Corridor size variation in spatially explicit/implicit models

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Abstract: We propose spatially implicit models described by ordinary differential equations which inherit the information of spatial explicit metapopulation models described by reaction-diffusion partial differential equations. Numerical simulations confirm that the proposed implicit models can capture the qualitative features of the explicit ones and may reveal as an effective tool to extract predictive information through a further theoretical analysis.

Key–Words: Habitat fragmentation, cyclic metapopulation dynamics, spatially implicit and implicit models.

1 Introduction

The ecological effects of human impacts induce different changes in the habitats. Habitat fragmentation is one of the classical consequences of human population growth: indeed, given human population activities and urban sprawl, habitats are often fragmented into patches connected via migration corridors set in non habitat portions of the landscape [6]. For cyclic predator-prey population dynamics, on which we focus our attention, experimental and theoretical results suggest that the subdivision of an habitat patch into smaller pieces may provide positive effects on their stability [9, 1]; on the other side a size reduction of migration corridors abates the amount of the individuals that are able to migrate from a patch to another and species are confined in more and more isolated patches. When increasing fragmentation produces patches too small to sustain local populations, the worst consequence of the reduction of the size of migration corridors is the extinction of the species. This motives us to consider the effects of such reduction on the permanence or the extinction of cyclic populations living in a fragmented habitat, characterized by patches whose extension and vegetation type is not suited for hosting a viable and stable population of predators.

Metapopulation dynamics, i.e. the dynamics of a “population of populations” [11], represent an effective tool for investigating the dispersal of species population in fragmented habitat. As concerns ecological cyclic processes, starting from the Jansen’s paper [10], mathematical models describing dynamics in patchy landscapes are generally spatially implicit, meaning that they have no spatial dimension and all patches are accessible via dimensionless corridors. As a consequence, the models are described by means of ordinary differential equations coupled through diffusion coefficients that model the migration of species from a patch to another. Lotka-Volterra (LV) [14] systems as well as its modifications like Rosenzweig-MacArtur (RM) [15], May [12] and Variable Territory (VT) [19] are the most widely used differential equations considered in this context.

In recent years, the consideration of spatial processes in ecological systems is growing and spatially explicit modeling reveals more effective for the ecological understanding of such kind of phenomena [2, 4, 16, 20]. As concerns cyclic population dynamics, a numerical study provided in [17] investigates the effects of habitat fragmentation through spatially explicit models i.e. models which take into account the spatial dimension. Unfortunately, the integration of the spatial dimension is difficult and expensive both practically, to parametrize spatially-explicit models [13], and numerically, to provide accurate solutions [7]. Furthermore, it leads sometimes to qualitatively similar prediction found by alternative approaches as, for example, the graph theory which has minimal data requirements and efficient algorithms [1, 21]. As concerns cyclic population dynamics, by reducing spatially explicit models into spatially implicit equivalent ones it is possible to capture the main features of the spatially explicit models and use standard mathematical tools to study the solution behaviour [18].

By following a metapopulation approach similar to the one provided in [7], we firstly numerically investigate the answer of the spatially explicit reaction-diffusion RM model to the variation of corridor entrance size; the results are then compared with the
ones provided by a new reduced implicit model where the spatial dependence is taken into account via relationships which link growth and death rates of prey and predators with the sizes of each patch and of the corridor entrances. In so doing, we were motivated by the results in [18]; indeed the implicit model, described by ordinary differential equations, may reveal an effective tool for a theoretical investigation about the effects of both the reduction of patches and migration corridor entrance sizes that is the aspect of the fragmentation process on which this paper is focused.

2 The spatially explicit model

In this section we introduce the most general metapopulation model as composed of \( N \) patches where the movement of each predator-prey subpopulation is modeled by a random Fickian diffusion and a reaction term:

\[
\frac{\partial n_i}{\partial t} = D^{(n)}_i \Delta n_i + f(n_i, p_i) + \sum_{j=1}^{N} W^{(n)}_{i,j}(x)(n_j - n_i)
\]

\[
\frac{\partial p_i}{\partial t} = D^{(p)}_i \Delta p_i + g(n_i, p_i) + \sum_{j=1}^{N} W^{(p)}_{i,j}(x)(p_j - p_i)
\]

for \( i = 1, \ldots, N \), where \( n_i = n_i(x, t) \) and \( p_i = p_i(x, t) \) represent the concentrations of prey and predator populations at each time \( t \) and position \( x \) within the patch \( \Omega_i \subset \mathbb{R}^m \), \( 1 \leq m \leq 3 \), then \( \Delta = \sum_{j=1}^{m} (\partial^2 / \partial x_j^2) \) is the Laplacian operator, \( D^{(n)}_i, D^{(p)}_i \) are the diffusivity coefficients for prey and predator in each patch \( \Omega_i \). The matrices \( W^{(n)}_{i,j}(x) \) and \( W^{(p)}_{i,j}(x) \) are supposed symmetric and their entries represent the migration rates between patches \( \Omega_i \) and \( \Omega_j \) for prey and predator, respectively, at position \( x \). We assume that migration occurs only at given positions in the patch which correspond to the corridor entrance, and that the corridors have no physical length. By defining as \( C_{i,j} \) the entrance of the corridor connecting \( \Omega_i \) to \( \Omega_j \), we have that \( C_{i,j} = C_{j,i} \) and \( C_{i,j} \subset \Omega_i \cap \Omega_j \). Moreover, we suppose migration rates are constant values in each corridor, i.e. \( W^{(n)}_{i,j}(x) = w^{(n)}_{i,j} \) and \( W^{(p)}_{i,j}(x) = w^{(p)}_{i,j} \) for every \( x \in C_{i,j} \), with \( w^{(p)}_{i,j}, w^{(n)}_{i,j} > 0 \), otherwise \( W^{(n)}_{i,j}(x) = W^{(p)}_{i,j}(x) = 0 \).

The general form of the reaction terms is

\[
\begin{align*}
    f(n, p) &= n H(n) - p F(n) \\
    g(n, p) &= p G(n) - p L(n, p)
\end{align*}
\]

where the function \( H(n) \) is the intrinsic growth rate of prey, \( F(n) \) gives the functional response of the prey to the predator, \( G(n) \) is the prey-dependent growth rate of the predator and \( L(n, p) \) represents the prey-dependent functional response of the predator to the prey. As in [3] and [5] the reaction terms \( f(n, p) \) and \( g(n, p) \) of LV, RM, May and VT models have a different form for growth according to the following table:

<table>
<thead>
<tr>
<th>MODEL</th>
<th>H(n)</th>
<th>F(n)</th>
<th>G(n)</th>
<th>L(n, p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LV</td>
<td>( r )</td>
<td>c.n,</td>
<td>( \chi n )</td>
<td>( \delta )</td>
</tr>
<tr>
<td>RM</td>
<td>( r - n )</td>
<td>( \frac{c}{k} )</td>
<td>( \frac{c}{d + n} )</td>
<td>( \frac{\chi c n}{d + n} )</td>
</tr>
<tr>
<td>MAY</td>
<td>( r - n )</td>
<td>( \frac{c}{k} )</td>
<td>( \frac{c}{d + n} )</td>
<td>( s )</td>
</tr>
<tr>
<td>VT</td>
<td>( r - n )</td>
<td>( \frac{c}{k} )</td>
<td>( \frac{c}{d + n} )</td>
<td>( \frac{\chi c n}{d + n} )</td>
</tr>
</tbody>
</table>

System (1) is completed with suitable initial conditions \( n_i(x, 0) = n_{i,0}(x) \) and \( p_i(x, 0) = p_{i,0}(x) \) for \( x \in \Omega_i \), and homogeneous Neumann boundary conditions \( \frac{\partial n_i(x, t)}{\partial v_i} = 0 \) for \( x \in \partial \Omega_i \times \mathbb{R} \), where \( v_i \) is the outward normal vector to the boundary \( \partial \Omega_i \), for \( i = 1, \ldots, N \). The choice of zero-flux boundary conditions means that the species cannot leave their patches, except via migration.

The case when two-patch metapopulation evolving in a two-dimensional space with functions \( f \) and \( g \) related to the RM model and a circular corridor entrance of fixed size was considered in [7] (see Figure 1).

In this paper we restrict our analysis to the two-patch one-dimensional case where the corridor entrances are segments (see Figure 2). For our purpose we evaluate the change in the dynamics with respect to the length \( L \) of the corridor entrance, taken as a parameter. In more details, let \( M_1 \) and \( M_2 \) be the length of the two patches we are considering, then we set \( C_{1,2} = C_{2,1} = [0, L] \subset \Omega_i = [-b_1^{(i)}, b_2^{(i)}] \) where

![Figure 1: An illustration of the two-patches two-dimensional metapopulation model with fixed corridor entrance as considered in [7]](image-url)
Figure 2: The one-dimensional metapopulation model with two patches $\Omega_1$, $\Omega_2$ and variable corridor entrance size $L$.

$b^{(i)}$ and $b^{(j)}$ depend on $L$ according to

$$b^{(i)} = (M_i - L)/s,$$
$$b^{(j)} = ((s - 1) M_i + L)/s$$

for $i,j = 1, 2$. Hence, while the domain sizes $M_1$ and $M_2$ of both patches are kept constant, the entrance size $L$ of the corridors varies from 0 to $M = \min\{M_1, M_2\}$. Of course, for $L = 0$ there is no migration and the metapopulation decouples in two separate predator-prey systems. For $L = M$ all positions, at least in one of the two patches, correspond to entrance positions of the corridor.

The model is described as follows

$$\frac{\partial n_1}{\partial t} = D_1^{(n)} \frac{\partial^2 n_1}{\partial x^2} + f(n_1,p_1) + W_{1,2}^{(n)}(x)(n_2 - n_1)$$
$$\frac{\partial n_2}{\partial t} = D_2^{(n)} \frac{\partial^2 n_2}{\partial x^2} + f(n_2,p_2) + W_{2,1}^{(n)}(x)(n_1 - n_2)$$
$$\frac{\partial p_1}{\partial t} = D_1^{(p)} \frac{\partial^2 p_1}{\partial x^2} + g(n_1,p_1) + W_{1,2}^{(p)}(x)(p_2 - p_1)$$
$$\frac{\partial p_2}{\partial t} = D_2^{(p)} \frac{\partial^2 p_2}{\partial x^2} + g(n_2,p_2) + W_{2,1}^{(p)}(x)(p_1 - p_2)$$

where again $n_i$ and $p_i$ are the population concentrations of prey and predators at any time $t$ and position $x$ within the two patches $[-b^{(i)}_1, b^{(i)}_2] \subset \mathbb{R}$, $i = 1, 2$.

### 3 The reduced spatially implicit model

In [18] the authors considered a spatially implicit model that was able to give results similar to the ones provided by the spatially explicit models introduced in [17]. In order to get the desired model simplification the authors assumed a prey population evolving according to the LV model in a one-dimensional patch $\Omega = [-b_1, b_2]$ of length $M$, with homogeneous Dirichlet boundary conditions $n(-b_1, t) = n(b_2, t) = 0$, in absence of predators. In their frame no migration is accounted for. The equation describing the dynamics thus simplifies as follows

$$\frac{\partial n}{\partial t} = D^{(n)} \frac{\partial^2 n}{\partial x^2} + r n$$

and it is solved by the method of Fourier series (see e.g. [8]). The solution is then dominated by the first eigenvalue $\lambda = r - D^{(n)} \left(\frac{\pi}{M}\right)^2$, which can be used to discriminate between an exponential growth ($\lambda > 0$) and an exponential decay ($\lambda < 0$) of the prey population. The solution corresponding to the first (principal) eigenvalue can be seen as the exact solution of a ODE

$$\frac{dn}{dt} = \left(r - D^{(n)} \left(\frac{\pi}{M}\right)^2\right)n$$

with a modified growth rate of the prey which depends on the size of the patch and on the diffusion coefficient $D^{(n)}$ according to the relation

$$r_M = r - D^{(n)} \left(\frac{\pi}{M}\right)^2.$$  

Following the same reasonement, in absence of preys and migration, the predator population would decade according to

$$\frac{\partial p}{\partial t} = D^{(p)} \frac{\partial^2 p}{\partial x^2} - \delta p.$$  

Hence, we can define

$$\delta_M = \delta + D^{(p)} \left(\frac{\pi}{M}\right)^2, \quad i = 1, 2.$$  

and, in the case of the May model, we define the predator growth rate as

$$s_M = s - D^{(p)} \left(\frac{\pi}{M}\right)^2.$$  

Biologically, the previous assumptions means that the carrying capacity for each population depends on the
size $M$ of the patch. As final result, the original spatially explicit dynamics is converted into an implicit one, by retaining the spatial dependence as patch size dependence for each model parameter. In the present paper we extend the above approach to the model described in (1) for $N$ patches connected through migration corridors. The growth rates for preys and predators, as well as the death rate of the predator in each patch are changed accordingly. Moreover we attempt to incorporate in the migration rates the dependence on the size $L$ of the corridor. To this purpose we consider the simplified model

$$\frac{\partial n_i}{\partial t} = D_i^{(n)} \frac{\partial^2 n_i}{\partial x^2} - w_{i,j}^{(n)} n_i$$

for $i, j = 1, 2$, with $i \neq j$ and $x \in [0, L]$ and suppose that homogeneous zero Dirichlet boundary conditions are set. The idea is to consider the whole domain as a corridor and to focus on the decreasing of the prey population due to the outgoing migration. Hence, we assume that there is no predator in the domain and no contribute comes from the intrinsic growth rate of the prey nor from the incoming migration of the population living in the other patch. By assuming that the rate of migration is affected by the first eigenvalue $A_1 e^{-w_{i,j}^{(n)} - D_i^{(n)} \left(\frac{\pi}{L}\right)^2}$ of the solution

$$n_i(x, t) = \sum_{m=1} A_m e^{-w_{i,j}^{(n)} - D_i^{(n)} \left(\frac{\pi}{L}\right)^2} t \sin \frac{m \pi x}{L}$$

we get the definition of a new migration coefficient dependent on the size $L$ of the corridor entrance:

$$w_{i,j}^{(n, L)} = w_{i,j}^{(n)} + D_i^{(n)} \left(\frac{\pi}{L}\right)^2, \quad L > 0,$$

$$w_{i,j}^{(n, 0)} = 0, \quad i, j = 1, 2, \ i \neq j.$$  

Similarly, we define

$$w_{i,j}^{(p, L)} = w_{i,j}^{(p)} + D_i^{(p)} \left(\frac{\pi}{L}\right)^2, \quad L > 0,$$

$$w_{i,j}^{(p, 0)} = 0, \quad i, j = 1, 2, \ i \neq j.$$  

Notice that, in the general case, the matrices with entries $w_{i,j}^{(n, L)}$ and $w_{i,j}^{(p, L)}$ are not symmetric.

Finally, we provide the following simplified version of the metapopulation model (3)

$$\frac{dn_1}{dt} = n_1 H_{M_1}(n_1) - p_1 F(n_1) + w_{1,2}^{(n, L)} (n_2 - n_1)$$

$$\frac{dn_2}{dt} = n_2 H_{M_2}(n_2) - p_2 F(n_2) + w_{2,1}^{(n, L)} (n_1 - n_2)$$

$$\frac{dp_1}{dt} = p_1 G_{M_1}(n_1) - p_1 L M_1(n_1, p_1) + w_{1,2}^{(p, L)} (p_2 - p_1)$$

$$\frac{dp_2}{dt} = p_2 G_{M_2}(n_2) - p_2 L M_2(n_2, p_2) + w_{2,1}^{(p, L)} (p_1 - p_2),$$

where, as in [18], the new functions $H_M(n)$, $G_M(n)$, $L_M(n, p)$ are modified as follows:

<table>
<thead>
<tr>
<th>MODEL</th>
<th>$H_M(n)$</th>
<th>$G_M(n)$</th>
<th>$L_M(n, p)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>LV</td>
<td>$r_M$</td>
<td>$\chi c n$</td>
<td>$\delta_M$</td>
</tr>
<tr>
<td>RM</td>
<td>$r_M - \frac{n}{k} \frac{\chi c n}{d+n}$</td>
<td>$\delta_M$</td>
<td></td>
</tr>
<tr>
<td>MAY</td>
<td>$r_M - \frac{n}{k} s_M$</td>
<td>$\frac{q p}{n}$</td>
<td></td>
</tr>
<tr>
<td>VT</td>
<td>$r_M - \frac{n}{k} \frac{\chi c n}{d+n}$</td>
<td>$\delta_M + \frac{s q p}{n}$</td>
<td></td>
</tr>
</tbody>
</table>

4 The effect of corridor size variation: comparison between explicit and reduced implicit RM model

We are interested in comparing the influence of reducing the corridor entrance size $L$ on the behaviour of the solution for both the spatial explicit and reduced implicit models. With this aim we vary the size $L$ from the maximum between the patch sizes i.e. $L_{max} = \max\{M_1, M_2\}$ and the minimum value $L_{min} = 0$ which corresponds to separated habitats.

We start from the general system (1) with two patches, where we set $r_i = 1$, $D_i^{(n)} = 1$, $c_i = 1$, $k_i = 1$ ($i = 1, 2$); then we adopt the RM metapopulation model, as in [7], in order to have

$$\frac{\partial n_i}{\partial t} = \Delta n_i + n_i (1 - n_i) - \frac{n_i p_i}{d_i + n_i} + W_{i,j}^{(n)} (x) (n_j - n_i)$$

$$\frac{\partial p_i}{\partial t} = D_i^{(p)} \Delta p_i + \frac{\chi_i n_i p_i}{d_i + n_i} - \delta_i p_i + W_{i,j}^{(p)} (x) (p_j - p_i),$$

$$\Delta = \frac{\pi}{L}, \quad W_{i,j}^{(n)} (x) = w_{i,j}^{(n, L)} (x), \quad W_{i,j}^{(p)} (x) = w_{i,j}^{(p, L)} (x).$$
for \( i, j = 1, 2, i \neq j \). We perform numerical simulations for the solution of this problem in the case of one dimensional patches.

We suppose they have the same dimensions \( M_i = 300 \) and we set the corridor entrance \([0, L]\) in the center of both domains i.e. \( \Omega_i = [(M_i - L)/2, (M_i + L)/2] \), for \( i = 1, 2 \). We start from the stationary states for the predator and the prey in \( \Omega_1 \) and from the stationary state for preys and local extinction of predators in \( \Omega_2 \) that is

\[
\begin{align*}
n_i(x, 0) &= \delta_i d_i/(\chi_i - \delta_i), \quad x \in \Omega_i, \quad i = 1, 2, \\
p_1(x, 0) &= d_1 \chi_1(-\delta_1 + \chi_1 - d_1 \delta_1)/(\chi_1 - \delta_1)^2, \quad x \in \Omega_1, \\
p_2(x, 0) &= 0, \quad x \in \Omega_2.
\end{align*}
\]

The values for the parameters are chosen as follows

\[
d_1 = 1/5, \chi_1 = 1, \delta_1 = 1/2, D_1^{(p)} = 1, \text{ and } d_2 = 2/5, \chi_2 = 2, \delta_2 = 3/5, D_2^{(p)} = 1.
\]

In order to obtain a numerical approximation for the solution, the Matlab pde solver \texttt{pdepe} is exploited: the solver discretizes the equations with respect to the space and then uses \texttt{ode15s} matlab routine for stiff ODEs in order to solve the resulting system. We numerically integrate in the time interval \([0, 250]\) and the solution is plotted in the interval \([200, 250]\), in order to neglect the behaviour in the transient.

In the first simulations we do not consider the prey migration by setting \( w^{(n)} = w_{1,2}^{(n)} = w_{2,1}^{(n)} = 0 \), then we consider the case \( w^{(p)} = w_{1,2}^{(p)} = w_{2,1}^{(p)} = 1 \).

As a result, we find that for \( L > 0 \) preys and predators spread rapidly throughout the two patches and new dynamics arise; however in the corridor positions prey and predator tend to new equilibria that they reach when the corridor overlaps the whole domain. These approximate equilibrium values are given by

\[
\begin{align*}
n_1 &= 0.7347 \times 10^{-8}, \quad p_1 = 0.3301, \quad n_2 = 0.3306, \quad p_2 = 0.4891. \quad \text{In Figure 3 we plot the results obtained in correspondence with } L = 10, 150, 200, 300. \quad \text{In Figure 4 the same test is done by setting } w^{(p)} = 1e - 6.
\end{align*}
\]

We repeat the same tests with the reduced version of the RM model (5). We slowly vary the size of the corridor and we find that the qualitative behaviour of the implicit model dynamics is approximately the same of the spatial explicit one. For \( w^{(n)} = 0 \) and \( w^{(p)} = 1 \), new dynamics arise in correspondence with intermediate values of the corridor size and then new equilibria are reached as evidenced in Figure 5 on the top (the equilibria values are given by \( n_1 = 6.1464e - 005, p_1 = 0.3249, n_2 = 0.3500, p_2 = 0.4873 \)). The results shown in Figure 5, on the bottom, are obtained by setting \( w^{(p)} = 1e - 6 \) and

Figure 3: Spatially explicit RM model: predator-prey dynamics in time interval \([200, 250]\) with \( w^{(n)} = 0 \) and \( w^{(p)} = 1 \).

Figure 4: Spatially explicit RM model: predator-prey dynamics in time interval \([200, 250]\) with \( w^{(n)} = 0 \) and \( w^{(p)} = 1e - 6 \).
confirm the behaviour of the predator-prey population predicted by spatial explicit model: whenever the size of the corridor is strictly positive we observe that the predator-prey dynamics spread in both the patches till the predator-prey populations reach limit cycles, which occurs when the corridor takes the same size of the domain.

5 Conclusion

The analysis of spatial processes in ecological systems allows us to set up theoretical models which may provide results closer to the real investigated phenomena. In this paper, a first numerical investigation about the effect of the variation of the corridor size in metapopulation cyclic dynamic has been provided. By focusing on the one dimensional two-patch case, we performed some numerical test on the spatially explicit model introduced in [7]; hence, by following the approach proposed in [18], we proposed a reduced spatially implicit model where the size of both the domain and the corridor are taken into account by means of nonlinear relationships that interlace growth and migration rates with diffusive coefficients which define the spatial explicit model. Our preliminary numerical investigation confirms that the proposed implicit model well reproduces the qualitative answers of the related spatially explicit one. Hence, a further theoretical investigation is justified in order to provide a complete analysis about the answer of the metapopulations dynamics to the variation of the corridor size.

References:


