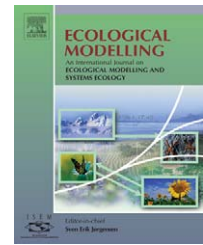


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# Effect of movement frequency on global host–parasitoid spatial dynamics with unstable local dynamics

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## ABSTRACT

We present a spatial host–parasitoid model where individuals move on a square lattice of patches. Local interactions between hosts and parasitoids within patches are described by the Nicholson–Bailey model. Dispersal between patches is represented by a series of movement events from a patch to neighbouring patches. We study the effect of the number of movement events on the stability of the host–parasitoid system. The aim of this work is to determine conditions on this number for using a reduced model (called aggregated model) to predict the total host and parasitoid population dynamics. When the number of movement events is small, the system is usually persistent and spatial patterns are observed, such as spiral waves or chaotic dynamics. We show that when this number is larger than a critical value, spatial homogeneity is observed after some transient dynamics and the system does not persist; in that case the reduced model can be used. Our results show that the critical value is relatively small and that the reduced model can be used in realistic situations.

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## 1. Introduction

A classical model describing host–parasitoid interactions is the Nicholson–Bailey model. This model predicts non-persistence of the community. However, early spatial models have demonstrated that the system can become persistent when individuals perform movements to neighbouring patches on a square lattice (Hassell et al., 1991). Spatial models extend possibilities of population dynamics models to the study of spatial structures, exhibiting singular spatial patterns. Spatial host–parasitoid dynamics models usually combine two sub-models, one describing local host–parasitoid interactions on each patch and the other describing dispersal among patches (see the review by Briggs and Hoopes, 2004). In an earlier work, Hassell et al. (1991) considered spatial environ-

ment as a two-dimensional network of patches connected by migration. Their model, and related models (e.g., Rohani and Miramontes, 1995), were mostly developed to study the persistence of the host–parasitoid system and the spatial structures that may emerge such as spiral waves, spatial chaos or crystal structures. In these spatial models, dispersal and local interactions are performed once per generation. The dispersal process consists of movements from one patch to neighbouring patches, or of one global event of dispersal (Travis and French, 2000). However, hosts and parasitoids can visit several patches in their lifetime in order to choose the most favourable habitat (Bell, 1990). This situation is likely to occur for most host–parasitoid associations involving winged adults like wasps, butterflies, flies or midges (Godfray, 1994; Hochberg and Ives, 2000). To take this into account, multiple events of

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migration per generation should be considered, giving individuals the opportunity to disperse in a relatively small domain around the patch in which they emerged.

In a recent work, Lett et al. (2003) studied the effects of repeated dispersal events on the global dynamics of a host–parasitoid system (see also Bernstein et al., 1999). They considered a system consisting of two patches connected by migration. Local host–parasitoid interactions were described by the Nicholson–Bailey model, and dispersion corresponded to a migration between patches with a constant proportion of migrants. Migration events could be repeated several times, while local interactions only occur once per generation. Considering several migration events implies the existence of two different time scales: there is a slow dynamics, the local interactions, and a fast one, the dispersal.

The existence of two time scales allows using aggregation of variables methods to describe global population dynamics, for continuous or discrete time models (Auger and Roussarie, 1994; Auger and Poggiale, 1998; Arino et al., 1999; Bravo de la Parra et al., 1999; Auger and Bravo de la Parra, 2000). It is possible to build a reduced model (referred to as the aggregated model) of the original model (the complete model), with fewer global variables. The aggregated model is obtained from the complete model by making the approximation that the fast dynamics tends to a stable attractor, like an equilibrium. The validity of the aggregated model depends on the difference between time scales. In Lett et al., it appeared that for more than five events of migration, the solutions of the complete and the aggregated models were very close in the case of a stable fixed point or for a cyclic attractor. Lett et al. (2005), have considered a linear network of spatial patches connected by frequent migration events. Their results have shown that the aggregated model could be used to predict stability of the complete system.

The aim of the present work is to reconsider host–parasitoid spatial interactions on a square grid of patches when individuals perform the same proportion and number of movement events for hosts and parasitoids. We use the classical Nicholson–Bailey model to describe local interactions and constant migrant proportions from patch to patch. We study the influence of the number of movement events on the persistence of the host–parasitoid community. Our key objective is to

determine the number of movement events needed to approximate the dynamics of the complete model by the dynamics of the aggregated model.

## 2. Presentation and reduction of the model

### 2.1. The classical Nicholson–Bailey model

We first briefly recall the Nicholson–Bailey host–parasitoid model. In a homogenous environment, the host–parasitoid association dynamics is described by a system of two equations:

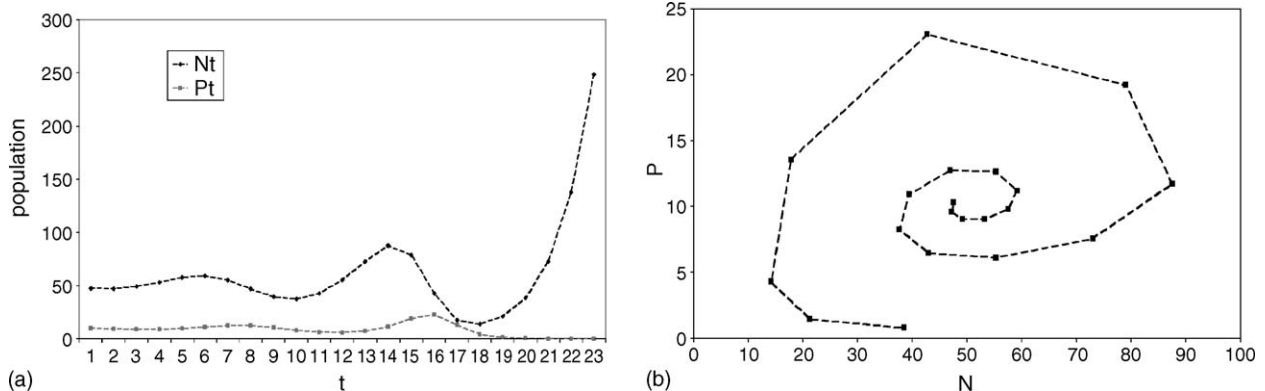
$$n_{t+1} = \lambda n_t e^{-ap_t}, \quad p_{t+1} = cn_t(1 - e^{-ap_t}) \quad (1)$$

where  $n_t$  and  $p_t$  are the host and parasitoid densities, respectively, at time step  $t$ . Parameter  $\lambda > 1$  corresponds to the host growth rate,  $a$  the parasitoid searching efficiency, and  $c$  the number of parasitoids emerging from one infected host. The dynamics of this system is well known. There exists a unique positive equilibrium given by:  $N^* = (\lambda \ln(\lambda))/(ac(\lambda - 1))$  and  $P^* = \ln(\lambda)/a$ , which is unstable for any set of parameters. Numerical simulations of host and parasitoid dynamics show growing oscillations (Nicholson and Bailey, 1935) driving one or both populations very close to zero. Below some critical density values the populations can be considered as extinct (see Fig. 1) and therefore, the Nicholson–Bailey model predicts non-persistence of the host–parasitoid community.

### 2.2. The complete spatial model

In an environment consisting of a square lattice with  $A \times A$  patches, we consider a spatial model derived from the Nicholson–Bailey model. The dynamics involves two phases: the first one corresponds to local host–parasitoid interactions. On every patch, local dynamics are ruled by the same set of equations than for the classical Nicholson–Bailey model (1).

The second phase corresponds to dispersal. In one movement event, a constant proportion  $\mu_n$  and  $\mu_p$  of hosts and parasitoids leave their patch for one of the eight neighbouring patches. The following equations describe the dispersal



**Fig. 1 – (a) Time series of a Nicholson–Bailey host–parasitoid system with parameters  $\lambda = 2$ ,  $a = 0.068$ ,  $c = 0.4$ . The parasitoids get extinct after 21 generations and the host population grows unboundedly. (b) Phase portrait corresponding to the previous system.**

process on one patch for one movement event:

$$\begin{aligned} n_{t+1} &= (1 - \mu_n)n_t + \frac{\mu_n}{8} \sum_{\text{neighbours}} n_t, \\ p_{t+1} &= (1 - \mu_p)p_t + \frac{\mu_p}{8} \sum_{\text{neighbours}} p_t \end{aligned} \quad (2)$$

We use reflexive boundaries where individuals going out of the lattice return to the place they come from.

For each generation, movement events can be repeated  $k$  times, allowing individuals to reach farther patches and to cover a larger area with radius  $k$ .

At each generation, we consider the  $2A^2$ -dimension vector  $V_t$  which  $A^2$  first elements (resp. last elements) correspond to the host (resp. parasitoids) densities on every patch. Local dynamics can be represented by a function  $F$ , which incorporates the two equations of (1) for each patch. One movement event over all patches can be described by a non-negative matrix  $M$ , corresponding to Eq. (2). The complete model can finally be written

$$V_{t+1} = F(M^k V_t) \quad (3)$$

In the particular case  $k=1$  this model is the same as the one used by Hassell et al. (1991).

The dispersal sub-model is deterministic, but describes underlying non-deterministic dynamics (random dispersal). Since Nicholson–Bailey model is also deterministic, so is the global model.

### 2.3. The aggregated model

When the number of movement events  $k$  per generation becomes large, the dispersal process is fast in comparison to local interactions, and then we can use aggregation methods: we build a reduced model that governs total host and parasitoid population densities over the grid. To build this model, we proceed in two steps: first we neglect the slow process (local interactions) and study the fast one (dispersal) only. This fast process has a stable positive equilibrium, called the fast equilibrium, which corresponds to uniform host and parasitoid density distributions among patches, with the same proportion  $1/A^2$  of individuals on each patch (for further details about aggregation we refer to Lett et al., 2003 in the case of a two patch system and also to Lett et al., submitted, for a linear chain of patches).

On the second step we assume that at each generation  $t$  the fast equilibrium is reached, and substitute in every patch the values of host and parasitoid densities at the fast equilibrium. By adding the number of individuals over all patches, we obtain a reduced model (4) governing the total host and parasitoid densities at time step  $t$ , given by  $N_t$  and  $P_t$ , respectively

$$N_{t+1} = \lambda N_t e^{-a(P_t/A^2)}, \quad P_{t+1} = cN_t(1 - e^{-a(P_t/A^2)}) \quad (4)$$

The aggregated model is the same as the Nicholson–Bailey model, but governing the total densities and with a global searching efficiency parameter  $a/A^2$ . Therefore, the dynamics of the aggregated model predicts growing oscillations of

the total host and parasitoid densities and a non-persistent host–parasitoid association. In the next sections, we are going to look for the conditions which allow using the aggregated model to describe the dynamics of the complete system.

## 3. Results

The complete model has been previously studied by Hassell et al. (1991) under the hypothesis of one movement event per generation ( $k=1$ ). They show that considering the host–parasitoid association within a spatial context can lead to a persistent system. Above a certain size of lattices ( $15 \times 15$  patches for  $\mu_n=1$ ), the global dynamics of the system is stable, in the sense that host and parasitoid total densities stay bounded, with both populations persisting. Additionally, different spatial structures may appear, like spiral waves, crystal lattices and spatial chaos, depending on the values of  $\mu_n$  and  $\mu_p$ , ranging from 0 to 1 (see Hassell et al., 1991; Comins et al., 1992; Rohani and Miramontes, 1995). We now study the effect of increasing the number of movement events  $k$  on the global dynamics of hosts and parasitoids, and compare the complete model and aggregated model dynamics. In the following simulations, we always use the same set of parameters,  $a=0.2$ ,  $\lambda=2$ ,  $c=0.4$  and a constant proportion of migrants  $\mu_n=\mu_p=1$  (henceforth called the default set of parameters), to make the comparison of the different results easier. We have used other sets of parameters (results not shown) leading to the same qualitative results and conclusions. In the discussion, we show the effects on the results of changes in the proportions of migrants  $\mu_n$  and  $\mu_p$ .

### 4. Effect of migration frequency on spatial dynamics of the complete model

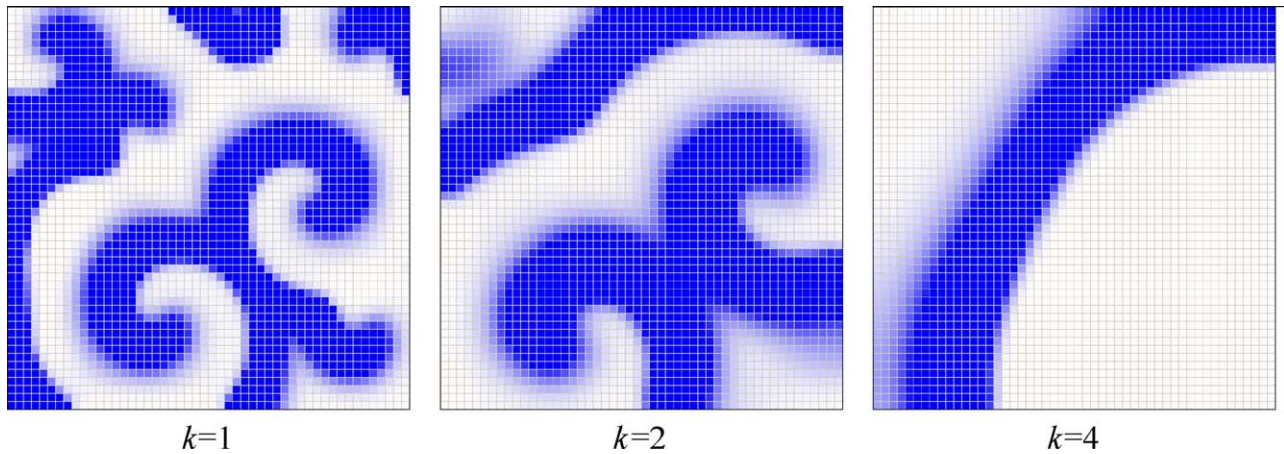
For the complete model, we observe the spatial patterns obtained in the simulations for different values of  $k$ . Simulations start with one patch containing 20 hosts and 20 parasitoids. For  $k=1$ , spatial patterns eventually appear after a transient dynamics, like in Hassell et al. (1991). Since the model is deterministic, those spatial patterns only depend on the parameters of the model and initial distribution of hosts and parasitoids. Influence of the initial distribution will be discussed later.

For increasing values of  $k$ , we observe that the size of spatial patterns grows (Fig. 2). For  $k=1$ , we observe several small spiral waves while for  $k=2$  and 4, there are, respectively 3 and 1 bigger spiral waves. Increasing parameter  $k$  acts like a zoom effect. For even higher value of  $k$ , spiral waves become too large to fit in the grid and the persistence of both populations cannot be obtained.

## 5. Comparison of the complete and aggregated models

### 5.1. Influence of migration frequency

The aggregated model is a classical Nicholson–Bailey model (4), predicting growing oscillations of host and parasitoid total



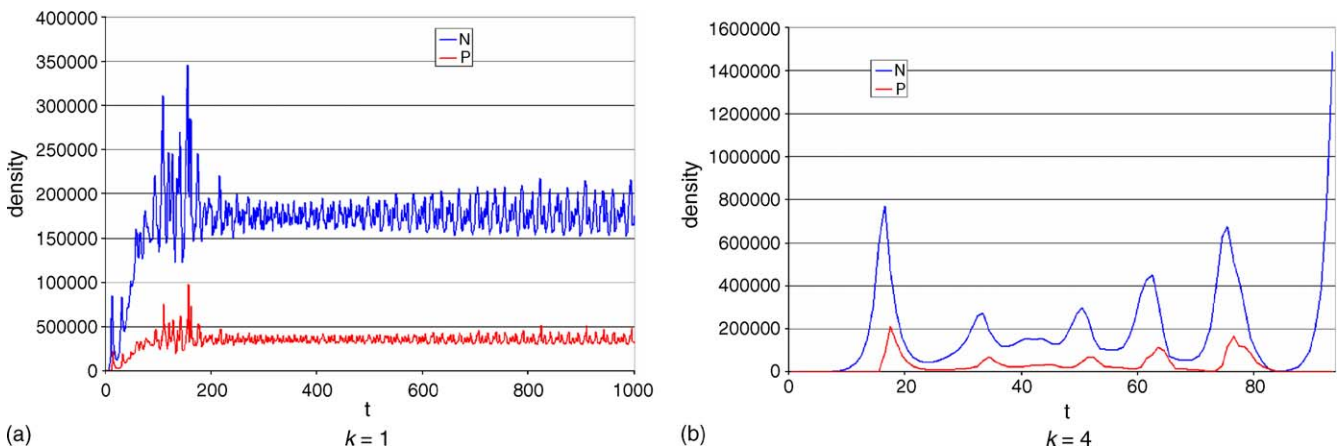
**Fig. 2 – Spatial patterns of host density obtained with the Nicholson–Bailey model spatialized on a 50 × 50 patches lattice, using the default set of parameters  $a = 0.2$ ,  $\lambda = 2$ ,  $c = 0.4$  and  $\mu_n = \mu_p = 1$ , for an increasing number of movement events  $k$  per generation. High density corresponds to dark colour.**

densities and non-persistence of the association. In the complete model, the number of movement events  $k$  influences the dispersal speed and has a big influence on the persistence of the populations. The time evolution of host and parasitoid densities is represented in Fig. 3 for a low (1, Fig. 3a) and a high (4, Fig. 3b) value of  $k$ , starting from the same initial condition (one patch with 20 hosts and 20 parasitoids). For the low value of  $k$ , spatial structures come along with persistence, both population densities becoming quasi-periodic after a transient period. In that case, the complete system is persistent while the aggregated model predicts non-persistence. Thus, for low  $k$  values, the aggregated model is not useful to predict the dynamics of the complete model. For the high value of  $k$ , total densities of hosts and parasitoids present unboundedly growing oscillations. After some generations, we observe that the system is not persistent. In this case, the complete model and the aggregated one are in good agreement as both lead to unbounded density oscillations and non-persistence.

**5.2. Dependence on initial condition**

Two simulations running with the same set of parameters but with two different initial conditions may lead to different results. When starting with barely uniform densities, the system is more likely to show unbounded oscillations than with an initial condition with singularities, where persistence is easier to obtain. For example, Fig. 3a shows the dynamics obtained with initially one patch containing 20 hosts and 20 parasitoids. In that case, both populations persisted. With a more uniform initial condition (e.g.,  $15 \pm 5$  hosts and parasitoids on every patch), we usually observed unbounded oscillations.

For every initial condition, there exists a value of  $k$  under which the system is persistent, and above which it is not. We tested various types of initial conditions: a pack of individuals randomly distributed at the centre of the grid, one patch containing individuals and spiral waves. The initial condition that appeared to be the most “stabilizing” was the last one as larger



**Fig. 3 – Time evolution of host and parasitoids densities for  $k = 1$  (a), and  $k = 4$  (b), with the default set of parameters and a 50 × 50 patches lattice.**



**Table 1 – Value of the threshold  $\tilde{k}$  for different sizes of the lattice, using the default set of parameters**

A	$\tilde{k}$
30	3
50	5
100	11

values of  $k$  were required to get unbounded oscillations. Such a condition is obtained by running simulations using a low value of  $k$ , not leading to extinction. For example, for a  $50 \times 50$  lattice, we run a simulation for  $k=1$ , with an initial condition consisting of 20 hosts and 20 parasitoids on one patch, like in Fig. 3a. After the transient dynamics, we store the density distribution (the spiral wave) and use it as initial condition for other simulations.

## 6. Migration frequency threshold

As we noticed that for any initial spatial distribution there exists a value of  $k$  above which the system is unstable, we tried to determine a global threshold value  $\tilde{k}$  above which, for any initial condition, the system would exhibit unbounded oscillations. In our simulations, it is for the initial condition with spiral waves that we need the highest value of  $k$  for the system to be unstable. For this reason, the value of the global threshold  $\tilde{k}$  was chosen as the critical value of  $k$  for this specific type of initial conditions. Under this critical value, there were some cases where spatial structures maintained and both populations persisted. Above this value, the complete model behaved like the aggregated one, for any initial condition, as far as we could test. To compute the threshold  $\tilde{k}$ , we run simulations for different values of  $k$  over a large number of time steps (10,000 steps) with the spiral wave initial condition. For a given value of  $k$ , if one population goes extinct within this period, we consider that  $k$  is over or equal to  $\tilde{k}$ . If both populations maintain after 10,000 steps, we assume that we are in the situation of a persistent system and consider that  $\tilde{k}$  is larger than  $k$ . Table 1 shows the threshold value obtained for different sizes of the lattice, using the default set of parameters.

## 7. Effect of the proportion of migrants

The number of movement events  $k$  is not the only parameter that influences dispersal. The proportion of migrants  $\mu$  is also a major parameter for dispersal. We expect that both parameters are important and must be taken into account to

characterize the dispersal process. The product  $\mu k$  is therefore expected to be a good global indicator of dispersal and there should be a threshold value for this product above which the host–parasitoid association is not persistent. In the results shown previously, we considered a proportion of migrants equal to 1. We now try other values of  $\mu = \mu_n = \mu_p$  ranging from 0 to 1, keeping the same values for the other parameters  $a=0.2$ ,  $\lambda=2$ ,  $c=0.4$ , and for a  $50 \times 50$  patches lattice. Both critical value  $\tilde{k}$  and the corresponding product  $\tilde{\mu k}$  are represented in Table 2.

According to Table 2, for each value of  $\mu$  there exists a threshold value  $\tilde{k}$  above which the complete model behaves like the aggregated one. For  $\mu > 0.3$ , the corresponding product  $\tilde{\mu k}$  is approximately constant in the range [4.5,5].  $\mu$  and  $k$  have a similar effect on the dynamics. At constant  $k$ , an increase of  $\mu$  corresponds to a larger proportion of migrants to the neighbouring patches. At constant  $\mu$ , an increase of  $k$  permits dispersal to farther patches. Therefore, an increase of  $k$  or  $\mu$  favours individual dispersal.

The value of the product  $\mu k$  allows making suitable predictions about the persistence of the system with a threshold value of about 5 for a  $50 \times 50$  grid. It must be noted that this threshold is rather realistic. Indeed if  $\mu=1$ , the threshold value is obtained when  $k=5$ , which corresponds to a dispersal from the departure patch in a disk of radius 5 which has to be compared to the size of the grid equal to 50.

## 8. Discussion and conclusion

The fact that for high values of migration frequency  $k$  the complete model behaves like the aggregated one is intuitive, because repeated movements tend to reduce the spatial variability among patches of the lattice. When  $k$  increases, population densities get more uniform, and for high enough values of  $k$  spatial structures eventually disappear. When the population densities are spatially uniform, we can use the aggregated model given by Eq. (4) which is defined according to this assumption.

What is more unexpected is that our numerical simulations have shown that the value of the threshold  $\tilde{k}$  (or  $\tilde{\mu k}$ ) above which the aggregated model is a valid approximation of the complete one is relatively small compared to the grid size (about 10% of it). This means that species do not have to move very fast for the aggregated model to be valid. For many species, flying species in particular, one can expect that migrant individuals cannot only reach the nearest patches but also farther ones. Therefore, our results show that it is often possible to use the aggregated model to make suitable predictions about the asymptotic behaviour of the complete spatial

**Table 2 – Second row: critical value  $\tilde{k}$  above which the system is not persistent, for different values of  $\mu$ , for parameters  $a=0.2$ ,  $\lambda=2$ ,  $c=0.4$  and for a  $50 \times 50$  grid**

$\mu$	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1
$\tilde{k}$	44	15	15	12	9	8	7	6	5	5
$\tilde{\mu k}$	4.4	3	4.5	4.8	4.5	4.8	4.9	4.8	4.5	5

Third row: corresponding values of the product  $\tilde{\mu k}$ .

host–parasitoid system. We also considered other values for the parameters  $a$ ,  $\lambda$  and  $c$  than the ones used above, leading to the same qualitative results. The critical value of  $\tilde{k}$  obtained was found to be relatively independent of the specific values of these parameters.

As a consequence, our work has shown that aggregation methods can be used in realistic biological situations to make suitable predictions about the global behaviour of the host–parasitoid community.

Dispersal speed has a strong influence on the persistence of spatial structures. Hassell et al. (1991) have determined the behaviour of their system for small values of dispersal speed. They have found domains in the  $(\mu_n, \mu_p)$  parameter space where spatial structures occur and populations persist. Our results have shown that the product  $\mu k$  allows defining general domains of persistence and non-persistence of the system. For small values of this product, the host–parasitoid association is generally persistent while it is not for higher values. Hassell et al. (1991), mentioned that for  $\mu_n$  and  $\mu_p$  very close to 0, the system was not persistent. It would be worth investigating the existence of a lower and upper limit for the value of the product  $\mu k$  for which the system is generally persistent. We also plan to study the relative influences of the proportion of migrants within hosts  $\mu_n$  and parasitoids  $\mu_p$ , and of the number of movement events for hosts  $k_n$  and parasitoids  $k_p$ , on the spatial dynamics and persistence of the system.

Introducing several movement events per generation enables us to take into account situations that are more relevant from a biological point of view. Using aggregation methods, it is possible to determine the global dynamics of the host–parasitoid system for relatively low values of the product  $\mu k$ . Migration speed appears to determine to a large extent the stability of the model. However, other processes that can influence stability, like environmental variability or asymmetrical migration, which induce spatial asynchrony and break spatial uniformity, have not been considered in our model. Furthermore, we focused on a fixed proportion of migrants, but density-dependent proportions of migrants should also be considered (French and Travis, 2001).

The present model is deterministic, but the processes described are intrinsically probabilistic, regarding as well to migration as to parasitism. It would be an interesting addition to make an individual-based model that would describe those processes explicitly. It would be also natural to introduce random events by considering more interlaced processes. In the present model, migration events always take place before the demographic event. The demographic event on each patch could occur randomly in the middle of the  $k$  events of migra-

tion. In that case, parasitism would not occur at the same time on all the patches, which could induce different dynamics.

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