respect to parameters α and β for λ = 1.1 using the usual stability condition based on the calculation of the trace and the determinant of the Jacobian Matrix (Fig. 9a) or the approximate CV^2 > 1 condition (19) (Fig. 9b). This result shows that the CV^2 > 1 rule works well for spatially homogeneous conditions and low values of host growth rates, but it does not otherwise.

3.6. Effect of the host growth rate on stability

Figs. 7c, 8a and 9a can be compared as they only differ in the value of host growth rate, with λ_i = 1.1, λ_i = 2 and λ_i = 3,

$i \in \{1, \ldots, A\}$, respectively. This comparison shows that an increase in the host growth rate promotes stability, which confirms previous results obtained on two patches (see Fig. 8 in Lett et al., 2003). When the dispersal of parasitoids was considered as independent of host density, the opposite result was obtained (see Fig. 3 in Lett et al., 2003, for two patches; this result holds for a higher number of patches). However, in this situation we also observed that for small host growth rates stability was obtained when hosts and parasitoids migrated mainly to different patches, whereas for high host growth rates, they had to go to the same patch. Here, because of the host-density dependent dispersal of parasitoids, we ''force'' parasitoids to go where hosts go. So both results actually suggest that an increase in host growth rate promotes stability in situations where hosts and parasitoids aggregate on the same patches.

4. Discussion

In this work, we have limited our study to a chain of patches. This is not too restrictive because under some conditions, a two-dimensional network of patches can be represented by a reduced model corresponding to a one-dimensional chain of patches. In order to perform such a reduction, some symmetry conditions must hold, see the case of a two-dimensional network of patches with radial symmetrical dispersal from a central patch to external patches in an appendix of Lett et al. (2005). However, in most cases, a two-dimensional network cannot be reduced to a one-dimensional chain of patches. Thus, to be more general and realistic, it would be needed to study the case of a two-dimensional network of patches.

This model can be seen as a discrete version of a reaction-diffusion model with a parasitoid diffusion coefficient depending on the host population density. Such a model has been developed in the continuous case (see Section 9.3 in Murray, 1993). An increase of the time scale factor k of the diffusion process in our model would have the same effect than an increase of the diffusion coefficient in a continuous time model. In our model, the parameter k can also be associated to the radius of the distribution after dispersal: k is the maximum number of patches an individual can go through during one generation. If all insects start on one patch, they all can be found within a distance of k patches

from the starting patch. This allows the model to be more flexible than models considering only dispersal on the nearest neighbours: patch size can be chosen arbitrarily small compared to the distance insects can travel in one generation, thus it would not be relevant to prevent individuals for moving farther. Furthermore, multiple host density-dependent elementary dispersal events allow parasitoid to leave the patch if no hosts are present, preventing the unrealistic situation where parasitoids would stay on an empty patch. In addition, this dispersal model is less extreme than the ideal free distribution, which does not describe the intrinsic process of dispersal, allowing individuals to reach any patch in the environment, regardless of their mobility.

The simplicity of our description comes from the fact that we assume the decomposition of the dispersal process in k elementary dispersal events. This allows ending up with some constant host and parasitoid distributions so that a simple global model governing the total host and parasitoid densities can be derived. The advantage of this method is to calculate explicitly the host and parasitoid spatial distributions as the fast equilibrium from the dispersal model instead of using spatial distributions that are given *a priori*. Our study allows obtaining an aggregated model that governs the total host and parasitoid densities. This model has only two variables, which are global densities for hosts and parasitoids, and is much more tractable than the complete model. In the most favourable cases it could be analysed analytically. Otherwise, as in this work, the existence of a non-trivial positive equilibrium for the aggregated model can be proved and stability conditions for the reduced model can be checked numerically. The stability condition for the complete model would be much more difficult to obtain for a chain with a large number of patches. Stability conditions of the aggregated model can be compared to other stability criteria that were already proposed, like the $CV^2 > 1$ rule. This rule is known to work better when the host growth rate is small (Hassell et al., 1991b; Taylor, 1993). The advantage of the local stability condition is that it is valid for any value of the parameter set. Our work was able to confirm that the $CV^2 > 1$ rule and local stability condition predict similar stability areas, the agreement between the two methods becoming better when the host growth rate gets smaller.

The expression of the aggregated model (18) differs from the Nicholson–Bailey model given in the local model (9), thus there is always a functional emergence in this system. Furthermore, the aggregated model provides three types of asymptotic behaviour: unstability, asymptotically stable equilibrium or trajectories tending towards an attracting closed invariant curve. Fig. 8 shows the corresponding domains for some sets of parameters. The local Nicholson–Bailey submodel always provides unstability, thus in grey and black domains (Figs. 7 and 8), there is a dynamical emergence. Hence, density-dependent dispersal promotes emergence, which makes the aggregated model a useful tool to analyse the global dynamics of the system.

In the future, we would like to consider the case of a two-dimensional network of patches connected by density dependent dispersal at a fast time scale. In that case too, aggregation methods would allow building a reduced global model which could be useful to make suitable predictions about the emergence of global dynamics of the complete system.

Appendix A

In this appendix, we are proving that the complete model can be reduce into an aggregated model that will be used to study its asymptotic behaviour.

First of all, let us summarize the results concerning the reduction of this kind of systems that are proved in Sanz et al. (submitted). The model evolves in discrete time and is driven by two processes with different time scales: slow and fast. Such processes are defined respectively by two mappings

$$S, F : \Omega_N \to \Omega_N, \quad S, F \in C^1$$

where $\Omega_N \subset \mathbb{R}^N$ is a non-empty open set. The time step of the model corresponds to the slow dynamics. The effect of the fast process over this time interval, which is much larger than its own, it is assumed to act k times before the slow process acts. So, denoting by $X_{k,t} \in \mathbb{R}^N$ the vector of state variables at time t, the complete system is defined by

$$X_{k,t+1} = S(F^k(X_{k,t})) \tag{A1}$$

where F^k denotes the k-fold composition of F with itself.

In order to reduce the system (A1), we have to impose some conditions on the fast process, which are specified in the following hypothesis:

Hypothesis 1. For each initial condition $X \in \Omega_N$, the fast dynamics tends to an equilibrium. That is, there exists a mapping $\bar{F} : \Omega_N \to \Omega_N$ such that for all $X \in \Omega_N$

$$\lim_{k \to \infty} F^k(X) = \bar{F}(X).$$

Moreover, there exist a non-empty and open set $\Omega_q \subset \mathbb{R}^q$ with $q < N$, and two mappings $G : \Omega_N \to \Omega_q$ and $E : \Omega_q \to \Omega_N$ such that $\bar{F}$ can be expressed as

$$\bar{F} = E \circ G$$

where G represents the so-called global variables and E the equilibrium reached by the fast dynamics for the corresponding value of the global variables.

Assuming Hypothesis 1, one can associate to the complete system (A1) the following reduced or aggregated system:

$$Y_{n+1} = G \circ S \circ E(Y_n) \tag{A2}$$

where $Y_n := G(X_n)$. Observe that the system (A1) evolves in $\mathbb{R}_+^N$ whereas its aggregated counterpart (A2) evolves in $\mathbb{R}_+^q$, where q can be much smaller than N. The following theorem states when and how one can use the aggregated system to study the asymptotic behaviour of the complete system.

Theorem 1. Let us assume that $\bar{F} \in C^1(\Omega_N; \Omega_N)$ and that $\lim_{k \to \infty} F^k(X) = \bar{F}(X)$ and $\lim_{k \to \infty} DF^k(X) = D\bar{F}(X)$ uniformly on any compact set $K \subset \Omega_N$. Let $Y^* \in \mathbb{R}^q$ be a hyperbolic fixed point of (A2) which is asymptotically stable (resp. unstable). Then there exists $k_0 \in \mathbb{N}$ such that for each $k \geq k_0$, $k \in \mathbb{N}$, there exists a hyperbolic fixed point X_k^* of (A1) which is asymptoti-

cally stable (resp. unstable) and that satisfies $\lim_{k\to\infty} X_k^* = S\circ E(Y^*)$. Moreover, let $X_0 \in \Omega_N$, if the solution Y_t of (A2) corresponding to the initial condition $Y_0 = G(X_0)$ is such that $\lim_{t\to\infty} Y_t = Y^*$ then, for each $k \geq k_0$, $k \in \mathbb{N}$, the solution $X_{k,t}$ of (A1) corresponding to X_0 verifies $\lim_{t\to\infty} X_{k,t} = X_k^*$.

The theorem states that, under certain conditions, one can approximate the hyperbolic fixed points of the complete system, as well as their basins of attraction in case they are stable, by performing their study in the aggregated system. Though it is not stated in the theorem, the results are also valid for hyperbolic periodic solutions (see Sanz et al., submitted).

The remainder of this appendix is devoted to show that model (11) matches with the assumptions of Theorem 1. Let us denote $\Omega_{2A} = \mathbb{R}_+^{2A}$ and $\Omega_2 = \mathbb{R}_+^2$. Let $N = (n_1, \ldots, n_A)^T$ and $P = (p_1, \ldots, p_A)^T$ be the population vectors of hosts and parasitoids, respectively. Let also $n = \sum_{i=1}^A n_i$ and $p = \sum_{i=1}^A p_i$ stand for the total number of hosts and parasitoids which will play the role of global variables and therefore will be the state variables for the aggregated system. Finally, we denote the population vectors for the complete and the aggregated system $X = (N,P)^T \in \mathbb{R}^{2A}$ and $Y = (n, p)^T \in \mathbb{R}^2$.

Functions F and S of system (A1) for model (11) are those defined by Eqs. (3) and (10) as follows:

$F(X) = M(N)X$ or, in terms of N and
P, $F(N,P) = (M_h N, M_p(N)P)$,
$S(X) = (h_1(n_1, p_1), \ldots, h_A(n_A, p_A), k_1(n_1, p_1), \ldots, k_A(n_A, p_A))^T$

We will refer in the sequel to the norm $||.||_1$ in $\mathbb{R}^m$ corresponding to the sum of the absolute values of the components of the vector.

From their definitions, it is obvious that $S, F \in C^1(\Omega_{2A}; \Omega_{2A})$. To start checking Hypothesis 1, we need to calculate $\lim_{k\to\infty} F^k(X)$. The expression of $F^k(X)$ is easily written in terms of N and P:

$$F^k(N,P) = \left(M_h^k N, \prod_{j=1}^k M_p(M_h^{k-j}N)P \right)$$

and thus, we need to calculate the limit of two sequences of matrices

$$\lim_{k\to\infty} M_h^k \quad \text{and} \quad \lim_{k\to\infty} \prod_{j=1}^k M_p(M_h^{k-j}N)$$

As M_h is a regular stochastic matrix, calling v^* its unique positive eigenvector associated to eigenvalue 1 with $||v^*||_1 = 1$, it is well known that

$$\lim_{k\to+\infty} M_h^k = (v^*|\cdots|v^*) =: \bar{M}_h \qquad (A3)$$

Straightforward calculations lead to

$$v^* = \left(\frac{1-\alpha}{1-\alpha^A}, \ldots, \frac{1-\alpha}{1-\alpha^A}\alpha^{i-1}, \ldots, \frac{1-\alpha}{1-\alpha^A}\alpha^{A-1} \right).$$

For the limit $\lim_{k\to\infty}\prod_{j=0}^k M_p(M_h^{k-j}(N))$, let us observe that we have the product of the elements of a convergent sequence of stochastic matrices, namely $\{M_p(M_h^k N)\}_{k\in\mathbb{N}}$, which limit is

$$\lim_{k\to+\infty} M_p(M_h^k N) = M_p(\lim_{k\to+\infty} M_h^k N) = M_p(\bar{M}_h N) = M_p(v^*n)$$

As $M_p(v^*n)$ is a regular stochastic matrix and each matrix $M_p(M_h^k N)$ is column-allowable (i.e., it has, at least, one positive entry in each column), following the proof of Proposition 3.1 in Blasco et al. (2001), which is based on the results in page 96 of Seneta (1981), we obtain that

$$\lim_{k\to\infty} \prod_{j=1}^k M_p(M_h^{k-j}N) = (\mu^*(v^*n)|\cdots|\mu^*(v^*n)) =: \bar{M}_p(v^*n)$$

where $\mu^*(v^*n)$ stands for the unique positive eigenvector of matrix $M^*(v^*n)$ associated to eigenvalue 1 with $||\mu^*(v^*n)||_1 = 1$. Straightforward calculations give us the following explicit expression for $\mu^*(v^*n)$

$$\mu^*(v^*n) = \left(\frac{1+n_1^{*\beta}}{A + \sum_{j=1}^A n_j^{*\beta}}, \ldots, \frac{1+n_A^{*\beta}}{A + \sum_{j=1}^A n_j^{*\beta}} \right).$$

where $n_i^* = \frac{1-\alpha}{1-\alpha^A}\alpha^{i-1}n$.
Then, we have

$$\bar{F}(X) = \lim_{k\to\infty} F^k(X) = (\bar{M}_h N, \bar{M}_p(v^*n)P) = (v^*n, \mu^*(v^*n)p) = E\circ G(X)$$

where $G:\Omega_{2A} \to \Omega_2$ is $G(X) = G(N, P) = (n, p)$, n and p being the global variables, and $E:\Omega_2 \to \Omega_{2A}$ is $E(n, p) = (v^*n, \mu^*(v^*n)p)$, which gives the equilibrium of fast dynamics for the particular values n and p of the global variables.

And finally the corresponding aggregated system reads as follows

$$(n_{t+1}, p_{t+1}) = Y_{t+1} = G\circ S\circ E(Y_t) = G\circ S\circ E(n_t, p_t)$$

that is

$$n_{t+1} = n_t \sum_{i=1}^A \lambda_i v_i^* e^{-a_i\mu_i^*(v^*n_t)p_t}, \qquad p_{t+1} = n_t \sum_{i=1}^A c_i v_i^*(1 - e^{-a_i\mu_i^*(v^*n_t)p_t})$$

which agrees with Eq. (16).

Following the proof of Theorem 4.3 in Blasco et al. (2001) together with standard compactness arguments assure the uniform convergence on any compact set $K \subset \Omega_{2A}$ of $\lim_{k\to\infty} F^k(X) = \bar{F}(X)$ and $\lim_{k\to\infty} DF^k(X) = D\bar{F}(X)$, what allows applying Theorem 1 and so studying the stability of equilibria of system (11) through the same study for system (16).

Appendix B

B.1. Existence of fixed points

The fixed points to Eq. (16) are the solutions to equation

$$n = n\sum_{i=1}^A \lambda_i v_i^* e^{-a_i\mu_i^*(v^*n)p}, \qquad p = n\sum_{i=1}^A c_i v_i^*(1 - e^{-a_i\mu_i^*(v^*n)p})$$

On one hand, we have the trivial fixed point $(n, p) = (0,0)$ and, whenever $\sum_{i=1}^A \lambda_i v_i^* = 1$, the semi-trivial fixed points of the form $(n, p) = (n^*,0)$ with $n^* > 0$.

On the other hand, in the particular case in which $\lambda_i = \lambda$, $c_i = c$ and $a_i = a$ for $i = 1, \ldots, A$, direct calculations lead to the existence of a fixed point (n, p) where n is a solution to the

equation $\sum_{i=1}^{A} v_i^* \, e^{-a\mu_i^*(v^*n)n(1-(1/\lambda))} = (1/\lambda)$ and p is $p = nc(-(1/\lambda))$. It should be pointed out that in this case it is needed that $\lambda > 1$. The number of fixed points equals the number of solutions to equation $\sum_{i=1}^{A} v_i^* \, e^{-a\mu_i^*(v^*n)n(1-(1/\lambda))} = (1/\lambda)$.

In the general case, existence of a non-trivial positive equilibrium has to be checked numerically.

B.2. Stability of the fixed points

Regarding stability questions, let us consider the function

$$H(n, p) = \left(n\sum_{i=1}^{A} \lambda_i v_i^* \, e^{-a_i\mu_i^*(v^*n)p}, \quad n\sum_{i=1}^{A} c_i v_i^* (1 - e^{-a_i\mu_i^*(v^*n)p}) \right)$$

The Jacobian matrix reads as

$$JH(n, p) = \left(\begin{array}{cc} \sum_{i=1}^{A} \lambda_i v_i^* \, e^{-a_i\mu_i^*(v^*n)p} - n\sum_{i=1}^{A} \lambda_i v_i^* a_i(\mu_i^*(v^*n))' \, p \, e^{-a_i\mu_i^*(v^*n)p} & -n\sum_{i=1}^{A} \lambda_i a_i v_i^* \mu_i^*(v^*n) \, e^{-a_i\mu_i^*(v^*n)p} \\ \sum_{i=1}^{A} c_i v_i^*(1 - e^{-a_i\mu_i^*(v^*n)p}) + n\sum_{i=1}^{A} c_i v_i^* a_i(\mu_i^*(v^*n))' \, p \, e^{-a_i\mu_i^*(v^*n)p} & n\sum_{i=1}^{A} c_i a_i v_i^* \mu_i^*(v^*n)(1 - e^{-a_i\mu_i^*(v^*n)p}) \end{array} \right)$$

It is well known that a fixed point (n, p) is asymptotically stable if, and only if,

$$\mathrm{tr}(JH(n, p)) < 1 + det(JH(n, p)) < 2$$

Applying this condition, we get that the trivial fixed point $(n, p) = (0, 0)$ is asymptotically stable if, and only if $\sum_{i=1}^{A} \lambda_i v_i^* < 1$, and the semi-trivial fixed points $(n, p) = (n, 0)$ with $n > 0$ are not asymptotically stable.

Regarding the stability of possible positive non-trivial fixed points, we were unable to achieve a simple condition based on $\mathrm{tr}(JH(n, p))$ and $det(JH(n, p))$ even in the particular case in which $\lambda_i = \lambda$, $c_i = c$ and $a_i = a$ for $i = 1, \ldots, A$. Therefore, in the general case the stability conditions must be numerically checked.

Appendix C

In this appendix, we detail the calculation of the condition '$CV^2 > 1$'. In the aggregated model, the number of hosts and parasitoids after dispersal are respectively $v_i^* N_t$ and $\mu_i^* P_t$ for patch i, for $i \in \{1, 2, \ldots, A\}$, where N_t and P_t represent the total density of hosts and parasitoids at time step t. This means that for each of the $v_i^* N_t$ hosts on patch i, there are $\mu_i^* P_t$ parasitoids in its vicinity. In order to calculate the coefficient of variation CV of the number of parasitoids in the vicinity of each host, we first calculate the mean m and variance v.

$$m = \frac{1}{N_t}\sum_{i=1}^{A} v_i^* N_t \mu_i^* P_t = \sum_{i=1}^{A} v_i^* \mu_i^* P_t$$

and

$$v = \frac{1}{N_t}\sum_{i=1}^{A} v_i^* N_t (\mu_i^* P_t)^2 - m^2 = \sum_{i=1}^{A} v_i^* (\mu_i^* P_t)^2 - m^2$$

We now calculate CV^2:

$$CV^2 = \frac{v}{m^2} = \frac{1}{m^2}\sum_{i=1}^{A} v_i^* \mu_i^{*2} - 1$$

The condition '$CV^2 > 1$' can then be written $\sum_{i=1}^{A} v_i^* \mu_i^{*2} > 2\left(\sum_{i=1}^{A} v_i^* \mu_i^*\right)^2$

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