

Effects of asymmetric dispersal and environmental gradients on the stability of host–parasitoid systems

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We consider host–parasitoid systems spatially distributed on a row of patches connected by dispersal. We analyze the effects of dispersal frequency, dispersal asymmetry, number of patches and environmental gradients on the stability of the host–parasitoid interactions. To take into account dispersal frequency, the hosts and parasitoids are allowed to move from one patch to a neighboring patch a certain number of times within a generation. When this number is high, aggregation methods can be used to simplify the proposed initial model into an aggregated model describing the dynamics of both the total host and parasitoid populations. We show that as the number of patches increases less asymmetric parasitoid dispersal rates are required for stability. We found that the ‘ $CV^2 > 1$ rule’ is a valid approximation for stability if host growth rate is low, otherwise the general condition of stability we establish should be preferred. Environmental variability along the row of patches is introduced as gradients on host growth rate and parasitoid searching efficiency. We show that stability is more likely when parasitoids move preferentially towards patches where they have high searching efficiency or when hosts go mainly to patches where they have a low growth rate.

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Interspecific interactions always take place in a spatially heterogeneous environment, which influences both the ecological and evolutionary outcomes of the interactions (Hanski and Gilpin 1997, Thompson 1999, Hassell 2000). Taking into account this natural biological complexity is necessary to investigate ecological situations where intra-patch dynamics, inter-patch dispersal and species specific behavioral processes may vary spatially (reviewed by Hanski 1998). Recent theoretical investigations on the evolution of antagonistic interactions have underscored the role of differential dispersal rates of partners on local adaptations, particularly in host–parasite associations (Gandon et al. 1996, Kaltz and Shykoff 1998, Nuismer et al. 1999). Like dispersal, spatial heterogeneity of resource

quality appears to influence interspecific interactions (McLaughlin and Roughgarden 1992, Leibold 1996, Clarke et al. 1997). Because resource quality often changes progressively from a central favorable habitat to marginal unsuitable area (at both local and geographic scales), organisms face environmental gradients that may affect their evolution towards specialist or generalist habits (Hochberg and van Baalen 1998). In contrast to evolutionary or coevolutionary models, and despite the considerable amount of models developed for host–parasitoid associations (reviewed by Hassell 2000), the consequences of differential dispersal rates and environmental gradients on the persistence of these associations are not much documented.

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Spatial models of host–parasitoid interactions generally consider a series of patches with Nicholson-Bailey dynamics within each patch and dispersal between patches. In such environments, the persistence of host–parasitoid interactions is expected under various conditions (reviewed by Hassell and Wilson 1997, Hassell 2000), in particular (i) under global dispersal, i.e. redistribution of hosts and parasitoids among all patches each generation according to fixed distributions (Hassell and May 1973, Hassell et al. 1991b), provided these distributions are heterogeneous enough (see the ‘ $CV^2 > 1$ rule’, Pacala et al. 1990, Hassell et al. 1991b, Taylor 1993); (ii) under local dispersal, i.e. when hosts and parasitoids move to adjacent patches only, if the number of patches is large enough to ensure asynchronous dynamics between patches (Hassell et al. 1991a, Comins et al. 1992, Rohani and Miramontes 1995); (iii) under spatial or spatio-temporal heterogeneity among patches, in host growth rate and parasitoid searching efficiency (Reeve 1988, Holt and Hassell 1993, Taylor 1998), parasitoid emergence rate (Holt and Hassell 1993, Taylor 1998), initial host and parasitoid densities (Adler 1993, Taylor 1998) or host carrying capacity (Allen et al. 2001).

In spatial models of host–parasitoid dynamics, dispersal is either included implicitly as the process resulting in a fixed redistribution of individuals over patches, or, when explicitly integrated, occurs only one time in an individual’s life. However, at local geographic scale, both host and parasitoids are able to visit several patches in their lifetime and their learning abilities allow them to choose among most favorable habitats (Bell 1990, Godfray 1994). A more realistic situation thus requires one to consider the dispersal process as a series of movement events whereby hosts and parasitoids experience different habitats and choose the most suitable ones. There are few empirical studies focusing on the relative movements of hosts and their parasitoids. Movements may vary according to local density of conspecific, or density of other species, with either negative or positive density-dependent dispersal rates (French and Travis 2001). Wild populations can also exhibit density-independent dispersal in response to their own ecological requirements including both biotic and abiotic factors (Jones et al. 1996). Temperature, humidity or landscape morphology can influence dispersal rates of host and parasitoids in a different way, leading to asymmetry in dispersal among interacting species. We thus have to explore situations where hosts and parasitoids can move independently in response to environmental gradients, including cases where they disperse in opposite directions.

In a recent paper (Lett et al. 2003), we pointed out the effects of asymmetry and frequency of movement events on the persistence of host–parasitoid interactions in a two-patch environment. We showed that persistence is likely to occur when the dispersal of parasitoids, in

particular, is asymmetrical, i.e. they move preferentially to one of the two patches. This asymmetry may result from a few highly asymmetrical movement events or from many slightly asymmetrical ones, so that movement frequency also plays a role. In the present paper, we extend the work to the situation where hosts and parasitoids are spatially distributed on a row of patches. We allow hosts and parasitoids to move from one patch to a neighboring patch a fixed number of times within each generation. When this number is low, our model is similar to models that assume local dispersal. When it is large, we can use the variables aggregation method (Auger and Poggiale 1998, Bravo de la Parra and Sanchez 1998, Auger and Bravo de la Parra 2000) to simplify the model into a reduced model. We show that the reduced model structure is close to that of models based on global dispersal. We use numerical simulations to determine when the reduced model is a valid approximation of the original one. Assuming that environmental heterogeneity along the row of patches results in gradients on demography and parasitism parameter values, we analyze under which conditions the host–parasitoid interactions are expected to be stable. We compare our results with those expected from the ‘ $CV^2 > 1$ rule’.

The model

A general structure of a model describing the dynamics of a host–parasitoid system is:

$$\begin{cases} N_{t+1} = \lambda N_t f(P_t) \\ P_{t+1} = c N_t [1 - f(P_t)] \end{cases} \quad (1)$$

where N_t and P_t are, respectively, the host density and the parasitoid density at generation t . Parameter λ is the growth rate of the host population and parameter c the average number of parasitoids that emerge from a single parasitized host. The function $f(P_t)$ is the proportion of hosts that are not parasitized between t and $t+1$. It is reasonable to assume that this proportion decreases with increasing values of P , that no host is parasitized when there is no parasitoid and that all hosts are parasitized when the number of parasitoids tends to infinity, i.e.:

$$\begin{aligned} f'(P_t) &< 0 \\ f(0) &= 1 \\ \lim_{P_t \rightarrow \infty} f(P_t) &= 0 \end{aligned} \quad (2)$$

When $f(P_t) = \exp(-aP_t)$, model (1) is the classical Nicholson–Bailey model, with the positive parameter a representing the searching efficiency of the parasitoids. The Nicholson–Bailey model has two fixed points, the origin (0,0) and another one which is positive when $\lambda > 1$. These two fixed points are unstable for all parameter values (Edelstein-Keshet 1988). Therefore, this model predicts non persistent host–parasitoid interactions.

This fixed point is locally stable when

$$-P^* \left[\frac{\sum_{i=1}^n [c_i v_i^* \mu_i^* f_i(\mu_i^* P^*)]}{\sum_{i=1}^n [c_i v_i^* (1 - f_i(\mu_i^* P^*))]} + \sum_{i=1}^n [\lambda_i v_i^* \mu_i^* f_i(\mu_i^* P^*)] \right] < 1 \quad (10)$$

In the particular case where $c_i = c$, $\lambda_i = \lambda$, $i \in \{1, 2, \dots, n\}$, Eq. 9 and 10 simplify. The unique positive fixed point (N^*, P^*) is defined by

$$\begin{cases} \sum_{i=1}^n [v_i^* f_i(\mu_i^* P^*)] = 1/\lambda \\ N^* = \frac{1}{c} \frac{\lambda}{\lambda - 1} P^* \end{cases} \quad (11)$$

It is locally stable when

$$-P^* \frac{\lambda^2}{\lambda - 1} \sum_{i=1}^n [v_i^* \mu_i^* f_i(\mu_i^* P^*)] < 1 \quad (12)$$

Results

From now on, we will use the Nicholson–Bailey model for the demography part of our model, i.e. $f_i(P_{i,t}) = \exp(-a_i P_{i,t})$, $i \in \{1, 2, \dots, n\}$. We recall that a system of disconnected patches with Nicholson–Bailey dynamics within each patch would lead to non persistent host–parasitoid interactions.

We first study the effects of dispersal asymmetry and number of patches on the stability of host–parasitoid interactions. We assume patch-independent values of host growth rate, parasitoid searching efficiency and average number of parasitoids emerging from one parasitized host, i.e. $\lambda_i = \lambda$, $a_i = a$ and $c_i = c$, $i \in \{1, 2, \dots, n\}$. Equations 11 and 12 become

$$\begin{cases} \sum_{i=1}^n [v_i^* \exp(-a \mu_i^* P^*)] = 1/\lambda \\ N^* = \frac{1}{c} \frac{\lambda}{\lambda - 1} P^* \end{cases} \quad (13)$$

$$a P^* \frac{\lambda^2}{\lambda - 1} \sum_{i=1}^n [v_i^* \mu_i^* \exp(-a \mu_i^* P^*)] < 1 \quad (14)$$

In this particular case, the aggregated model is the same as model D in Hassell and May (1973), except that here the host and parasitoid distributions (v_i^* and μ_i^*) are related to the dispersal asymmetry parameters α and β and the number of patches n , see Eq. A.1.

Equation 14 depends on four parameters only, α , β , n and λ , because from the first Eq. in 13 we can conclude that P^* is proportional to $1/a$. For every set of

parameters used we solved numerically the first Eq. in 13 for P^* and then checked if the condition of stability (Eq. 14) was true. For $\lambda = 2$ and increasing values of n , Fig. 2 shows the regions of the domain of the parameters α and β that assure the stability of the fixed point and, consequently, the persistence of the host–parasitoid interactions. The left part of the domains corresponds to $\beta < 1$, i.e. to parasitoids moving preferentially in the left direction on Fig. 1. On the right part of the domain we have $\beta > 1$ and the parasitoids move preferentially to the right. Similarly, up and down parts of the domains correspond to hosts moving preferentially to, respectively, right and left (Fig. 3). It appears from Fig. 2 that stable host–parasitoid interactions occur mainly for smooth dispersal asymmetry for hosts and steep dispersal asymmetry for parasitoids, in one or the other direction. Stability is more likely when the number of patches increases. This is essentially a consequence of an increase in the range of values of β leading to stability, as that of α does not change much with number of patches.

As noted by Holt and Hassell 1993, it is unlikely that variability in the demographic parameters λ and c only could stabilize the system. Indeed, if parasitism is spatially homogeneous, i.e. $\mu_i^* = 1/n$ and $f_i(P_{i,t}) = f(P_t)$, $i \in \{1, 2, \dots, n\}$, the aggregated model 8 simplifies into

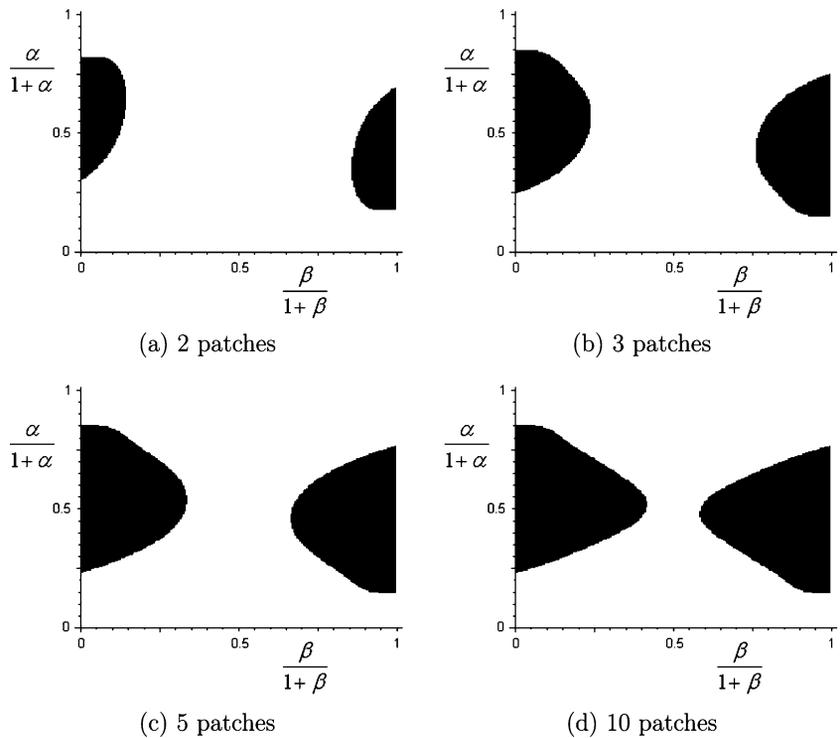
$$\begin{cases} N_{t+1} = \tilde{\lambda} N_t f(\tilde{P}_t) \\ \tilde{P}_{t+1} = \tilde{c} N_t [1 - f(\tilde{P}_t)] \end{cases} \quad (15)$$

with $\tilde{P}_t = P_t/n$, $\tilde{\lambda} = \sum_{i=1}^n \lambda_i v_i^*$ and $\tilde{c} = \sum_{i=1}^n c_i v_i^*/n$.

The aggregated model 15 has the same structure as the local model 1 on each patch. Consequently, with a Nicholson–Bailey model for demography, unstable local interactions imply unstable interactions for the whole system. The same can be said for the model of May 1978.

Therefore, we study the effects of dispersal asymmetry combined with environmental gradients on the stability of host–parasitoid interactions, for a fixed number of patches ($n = 5$ on Fig. 4). We consider a linear decrease of host growth rates λ_i on Fig. 4a; on Fig. 4b, we assume a linear decrease of parasitoid searching efficiencies a_i ; on Fig. 4c, the number of parasitoids emerging from a single parasitized host, c_i , decreases linearly with i ; finally, the three latter linear decreases are combined on Fig. 4d. Compared with Fig. 2, the domains of stability on Fig. 4 are now made of two asymmetrical areas because of the spatial heterogeneity among the patches. The differences between Fig. 2c and Fig. 4a are shown on Fig. 5a. The differences between Fig. 2c and Fig. 4b are shown on Fig. 5b. The differences between Fig. 2c and Fig. 4c are not shown; they look like on Fig. 5b but with smaller areas. From Fig. 5a we can see that a gradient in host growth rates promotes stability of the host–parasitoid system when hosts move preferentially towards patches with low growth rates. From Fig. 5b it appears that a gradient in parasitoid searching efficiencies makes stability more likely when parasitoids move

Fig. 2. Domain of stability (in black) of the aggregated model for different values of dispersal asymmetry parameters (α for the hosts and β for the parasitoids) and number of patches n . The boundaries obtained by simulation using $\lambda = 2$, $a = 0.05$ and $c = 1$ change with λ but not with a nor c .



preferentially towards patches with high efficiencies. A similar conclusion can be made for a gradient in the number of parasitoids emerging from a parasitized host.

In the aggregated model, it is assumed that the movement events are frequent enough to lead to an equilibrium before the demography and parasitism processes act. Consequently, hosts and parasitoids are redistributed among all patches each generation according to the equilibrium distributions, the geometric distributions given in Eq. A.1. The aggregated model is

therefore based on the same assumptions as models using global dispersal (Hassell and May 1973, Hassell et al. 1991b). For such models, it has been shown that the ‘ $CV^2 > 1$ rule’ (Hassell et al. 1991b, Taylor 1993) is an approximate criterion for stability (Eq. 14), CV being the coefficient of variation of parasitoids density in the vicinity of each host (Hassell et al. 1991b, Hassell 2000). We show in appendix C that here the $CV^2 > 1$ condition is equivalent to:

$$\sum_{i=1}^n v_i^* \mu_i^{*2} > 2 \left(\sum_{i=1}^n v_i^* \mu_i^* \right)^2 \quad (16)$$

For the aggregated model, the domains of stability expected from the ‘ $CV^2 > 1$ rule’ are shown on Fig. 6a and b for systems of 5 and 10 patches, respectively. They differ from the domains obtained using the condition of stability (Eq. 14), see Fig. 2c, d. However, it has already been noted that the ‘ $CV^2 > 1$ rule’ applies best for low values of host growth rate λ (Hassell et al. 1991b, Taylor 1993). This is confirmed by Fig. 6c and d showing the domains of stability using condition 14 and a lower value of λ (1.2 instead of 2 on Fig. 2).

So far, we have analyzed the stability of our host–parasitoid system through the aggregated model only. However, one should remember that the aggregated model is an approximation of the complete model. The conclusions we made using the aggregated model can be transposed to the complete model only if the former is a valid approximation of the latter. For $k \gg 1$, with k the

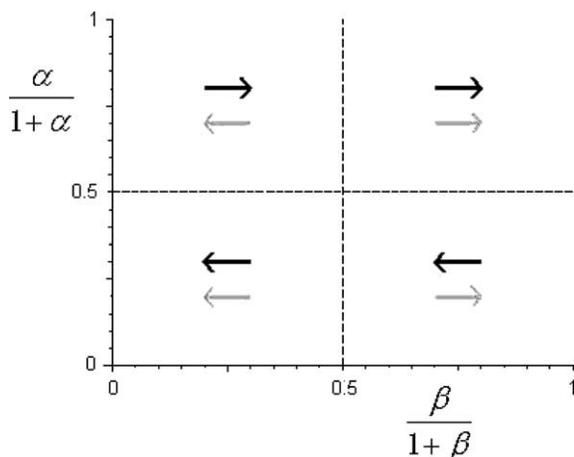


Fig. 3. Arrows indicating the preferred direction for hosts (black arrows) and parasitoids (grey arrows) following the dispersal process defined on Fig. 1.

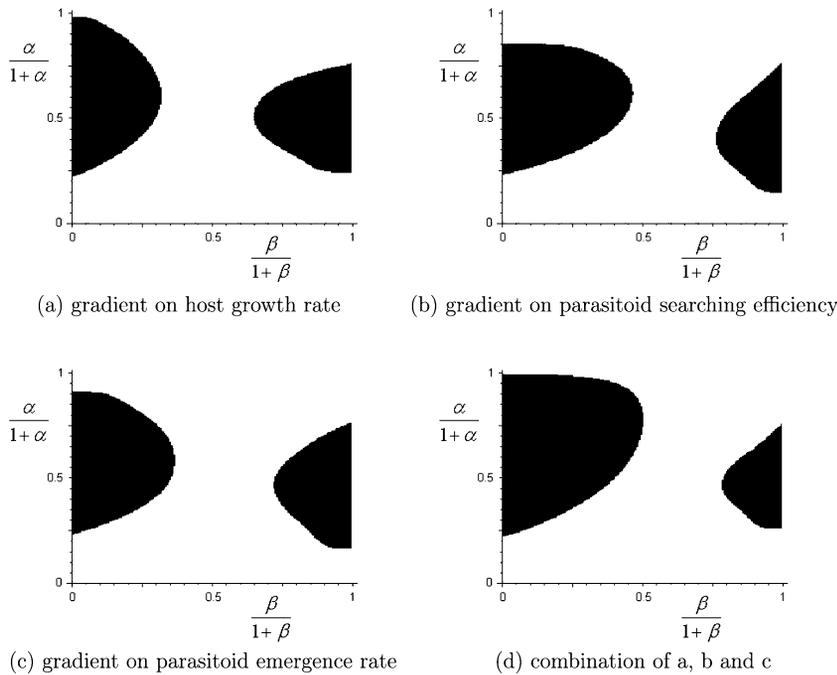


Fig. 4. Domain of stability (in black) of the aggregated model for different values of dispersal asymmetry parameters (α for the hosts and β for the parasitoids) with spatial heterogeneity among the n patches. (a) $\lambda_1 = 1.4\lambda$, $\lambda_2 = 1.2\lambda$, $\lambda_3 = \lambda$, $\lambda_4 = 0.8\lambda$, $\lambda_5 = 0.6\lambda$ (b) $a_1 = 1.8a$, $a_2 = 1.4a$, $a_3 = a$, $a_4 = 0.6a$, $a_5 = 0.2a$ (c) $c_1 = 1.8c$, $c_2 = 1.4c$, $c_3 = c$, $c_4 = 0.6c$, $c_5 = 0.2c$ (d) parameter values of a , b and c are combined. When they are not specified, the values of the parameters are $\lambda_{1-5} = \lambda$, $c_{1-5} = c$ and $a_{1-5} = a$. The boundaries obtained by simulation using $n = 5$, $\lambda = 2$, $a = 0.05$ and $c = 1$ change with n and λ but not with a nor c .

number of movement events performed by hosts and parasitoids within a generation, we know that the complete and aggregated models have the same dynamics. The question is how high k should be in the particular case of our system. We have addressed this question numerically by simulating the two models and comparing their dynamics for different parameter values and initial conditions. We call ϕ the proportion of individuals moving from a patch to a neighboring patch each movement event (in our model we have four such proportions, f , αf , g and βg , Fig. 1). What actually matters to get a good numerical consistency between the complete and aggregated models dynamics is to have high enough values of the product ϕk , so that low values of ϕ have to be counterbalanced by high values of k and vice versa. The product ϕk can be interpreted as the average number of movements from a patch to a neighboring patch performed by every individual each generation. Here we found that for the aggregated model to be a valid approximation of the complete model, this

number had to be of the order of magnitude 2, 5, 10, 15 and 40 for systems with, respectively, 2, 3, 4, 5 and 10 patches.

Discussion

In this paper, we have considered host–parasitoid systems spatially distributed on a row of patches connected by dispersal, and have analyzed the effects of dispersal asymmetry and environmental heterogeneity along the patches on the persistence of host–parasitoid interactions.

We have first studied the effects of dispersal asymmetry only, assuming that more individuals move in one direction than in the other. This situation could be the consequence of physical transport processes, with a main wind or water flow direction, for example (Horvath et al. 1996). We showed that such asymmetry in dispersal can lead to persistent interactions, which confirm previous

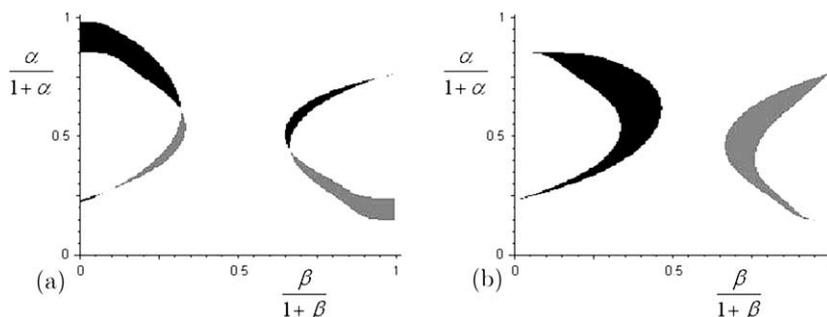
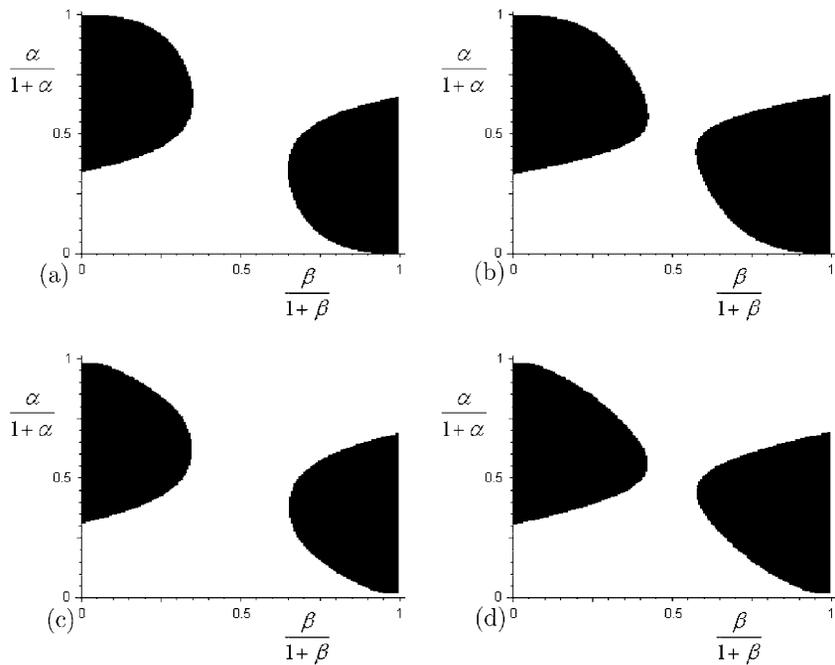


Fig. 5. Differences between Fig. 2c and (a) Fig. 4a (b) Fig. 4b. The grey zones correspond to parameter space areas where stability is obtained on Fig. 2c and not on (a) Fig. 4a (b) Fig. 4b. The black zones correspond to the opposite situation.

Fig. 6. Domain of stability (in black) of the aggregated model for different values of dispersal asymmetry parameters (α for the hosts and β for the parasitoids) (a) using the ‘ $CV^2 > 1$ rule’, $n = 5$ patches (b) using the ‘ $CV^2 > 1$ rule’, $n = 10$ (c) using condition of stability, $n = 5$ like in Fig. 2c but with $\lambda = 1.2$ (d) using condition of stability, $n = 10$ like in Fig. 2d but with $\lambda = 1.2$.



results (Lett et al. 2003) obtained on a two-patch system. Here we could also point out that persistent interactions become more likely when the number of patches increases. A similar conclusion was drawn for host–parasitoid models with local dispersal on a lattice (Hassell et al. 1991a, Comins et al. 1992). In our system, this was essentially due to an increase in the range of values of the parasitoid dispersal asymmetry parameter allowing stability. This result was shown for one value of host growth rate λ but remains true for other values. Changing the value of λ mainly affects which dispersal “strategy” of hosts and parasitoids lead to stability, as explained in Lett et al. (2003).

Then, environmental variability was introduced on the demography and parasitism parameters of the model, i.e. host growth rate λ , parasitoid searching efficiency a and number of parasitoids emerging from a parasitized host c . We assumed a linear decrease of the parameter values along the row of patches. Such gradients could reflect the influence of environmental variables such as temperature. Passive dispersal is known to create source–sink habitats with a gradient from good quality patches (sources) to poor quality ones (sinks; Dias 1996). We found that stability is more likely when parasitoids move preferentially towards patches where they have high values of a or c , or when hosts mainly go to patches where they have low values of λ . The latter result is somewhat counterintuitive, but it is in accordance with previous results indicating that stability is facilitated for low values of λ (Hassell and May 1973, Adler 1993, Lett et al. 2003). Analyzing host–parasitoid interactions on two patches with one patch free of parasitism (refuge),

Holt and Hassell (1993) also found that a high host growth rate in the refuge had to be counterbalanced by a low proportion of individuals there for the stability of the system to be possible. Similarly, Cosner and Lou (2003), using an advection–reaction–diffusion model on a spatially inhomogeneous habitat, concluded that movement towards “better” environments does not necessarily benefit a population.

Some of the stability areas obtained in the model correspond to contrary choices among hosts and parasitoids for the preferred dispersal direction. Contrary choices are possible, even if they are probably not the rule (Schreiber et al. 2000). They may occur when ecological requirements of interacting species differ, which is the case for instance for thermal niches in *Drosophila* and their parasitoids. Under certain conditions, we can also expect opposite dispersal in response to environmental gradients, and the results shown here suggest that this could enhance the system stability.

Following Holt and Hassell (1993), we showed that under spatially homogeneous parasitism, variability of λ or c can not stabilize the system when the Nicholson–Bailey or May models for demography are used. Using numerical simulations, Reeve (1988) and Taylor (1998) showed that such variability can however lead to persistent interactions, provided the proportions of dispersing individuals is small. Even when there is no spatial heterogeneity in parasitism nor demography, spatial heterogeneity in initial host and parasitoid densities can lead to persistent interactions (Adler 1993, Taylor 1998), though in specific conditions. These results stress that the conditions for persistence are not

restricted to the conditions for stability. In this paper, we analyzed the mathematical conditions for stability of the aggregated model fixed point using standard dynamical systems theory. Like in the two-patch model (Lett et al. 2003), numerical simulations indicated that persistent interactions could occur immediately outside the domains of stability. Otherwise the system showed amplified oscillations of host and parasitoid densities leading to extinction. Extinction occurred after a relatively small number of generations, except for special initial conditions set very close to the unstable fixed point of the model.

Our results support the validity of the ' $CV^2 > 1$ rule' as an approximation rule for stability when host growth rates are low and if there is no spatial heterogeneity among the patches other than individual distributions. In other situations, it is preferable to use the general condition of stability (10). This condition has been established for the aggregated model. This model is a valid approximation of the complete initial model provided the average number of movement events from a patch to a neighboring patch performed by the individuals (ϕk) is high enough. It is likely that these conditions are fulfilled for a number of natural host–parasitoid associations, even in the case of 10 patches with a ϕk value of 40. For example, *Drosophila* are able to travel more than 10 km per day (Coyne and Milstead 1987) and their parasitoid insects cover probably the same distance given their high rate of activity observed in some species (Fleury et al. 2000). At a local scale, where orchards are separated by only several 100 m, both *Drosophila* and their parasitoids could clearly travel more than forty times the distance separating adjacent orchards during their lifetime (several weeks). Evolutionary models of dispersal have shown that increased temporal variability in the habitat selects for higher dispersal rates (Travis and Dytham 1999), i.e. higher values of ϕ , and unstable local dynamics lead to selection for longer distances of dispersal (Murrell et al. 2002), i.e. higher values of k . Under such conditions, the validity of the aggregated model is therefore likely to be enhanced. These biological features not only justify the possible use of the aggregated model to analyze host–parasitoid dynamics, but also underline that models operating at a local scale need to consider several movement events within each demographical event.

In this paper we have focused on host–parasitoid systems along a row of patches, but our model can be easily extended to systems spatially distributed on an array of patches. In Appendix D we show that when radial and transverse movements between patches occur at different frequencies, such an extension is straightforward. This opens fresh perspectives for the application of the model to host–parasitoid associations in a fragmented patchy landscape. The present work has concerned density-independent dispersal for hosts and parasitoids.

We now have to consider dispersal driven by the local density of individuals, since it is likely that both intensity and direction of dispersal are negative or positive density-dependent traits (French and Travis 2001). Temporal variability in environmental conditions could also be taken into account, as it affects dispersal rates (Travis and Dytham 1999), local abundance of populations in sink habitats (Gonzalez and Holt 2002) and the persistence of host–parasitoid associations (Reeve 1988, Taylor 1998).

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Appendix A. Construction of the aggregated model

To construct the aggregated model, the first step consists of studying the dynamics resulting from the fast process, here the dispersal process. We can note that the dispersal matrix M (5) is a stochastic matrix (the sum of elements in each column equals 1) that keeps constant the total host density and the total parasitoid density. We denote these constants N and P , respectively. We look for the existence of a stable equilibrium population vector $V^* = (N_1^*, N_2^*, \dots, N_n^*, P_1^*, P_2^*, \dots, P_n^*)$ resulting from the dispersal. It is solution of the equation $V^* = MV^*$. Solving this equation leads to $N_i^* = \alpha^{i-1} N_1^*$ and $P_i^* = \beta^{i-1} P_1^*$, $i \in \{1, 2, \dots, n\}$. With $N = \sum_{i=1}^n N_i^*$ and $P = \sum_{i=1}^n P_i^*$ we finally get a relationship between the densities on each patch at the fast equilibrium and the total density, for the hosts and the parasitoids

$$\begin{aligned} N_i^* &= v_i^* N & v_i^* &= \frac{1 - \alpha}{1 - \alpha^n} \alpha^{i-1} \\ P_i^* &= \mu_i^* P & \mu_i^* &= \frac{1 - \beta}{1 - \beta^n} \beta^{i-1} \end{aligned} \quad (\text{A.1})$$

The second step in the construction of the aggregated model consists in assuming that between generations t and $t+1$ the fast system has reached its equilibrium. Then, adding the n host and the n parasitoid equations of the complete model (7) and substituting the fast equilibrium values (A.1) leads to the aggregated model, which governs the dynamics of the total host density and the total parasitoid density

$$\begin{cases} N_{t+1} = N_t \sum_{i=1}^n [\lambda_i v_i^* f_i(\mu_i^* P_t)] \\ P_{t+1} = N_t \sum_{i=1}^n [c_i v_i^* (1 - f_i(\mu_i^* P_t))] \end{cases} \quad (\text{A.2})$$

Appendix B. Analysis of the aggregated model

We look for the existence of a positive fixed point (N^*, P^*) of the aggregated model (A.2). It is solution of the equations

$$\begin{cases} 1 = \sum_{i=1}^n [\lambda_i v_i^* f_i(\mu_i^* P^*)] \\ P^* = N^* \sum_{i=1}^n [c_i v_i^* (1 - f_i(\mu_i^* P^*))] \end{cases} \quad (\text{B.1})$$

Because of the assumptions made on the functions f_i , $i \in \{1, 2, \dots, n\}$, see Eq. 2, the function on the left-hand side of the first equation in decreases monotonically with

P^* and takes the value $\sum_{i=1}^n \lambda_i v_i^*$ for $P^* = 0$. Consequently, when

$$\sum_{i=1}^n \lambda_i v_i^* > 1 \quad (B.2)$$

there is a unique positive value for P^* . The second equation then gives the corresponding value for N^* , which is also positive, because $f_i(\mu_i^* P^*) < 1$, $i \in \{1, 2, \dots, n\}$. Assuming that $\lambda_i > 1$, $i \in \{1, 2, \dots, n\}$, is sufficient to ensure that there is a unique positive fixed point (N^*, P^*) , because in this case, $\sum_{i=1}^n \lambda_i v_i^* > \sum_{i=1}^n v_i^* = 1$ so that condition is satisfied. This assumption requires that the host population on each patch would grow in the absence of parasitoid and connection with another patch.

To study the local stability of the positive fixed point, we calculate the Jacobian matrix

$$J^* = \begin{pmatrix} 1 & N^* \sum_{i=1}^n [\lambda_i v_i^* \mu_i^* f_i'(\mu_i^* P^*)] \\ \frac{P^*}{N^*} & N^* \sum_{i=1}^n [-c_i v_i^* \mu_i^* f_i'(\mu_i^* P^*)] \end{pmatrix} \quad (B.3)$$

Because $f_i'(\mu_i^* P^*) < 0$, $i \in \{1, 2, \dots, n\}$, both the trace and the determinant of J^* are positive. Consequently, local stability is assured when

$$\text{Tr}(J^*) < 1 + \text{Det}(J^*) < 2 \quad (B.4)$$

The first inequality is always satisfied. The condition for local stability of the positive fixed point (N^*, P^*) of the aggregated model is then $\text{Det}(J^*) < 1$, i.e. in terms of P^* only,

$$-P^* \left[\frac{\sum_{i=1}^n [c_i v_i^* \mu_i^* f_i'(\mu_i^* P^*)]}{\sum_{i=1}^n [c_i v_i^* (1 - f_i(\mu_i^* P^*))]} + \sum_{i=1}^n [\lambda_i v_i^* \mu_i^* f_i'(\mu_i^* P^*)] \right] < 1 \quad (B.5)$$

Appendix C. Application of the ‘ $CV^2 > 1$ rule’

In the aggregated model, the number of hosts and the number of parasitoids on each patch after the dispersal phase are given by, respectively, $v_i^* N_t$ and $\mu_i^* P_t$, $i \in \{1, 2, \dots, n\}$. We calculate the coefficient of variation of the number of parasitoids in the vicinity of each host as explained in Hassell (2000). Each of the $v_i^* N_t$ hosts experiences $\mu_i^* P_t$ parasitoids on patch i , which gives the following weighted mean and variance:

$$m = \frac{\sum_{i=1}^n v_i^* N_t \mu_i^* P_t}{\sum_{i=1}^n v_i^* N_t} = \sum_{i=1}^n v_i^* \mu_i^* P_t \quad (C.1)$$

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

Therefore, the condition $CV^2 > 1$ is:

$$\sum_{i=1}^n v_i^* \mu_i^{*2} > 2 \left(\sum_{i=1}^n v_i^* \mu_i^* \right)^2 \quad (C.2)$$

This condition can also be expressed in terms of α , β and n by substituting the expressions of v_i^* and μ_i^* given in A.1 into C.2.

Appendix D. From a network of patches to a row of patches

We consider a two-dimensional network of patches connected by dispersal like on Fig. 7a. We call $x_{i,t}$ the density of individuals at time step t on patch i , $i \in \{1, 2E, 2S, 2W, 2N, 3E, 3S, 3W, 3N\}$. When only the dispersal process acts, at time step $t+1$ we have:

$$\begin{aligned} x_{1,t+1} &= (1 - 4f_{12})x_{1,t} + f_{21}(x_{2E,t} + x_{2S,t} + x_{2W,t} + x_{2N,t}) \\ x_{2E,t+1} &= (1 - f_{21} - f_{23} - f_{2ES} - f_{2EN})x_{2E,t} + f_{12}x_{1,t} \\ &\quad + f_{32}x_{3E,t} + f_{2SE}x_{2S,t} + f_{2NE}x_{2N,t} \\ x_{2S,t+1} &= (1 - f_{21} - f_{23} - f_{2SE} - f_{2SW})x_{2S,t} + f_{12}x_{1,t} \\ &\quad + f_{32}x_{3S,t} + f_{2ES}x_{2E,t} + f_{2WS}x_{2W,t} \\ x_{2W,t+1} &= (1 - f_{21} - f_{23} - f_{2WS} - f_{2WN})x_{2W,t} + f_{12}x_{1,t} \\ &\quad + f_{32}x_{3W,t} + f_{2SW}x_{2S,t} + f_{2NW}x_{2N,t} \\ x_{2N,t+1} &= (1 - f_{21} - f_{23} - f_{2NW} - f_{2NE})x_{2N,t} + f_{12}x_{1,t} \\ &\quad + f_{32}x_{3N,t} + f_{2WN}x_{2W,t} + f_{2EN}x_{2E,t} \\ x_{3E,t+1} &= (1 - f_{32} - f_{3ES} - f_{3EN})x_{3E,t} + f_{23}x_{2E,t} + f_{3SE}x_{3S,t} \\ &\quad + f_{3NE}x_{3N,t} \\ x_{3S,t+1} &= (1 - f_{32} - f_{3SE} - f_{3SW})x_{3S,t} + f_{23}x_{2S,t} + f_{3ES}x_{3E,t} \\ &\quad + f_{3WS}x_{3W,t} \\ x_{3W,t+1} &= (1 - f_{32} - f_{3WS} - f_{3WN})x_{3W,t} + f_{23}x_{2W,t} \\ &\quad + f_{3SW}x_{3S,t} + f_{3NW}x_{3N,t} \\ x_{3N,t+1} &= (1 - f_{32} - f_{3NW} - f_{3NE})x_{3N,t} + f_{23}x_{2N,t} \\ &\quad + f_{3WN}x_{3W,t} + f_{3EN}x_{3E,t} \end{aligned} \quad (D.1)$$

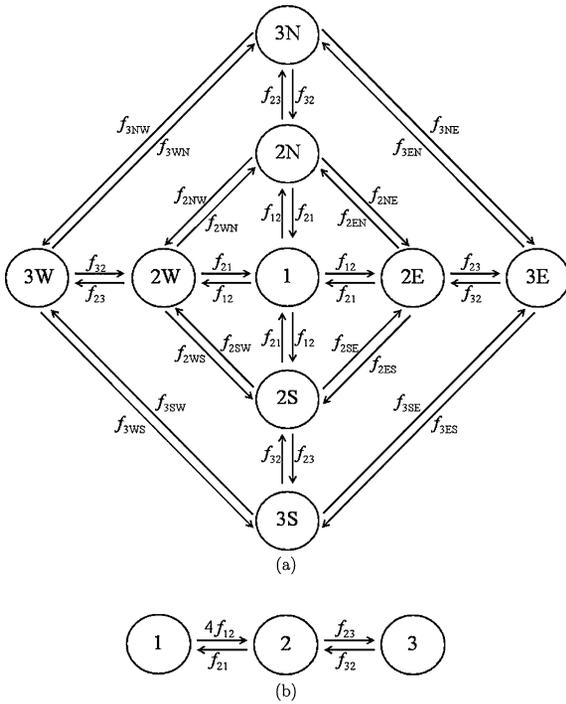


Fig. 7. A two-dimensional network (a) and a one-dimensional row (b) of patches connected by dispersal. Dispersal directions and associated proportions of moving individuals are indicated by arrows and parameters. The two dispersal processes shown here result in the same overall dynamics appendix

If we define $x_{2,t} = x_{2E,t} + x_{2S,t} + x_{2W,t} + x_{2N,t}$ and $x_{3,t} = x_{3E,t} + x_{3S,t} + x_{3W,t} + x_{3N,t}$, then the first equation in D.1 is:

$$x_{1,t+1} = (1 - 4f_{12})x_{1,t} + f_{21}x_{2,t} \quad (D.2)$$

Adding the four equations defining $x_{2E,t+1}$, $x_{2S,t+1}$, $x_{2W,t+1}$ and $x_{2N,t+1}$ in D.1 leads to:

$$x_{2,t+1} = (1 - f_{21} - f_{23})x_{2,t} + 4f_{12}x_{1,t} + f_{32}x_{3,t} \quad (D.3)$$

Similarly, adding the four equations defining $x_{3E,t+1}$, $x_{3S,t+1}$, $x_{3W,t+1}$ and $x_{3N,t+1}$ gives:

$$x_{3,t+1} = (1 - f_{32})x_{3,t} + f_{23}x_{2,t} \quad (D.4)$$

Equations D.2, D.3 and D.4 show that the inter-crown dispersal dynamics of the two-dimensional network of patches of Fig. 7a is the same as that of the one-dimensional row of patches of Fig. 7b.

In the situation where $f_{21} = f_{32} = f$ and $4f_{12} = f_{23} = \alpha f$, the dispersal processes of Fig. 7b and Fig. 1 are identical. In a two-dimensional context, this asymmetry in the dispersal process would represent attraction ($\alpha < 1$) or repulsion ($\alpha > 1$) towards the central patch. Using Eq. A.1 enables to determine the equilibrium frequencies of individuals on each crown of patches i.e. crown 1 (patch 1), crown 2 (patches 2E, 2S, 2W and 2N) and crown 3 (patches 3E, 3S, 3W and 3N). If one further assumes that transverse (intra-crown) movement events occur more frequently than radial (inter-crown) ones, then each crown of patches can be considered as isolated to calculate the equilibrium frequencies of individuals on each patch within each crown. This leads to calculate the solution of a 4 equations system (for crown 2 and crown 3) instead of the original 9 equations system, and the result holds for any supplementary crown that could be added. The aggregated model is then obtained by substituting the equilibrium values for each patch into the model which governs the dynamics of the total host density and the total parasitoid density, as explained in Appendix A.