Mathematical Biology

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Local stability analysis of spatially homogeneous solutions of multi-patch systems

Abstract. Multi-patch systems, in which several species interact in patches connected by dispersal, offer a general framework for the description and analysis of spatial ecological systems. This paper describes how to analyse the local stability of spatially homogeneous solutions in such systems. The spatial arrangement of the patches and their coupling is described by a matrix. For a local stability analysis of spatially homogeneous solutions it turns out to be sufficient to know the eigenvalues of this matrix. This is shown for both continuous and discrete time systems. A bookkeeping scheme is presented that facilitates stability analyses by reducing the analysis of a k-species, n-patch system to that of n uncoupled k-dimensional single-patch systems. This is demonstrated in a worked example for a chain of patches. In two applications the method is then used to analyse the stability of the equilibrium of a predator–prey system with a pool of dispersers and of the periodic solutions of the spatial Lotka–Volterra model.

1. Introduction

In most natural populations individuals are not evenly distributed across space. Consequently, the rôle played by spatial heterogeneity in both the dynamics and the persistence of populations has been a question of considerable interest to mathematical ecologists. Spatial structure can be explicitly incorporated into mathematical models in one of two ways, either as a continuous variable (as in reaction diffusion models) or as a discrete variable. In the latter case, a single population is considered as being made up of a collection of smaller subpopulations ('patches') between which individuals migrate. Such models have attracted considerable attention in recent years, partly because they are often more amenable to mathematical analysis and partly since their simulation is straightforward.

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A key question addressed by such investigations is the effect of dispersal on the stability of population dynamics. Because the absence of a stable homogeneous solution is a sufficient condition for the existence of a spatial pattern, stability analysis of spatially homogeneous solutions is a natural first step in analysing spatial systems. In this paper we describe a method for local stability analysis of spatially homogeneous solutions of multi-patch systems. In essence, the method involves finding the eigenvalues of the matrix that describes the spatial arrangement of the patches, and then reducing the multi-patch system to a collection of single–patch systems. This simplification of the local dynamics makes the model tractable so that standard techniques can be applied more easily. For instance, a bifurcation analysis of a low dimensional system can give information about the spatial pattern that develops when the homogeneous solution becomes unstable. These methods have the obvious advantage over simulations that they lead to more general results and hence to clearer insights.

Local stability analysis in multi-patch systems is a (spatially) discrete analogue of local stability analysis in reaction diffusion (Turing, 1952; Segel and Jackson, 1972; Murray 1989) and reaction dispersion (Kot, 1989; Neubert et al., 1995) systems. The discrete form covers cases where the geometry of the spatial domain cannot be described with a continuous spatial variable. This is of particular interest for ecological problems for which the effect of the spatial arrangement of the local populations on the stability of the global population is studied.

The analysis uses a novel method to keep track of all the nk population densities (k species in each of n patches) by arranging them as a k by n matrix. This avoids the need for the complex book-keeping which arises if the densities are kept as a vector of length kn. For instance, we do not need to employ the Kronecker product constructs which play a crucial rôle in the elegant study of continuous time multi-patch models by Othmer and Scriven (1971). Our analysis also provides a generalisation to the stability analysis of non-equilibrium homogeneous solutions. This generalisation can be used, for instance, to study the stability of spatially homogeneous limit cycles and can thus shed light on the biologically important issue of the synchronicity observed between populations, whose abundances undergo oscillatory behaviour, in different geographical regions (Lloyd and May, 1999; Jansen, 1999). Furthermore, we show that the same method can be applied to discrete time systems, and we thus generalise and extend results discussed by Rohani et al. (1996).

One of the main aims of this paper is to generalise previous analyses of the linear stability of spatially homogeneous solutions, and, by extension, of dispersal-driven instabilities (Turing, 1952; Segel and Jackson, 1972; Levin, 1974; Allen, 1975; Kot, 1989; Murray, 1989; Neubert et al., 1995; Rohani et al., 1996). It is unfortunate that the four cases of continuous or discrete time and continuous or discrete space have tended to be treated as four separate cases in the literature (Turing, 1952, is one notable exception in that both continuous and discrete spatial models are considered). The analyses in each of the four situations are, not surprisingly, very similar indeed, as are the conclusions drawn from them (although there are important differences between continuous and discrete time models regarding the bifurcations by which spatially homogeneous equilibrium solutions lose stability and the conditions which lead to such bifurcations; Kot, 1989; Neubert et al.,

1995). Considerable duplication of work has occurred as a consquence of this separation of cases, most notably in a number of recent papers concerning stability and dispersal-driven instability in discrete-time metapopulation models (Rohani et al., 1996; Rohani and Ruxton, 1999a,b).

In the next section we shall present the main result of this paper, for both continuous time and for discrete time systems, followed by the proofs of the results. Next we apply our result, firstly to analyse the stability of the equilibrium of a spatial predator–prey system, and secondly to analyse the stability of periodic solutions of a spatial predator–prey system. Finally, the applicability of the results and possible generalisations are discussed.

2. Main result

2.1. Continuous time

Consider a spatial system of n patches in which k species interact. It is assumed that, from the perspective of the species, all patches are identical environments and therefore that, in the absence of migration, the local dynamics in each patch is defined by

$$\begin{pmatrix} \dot{x}_{1,j} \\ \vdots \\ \dot{x}_{k,j} \end{pmatrix} = \begin{pmatrix} f_1(x_j) \\ \vdots \\ f_k(x_j) \end{pmatrix}$$

where the dot means differentiation with respect to time and x_j is the vector which holds the densities of all species in patch j: $x_j = (x_{1,j}, \ldots, x_{k,j})^T$. In vector notation this can be expressed as

$$\dot{x}_j = f(x_j) \tag{1}$$

where $f : \mathbb{R}^k \to \mathbb{R}^k$ is a vector function. Its Jacobian is denoted as

$$Df(x_j) = \begin{pmatrix} \frac{\partial f_1}{\partial x_{1,j}} & \cdots & \frac{\partial f_1}{\partial x_{k,j}} \\ \vdots & \ddots & \vdots \\ \frac{\partial f_k}{\partial x_{1,j}} & \cdots & \frac{\partial f_k}{\partial x_{k,j}} \end{pmatrix}.$$

The patches are coupled through dispersal. The population dynamics of the spatial system is completely defined by the combination of local dynamics and dispersal

$$\dot{x}_j = f(x_j) + \sum_{i=1}^{n} c_{ij} M x_i \tag{2}$$

where the $k \times k$ matrix M is diagonal, with elements m_h, and describes how migration differs between species. C is an $n \times n$ matrix $C = \{c_{ij}\}$ which describes the spatial structure of the system and is the same for all species. The density of species h in patch j changes through migration from patch i to j at rate $m_h c_{ij}$. Thus $c_{ii} < 0$, as diagonal elements of C represent individuals leaving a given patch, and $c_{ij} \geq 0$ for all $i \neq j$, as off-diagonal elements of C represent individuals arriving at

a given patch from another. (Note that we adopt the notation of the probabilistically oriented literature: c_{ij} describes the movement from i to j.)

In many biologically interesting situations, dispersal is a non-directional process, i.e. the (per-capita) rate of migration from patch i to patch j equals the rate of migration in the opposite direction. As an example, dispersal between two patches may depend only on the distance between them. In such situations, the matrix C is symmetric, but, although this has some implications which we shall discuss later, we emphasize that we do not require C to be symmetric.

Throughout this paper we shall assume that migration conserves the numbers of individuals and that all patches have equal sizes. Consequently, the number of migrants leaving a particular patch must equal the sum of these migrants arriving at other patches. We thus have $\sum_{j=1}^{n} c_{ij} = 0$ for all i, implying that C has a zero eigenvalue corresponding to the right eigenvector $(1, \ldots, 1)^T$. Using the additional properties of C mentioned above, it follows from Gershgorin's first theorem (see, for instance, Marcus and Minc, 1964) that all non-zero eigenvalues of C have negative real part. (Note that when patches are of different sizes, the rows of C need not sum up to zero. Since the model involves densities, as opposed to numbers, migration from patch i to patch j can cause a decrease in density in patch i that does not match the increase in density in patch j. The numbers of migrants leaving a particular patch and arriving at other patches from that particular patch should still match. Therefore $\sum_{j=1}^{n} w_{1j} c_{ij} = 0$, where w_{1j} is the size of the jth patch, obviously $w_1 = (w_{11}, \ldots, w_{1n})^T$ is a right eigenvector w_1 of C with eigenvalue 0. The analysis of systems with different patch sizes is otherwise completely analogous to the case of equal patch sizes.)

We shall analyse the local stability of spatially homogeneous solutions, defined as follows.

Definition. *A solution is* spatially homogeneous *or* flat *when the densities in all patches are identical, i.e. when $x_j(t) = s(t)$ for all t and for all $j = 1, \ldots, n$, with s taking values in $\mathbb{R}^k$.*

Not all matrices C allow for flat solutions. Flat solutions remain flat if the number of migrants leaving a patch matches the number of arriving migrants: the migration terms cancel. This will be the case if $\sum_{i=1}^{n} c_{ij} = 0$ for all j, in other words, if the matrix C has a left eigenvector $(1, \ldots, 1)$ associated with eigenvalue 0, we shall assume that this is the case throughout this paper. (This will clearly be the case if C is symmetric.) If the migration terms cancel for a flat solution, then a solution which is flat at one point in time will stay flat forever and the k dimensional subset of the state space in which flat solutions take their values is invariant. We denote such flat solutions by $S_{flat}(t) = (s(t), \ldots, s(t))$, where $s(t)$ is a solution of (1).

For large n, stability analysis of a $n \times k$ dimensional system is a daunting task. The following result simplifies the problem by reducing it to a stability analysis of n decoupled, k dimensional systems.

Theorem 1. *Let M be a $k \times k$ matrix and C a $n \times n$ matrix with n linearly independent eigenvectors, one of which is the left eigenvector $(1, \ldots, 1)$ with associated*

eigenvalue 0. Let $f : \mathbb{R}^k \to \mathbb{R}^k$ be a vector function which is at least once continuously differentiable and let $s(t)$ be a solution of (1) and $S_{\text{flat}}(t)$ the corresponding flat solution of (2).

The linearisation of the system (2) around $S_{\text{flat}}(t)$ can be transformed by a similarity transformation into n decoupled systems of the form

$$\dot{x} = (Df(s(t)) + \lambda_i M)\, x, \qquad i = 1, \dots, n \qquad (3)$$

where λ_i is an eigenvalue of C and $x(t) \in \mathbb{C}^k$.

The stability properties of $S_{\text{flat}}(t)$ can now be derived from those of the n decoupled systems. When $s(t) = \tilde{s}$ is a fixed point, the corresponding flat solution is locally asymptotically stable if the matrices $Df(\tilde{s}) + \lambda_i M$ do not have any eigenvalues with non-negative real parts. When $s(t) = s(t + T)$, i.e., the solution is periodic with period T, the flat solution is a linearly stable solution if all non-trivial Floquet multipliers of (3) for all i lie inside the unit circle. In all other cases the stability can, in theory, be assessed from the dominant Lyapunov exponents of (3).

We remark that C is guaranteed to have n linearly independent eigenvectors in the biologically important case when C is symmetric. In this situation, the eigenvalues of C will be real (as are the corresponding eigenvectors), but will not be necessarily distinct.

Because C has a zero eigenvalue, one of the systems (3) equals the linearisation of (1) around $s(t)$. Thus a spatially homogeneous solution can only be stable if $s(t)$ is a stable solution of (1); dispersal without loss therefore never stabilises a system of which the non-spatial variant is unstable. When $\dot{x} = Df(s(t))\, x$ is unstable, it can still be interesting to know the stability properties of the other linearised subsystems. If the Lyapunov exponents of the subsystems corresponding to non-zero eigenvalues of C are negative, then the differences in density between patches will decrease while the solution is in the neighbourhood of the homogeneous solution. This is particularly relevant when $s(t)$ is a chaotic solution of (1); the flat chaotic solution attracts only if the Lyapunov exponents of all the subsystems corresponding to non-zero eigenvalues of C are negative.

When the migration rates are identical for all species, the stability conditions for the spatial system follow directly from (1). Then, all systems (3) can be transformed to $\dot{\psi} = Df(s(t))\, \psi$ by substituting $\psi(t) = \exp(-\lambda_i mt)x(t)$, where m is the migration rate. A corollary is that a single species spatial system cannot be destabilised by diffusion (Okubo, 1980).

Finally, we note that in the case of an equilibrium flat solution, (3) is of the same form as the eigenvalue equation obtained in reaction diffusion systems (in which both space and time are taken to be continuous) when the stability of a wave-like spatial mode is considered (see, for instance, Murray, 1989). Notice that the eigenvalue λ of the matrix C which appears in (3) replaces the quantity $-k^2$, where k is the spatial wavenumber–the eigenvalue of the spatial eigenfunction–in the corresponding expression from the continuous spatial case.

2.2. Discrete time

Discrete time systems with dispersal are often implemented in two steps. In the first step the k species interact within their patch, and form the raw material for the next generation. This interaction transformation is defined by

$$\begin{pmatrix} x_{1,j}(t+1) \\ \vdots \\ x_{k,j}(t+1) \end{pmatrix} = \begin{pmatrix} f_1(x_j(t)) \\ \vdots \\ f_k(x_j(t)) \end{pmatrix}$$

or in vector notation

$$x_j(t+1) = f(x_j(t)) \tag{4}$$

Next the individuals disperse. Combination of the two steps yields

$$x_j(t+1) = f(x_j(t)) + \sum_{i=1}^{n} c_{ij} \, M \, f(x_i(t)) \tag{5}$$

This completely defines the spatial system. When the patches are arranged in some regular way, system (5) is called a coupled map lattice.

The interpretations of the matrices C and M differ from the previous case, since they now describe a discrete, rather than continuous, dispersal process. $c_{ij}m_h$ denotes the fraction of individuals of species h in patch i that migrates to patch j, and $1 + c_{ii}m_h$ the fraction of individuals of species h in patch i that does not leave during the dispersal step. Despite the differences in interpretation, similar assumptions are made concerning their structure: $c_{ii} < 0$ for all i, $c_{ij} \geq 0$ for all $i \neq j$, and $\sum_{j=1}^{n} c_{ij} = 0$ for all i. In addition, notice that, since a patch cannot produce more migrants than the number of individuals present, $c_{ii}m_h \geq -1$.

The local stability of a flat solution can be established using the following result:

Theorem 2. *Let M be a $k \times k$ matrix, C a $n \times n$ matrix with n linearly independent eigenvectors, one of which is the left eigenvector $(1, \ldots, 1)$ associated with eigenvalue 0. Let $f : \mathbb{R}^k \to \mathbb{R}^k$ be a vector function which is at least once continuously differentiable and let $s(t)$ be a solution of (4) and $S_{\text{flat}}(t)$ the corresponding flat solution of (5).*

The linearisation of the system (5) about $S_{\text{flat}}(t)$ can be transformed by a similarity transformation into the following set of equations

$$x(t+1) = (I + \lambda_i M) \, Df(s(t)) \, x(t), \tag{6}$$

where λ_i are the eigenvalues of C, I is the identity matrix and $x(t) \in \mathbb{C}^k$.

When $s(t) = \tilde{s}$ is a fixed point, the flat solution is stable when all eigenvalues of the matrices $(I + \lambda_i M) \, Df(\tilde{s})$ lie inside the unit circle. As before, since C has a zero eigenvalue, one of these matrices is precisely that which appears in the stability criterion of the single-patch system. Dispersal cannot, therefore, stabilise a system of which the non-spatial variant is unstable. When $s(t + \tau) = s(t)$, i.e.,

when $s(t)$ is periodic with period τ, the spatially homogeneous solution is linearly stable when all eigenvalues of the matrix

$$(\mathrm{I} + \lambda_i M) \, Df\,(s(\tau)) \, (\mathrm{I} + \lambda_i M) \, Df\,(s(\tau - 1)) \ldots (\mathrm{I} + \lambda_i M) \, Df\,(s(1)) \qquad (7)$$

for all i lie inside the unit circle. In all other cases the stability is likewise determined by the dominant Lyapunov exponents of (6), but their calculation is often cumbersome.

As in the continuous time case, equality of the migration rates ($m_h = m$ for all h) leads to further simplifications. As the matrices $\mathrm{I} + \lambda_i M$ equal $(1 + \lambda_i m)\mathrm{I}$, the eigenvalues of the matrix multiplying $x(t)$ in (6) are simply those of the single-patch Jacobian multiplied by $1 + \lambda_i m$ (Lloyd, 1996). As a consequence of the restrictions placed upon the entries of C, this factor has modulus less than or equal to one. Again, dispersion cannot destabilise the spatially homogeneous equilibrium (Lloyd, 1996; Rohani et al., 1996). Similarly, examining expression (7) shows that the stability of a spatially homogeneous periodic orbit is related in an obvious way to that of the corresponding single-patch periodic orbit.

The method presented here is particularly useful to construct the stability boundaries of complicated spatial systems from those of a simple spatial system. (Stability boundaries are curves in parameter space for which the subsystems given by (3) have at least one Lyapunov exponent of value zero (or, more simply in the case of an equilibrium, have at least one eigenvalue with real part equal to zero) or for which subsystems (6) have one or more multiplier with unit modulus.) As a simple spatial system consider, for instance, a matrix C with eigenvalues 0 and -1, which arises for certain two patch systems. Because a stability analysis for complicated spatial systems requires analysis of subsystems which only differ in their value of λ_i, the stability boundaries can be found by a scaling of all migration rates with $-\lambda_i^{-1}$. In this way results from small spatial systems can be extended to larger systems which possibly have more complicated arrangements of patches.

As before, we notice that for an equilibrium flat solution, (6) is of the same form as the eigenvalue equation that is obtained in reaction dispersal systems (in which space is continuous, but time discrete) when the stability of a wave-like spatial mode is considered (Kot, 1989; Neubert et al., 1995). Again, comparing the expressions obtained in the two cases, we see that the diagonal matrix $I + \lambda_i M$ plays an identical rôle to that of Kot's matrix K, whose diagonal elements are spatial Fourier transforms of the dispersal kernels for the different species.

3. Proofs

The main problem in a local stability analysis of a $k \times n$ dimensional problem is to keep track of all densities in an ordered fashion. To this end the $k \times n$ matrix

$$X = (x_1, \ldots, x_n) = \begin{pmatrix} x_{1,1} & \cdots & x_{1,n} \\ \vdots & \ddots & \vdots \\ x_{k,1} & \cdots & x_{k,n} \end{pmatrix}$$

is introduced. The columns of this matrix contain the densities of the k species in a particular patch, its rows the densities of a species in the n patches. The interaction

in a patch therefore works on the columns, and transport between patches on the rows. The local interaction is between different species in a patch and is given by the function

$$F(X) = (f(x_1), \ldots, f(x_n))$$

which works on the columns of X. Migration redistributes a species over the different patches, therefore migration works on the rows of X and can be expressed as a postmultiplication of X (or $F(X)$ for discrete time systems) by the matrix C. Different species in a patch migrate with different rates, which can be accomplished by a premultiplication of X (or $F(X)$) by M. The dispersal process can thus be written as $M X C$ (or $M F(X) C$).

Proof of Theorem 1. The dynamics of a continuous time spatial system (2) can be expressed as

$$\dot{X} = F(X) + M X C. \tag{8}$$

To analyse the stability of the homogeneous solution we consider the time evolution of a solution, X, which arises by making a small perturbation to the flat solution. Then we have the following equation for the time evolution of the perturbation

$$\dot{X} - \dot{S}_{\text{flat}} = F(X) - F(S_{\text{flat}}) + M (X - S_{\text{flat}}) C. \tag{9}$$

We can linearise about S_{flat} by writing $X = S_{\text{flat}} + \epsilon Y + \text{h.o.t.}$, where $0 < \epsilon \ll 1$ and h.o.t. indicates second and higher order terms in ϵ. The term $F(X)$ can be expanded in a Taylor series

$$\begin{aligned} F(X) &= F(S_{\text{flat}} + \epsilon Y + \text{h.o.t.}) \\ &= F(S_{\text{flat}}) + \epsilon Df(s(t))Y + \text{h.o.t.} \end{aligned}$$

Inserting this expression into (9) and comparing terms of first order in ϵ we obtain the following equation for the time evolution of Y

$$\dot{Y} = Df(s(t)) Y + M Y C.$$

Since C has n linearly independent eigenvectors, it can be diagonalised by a similarity transformation (this is a standard technique from linear algebra, see, for example, Hirsch and Smale, 1974), that is to say, there exists an invertible matrix A such that $A^{-1} C A = \Lambda$ where Λ is a diagonal matrix. The diagonal elements of the matrix Λ are the eigenvalues, λ of C, and the matrix A can be constructed using the eigenvectors of C. In particular, we set $A = (w_1, \ldots, w_n)$ where w_i is a right eigenvector of C, i.e. $C w_i = \lambda_i w_i$, and $A^{-1} = (v_1, \ldots, v_n)^T$ where v_i is a left eigenvector of C, i.e., $v_i C = \lambda_i v_i$. We shall choose $v_1 = (1, \ldots, 1)$ as the left eigenvector associated with $\lambda_1 = 0$.

Using the linear transformation $\Psi = Y A$, we transform the k by n matrix Y to $\Psi = (\psi_1, \ldots, \psi_n)$. For a continuous time spatial system, linearised in the neighbourhood of the spatially homogeneous solution S_{flat}, the derivative of Ψ with respect to time is

$$\dot{\Psi} = \dot{Y} A = Df(s(t)) Y A + M Y C A$$

$$= Df(s(t)) \Psi + M \Psi \Lambda$$

Because Λ is diagonal the dynamics of the columns of Ψ are decoupled and A transforms the linearised version of (2) to a system of n decoupled subsystems given by (3). The transformed variable Ψ is expressed in a coordinate system where the coordinate axes are invariant with respect to the linearised flow. $\square$

Proof of Theorem 2. For discrete time systems the same method can be applied. First (5) is rewritten in matrix notation as

$$X' = F(X) + M\,F(X)\,C \tag{10}$$

where the shorthands $X = X(t)$, $X' = X(t+1)$ are used. As in the proof of Theorem 1, we shall make a small perturbation about the flat solution, writing $X = S_{\text{flat}} + \epsilon Y + \text{h.o.t.}$, and then linearise around S_{flat}

$$X' - S'_{\text{flat}} = F(X) - F(S_{\text{flat}}) + M\,(F(X) - F(S_{\text{flat}}))\,C. \tag{11}$$

Expanding $F(X)$ in a Taylor series about S_{flat} and collecting terms of order ϵ gives the following equation for the time evolution of Y

$$Y' = Df(s(t))\,Y + M\,Df(s(t))\,Y\,C.$$

Again, we transform Y into Ψ with the matrix A that diagonalises C. The transformed variable Ψ changes over time as

$$\begin{aligned} \Psi' = Y'\,A &= Df(s(t))\,Y\,A + M\,Df(s(t))\,Y\,C\,A \\ &= Df(s(t))\,\Psi + M\,Df(s(t))\,\Psi\,\Lambda \end{aligned}$$

which are n decoupled systems, each of which can be rewritten as (6) for appropriate λ_i. $\square$

4. Examples and applications

In general there are no methods to determine the stability of a spatial system directly from the non-spatial system. However, the method described here can greatly reduce the numerical effort because it allows the extrapolation of results from a collection of uncoupled systems to more complex systems. We shall demonstrate this for a simple spatial system and then apply it to two spatial predator–prey models.

4.1. Example: a chain of patches

Above we showed how local stability analysis of a spatially homogeneous solution of a n-patch system can be reduced to an analysis of n uncoupled systems. We will demonstrate this for a chain of equally spaced patches of identical size. In such a chain every patch that is not at the end of the chain will lose half of its migrating individuals to the left and the other half to the right. Patches on the end will lose

only half their migrants because the other half will be reflected from the end of the chain. In this case C takes the form

$$
\begin{bmatrix}
-\frac{1}{2} & \frac{1}{2} & 0 \cdots & & \cdots & 0 \\
\frac{1}{2} & -1 & \frac{1}{2} & \ddots & & \vdots \\
0 & \frac{1}{2} & -1 & \frac{1}{2} & \ddots & \\
\vdots & \ddots & & & \ddots & \vdots \\
& & \ddots & & & 0 \\
\vdots & & \ddots & \frac{1}{2} & -1 & \frac{1}{2} \\
0 \cdots & & \cdots & 0 & \frac{1}{2} & -\frac{1}{2}
\end{bmatrix}
\tag{12}
$$

The right eigenvectors are (Othmer and Scriven, 1971; May, 1974)

$$
w_i = \frac{1}{n} \left(\cos \frac{(i-1)\pi}{2n}, \cos \frac{3(i-1)\pi}{2n}, \ldots, \cos \frac{(2n-1)(i-1)\pi}{2n} \right)^T
$$

with corresponding eigenvalues $\lambda_i = -1 + \cos \frac{(i-1)\pi}{n}$, where $i = 1, \ldots, n$. Note that for a stability analysis it is sufficient to know the eigenvalues; the eigenvectors need not be known since it is not necessary to explicitly calculate the matrix A.

4.2. Application 1: a predator-prey system with a localised predator disperser pool

In Weisser et al. (1997) a predator–prey system is studied in which the interaction between predator and prey is localised in patches and in which individual predators can migrate from patch to patch through a pool of dispersers. A pool of migrants stabilises the neutrally stable equilibrium of the Lotka–Volterra predator–prey model (Holt, 1985; Weisser and Hassell, 1996). When a Holling type II functional response is added to the model, a single, global pool stabilises the equilibrium if the destabilising influence is not too strong. Beyond a certain threshold the equilibrium becomes unstable (Namba, 1983; Holt, 1985; Weisser et al., 1997).

The above result is based on a single global pool through which all migrants disperse. A natural question is whether the stability domain expands or contracts when spatial interactions are explicitly included in the model. To answer this question, the global pool is subdivided into local pools. Migrants from each patch move into a pool belonging to the local patch from which they can travel to other pools. This results in the following local interaction:

$$
f(x_i) = \begin{pmatrix}
r H_i - \frac{H_i P_i}{1 + T_h H_i} \\
\frac{H_i P_i}{1 + T_h H_i} - (d + e) P_i + \iota Q_i \\
e P_i - (\iota + s) Q_i
\end{pmatrix}
$$

where $x_i = (H_i, P_i, Q_i)^T$. The variables H_i and P_i are the densities of, respectively, prey and predators in patch i and Q_i is the density of predator dispersers

in the local pool belonging to patch i. Within a patch, the prey population grows with rate r and predators die with rate d. Predators become dispersers with rate e and dispersers move back from the local pool to the patch with rate ι. The death rate in the patch is s and T_h is the predator's handling time for a prey item. For a suitable choice of parameters the system has a positive equilibrium x^*, defined by $f(x^*) = 0$.

Because only the migrants in the local pool can migrate to other local pools

$$M = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & m_Q \end{bmatrix}$$

where m_Q is the maximum rate with which migrants leave the local pool. We shall assume that the patches are arranged in a chain. This defines the multi-patch system.

We now want to find out whether spatial interactions can possibly destabilise the system. For this at least one of the equilibria of subsystems (3) should be unstable while the subsystem corresponding to $\lambda_i = 0$ is stable. In Weisser et al. (1997) a two patch model is studied, with the following connectivity matrix

$$C = \begin{bmatrix} -1 & 1 \\ 1 & -1 \end{bmatrix},$$

which has eigenvalues 0 and -2. It follows from the evaluation of the Routh-Hurwitz conditions that the matrix $(Df(x^*) - 2M)$ has at least one eigenvalue with positive real part if and only if

$$(2m_Q)^2 U + (2m_Q)V + W > 0 \tag{13}$$

where

$$U = \frac{\iota e}{\iota + s} + r(d + \frac{es}{\iota + s})T_h$$
$$V = U(\iota + s - U) + r(d(\iota + s) + es)T_h$$
$$W = r(d + \frac{es}{\iota + s})\big[(T_h(\iota + s + d + e) - 1)(\iota + s - U)$$
$$+ (\iota + s - (d(\iota + s) + es)T_h)\big]$$

Note that for $m_Q = 0$ the model reduces to the single patch case (equivalent to the subsystem with $\lambda_i = 0$) so that $W < 0$ is the stability condition for the single patch model. As is shown in Fig. 1a, the two-patch model can indeed be unstable while the single patch model is stable (Weisser et al., 1997). The spatial interactions can thus destabilise the interaction.

Fig. 1a shows the region in parameter space in which a flat solution in a chain of two patches is unstable. This can be constructed from the results in Weisser et al. (1997) by realising that in their model the only non-zero eigenvalue of C is -2. The stability condition for a chain of two patches can be found by replacing $2m_Q$ by m_Q in condition (13).

The region is rather small. To see whether this region will expand or contract with increasing chain length, an extra patch is linked to the chain. For a chain of
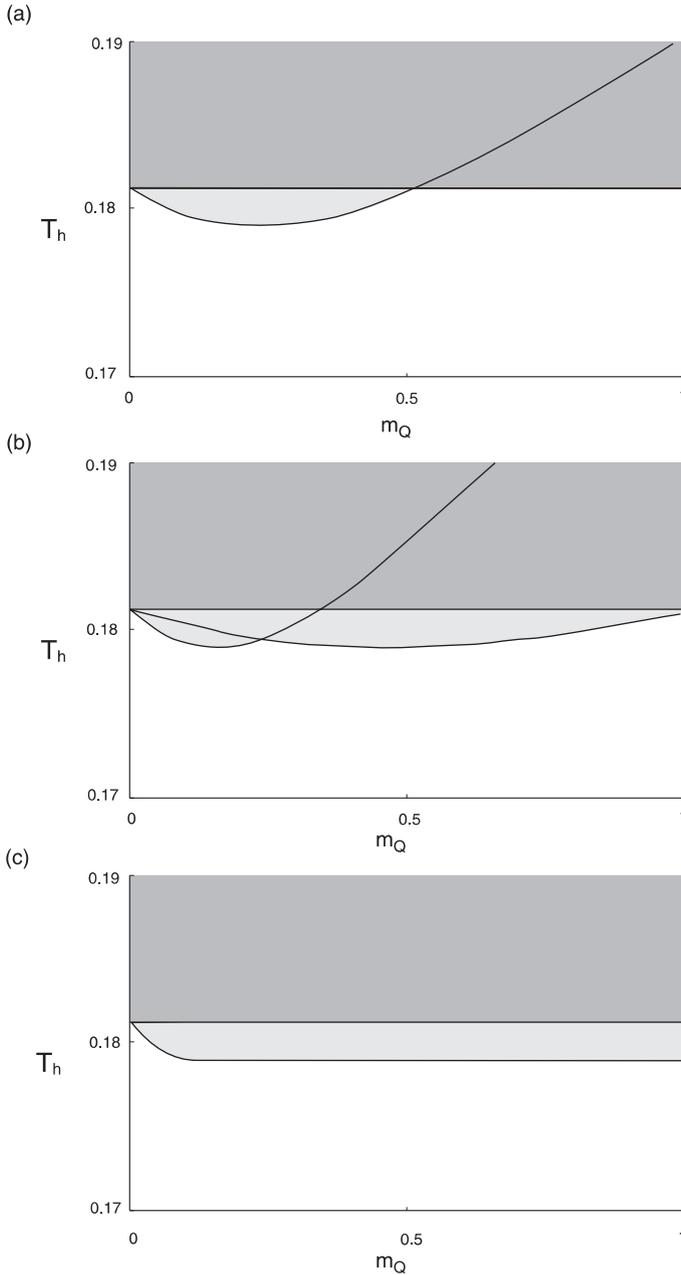
(a)

(b)

(c)

Fig. 1. Stability of the equilibrium of a predator–prey system with a localised predator dis-
perser pool, depending on the predator handling time, T_h and the predator migration rate,
m_Q. In the dark shaded region the equilibrium in unstable in the non-spatial model, in the
lighter shaded region the equilibrium of the spatial model is unstable, while it is stable in
the non-spatial model. In the unshaded region the equilibrium is stable in the spatial and
non-spatial models: (a) for a chain of two patches, (b) for a chain of three patches, (c) for a
chain of patches of infinite length. Parameters: $r = 1$, $e = 1$, $\iota = s = 0.2$ and $d = 1.5$.

three patches the eigenvalues of C are 0, $-1/2$ and $-3/2$. In Fig. 1b the unstable region in Fig. 1a is copied twice after a scaling with $-\lambda_i^{-1}$. Clearly the region in which the equilibrium is unstable becomes larger. For a given handling time, the equilibrium of a longer chain is unstable for a larger range of migration rates. If the two patch system is stable for all migration rates, all chains of longer length are always stable.

The region of instability generally increases with increasing chain length. For an infinitely long chain the homogeneous solution is unstable for all migration rates above a lower boundary (Fig. 1c). Even for very large migration rates we do find instability. The reason for this is that, for an infinitely long chain, the eigenvalues of C can take values close to 0. Therefore even very large migration rates can be scaled back to values for which the two patch model is unstable. The lower value of the migration rate for which instability is found happens to be exactly half the value of the lower stability boundary of a chain of two patches (this is because the smallest eigenvalue of C goes to -2 as the number of patches goes to infinity). A general conclusion is that the region of instability increases with the addition of more patches to the chain. If the patches are not arranged in a chain but in a different geometrical arrangement a similar result can be expected to hold.

4.3. Application 2: the spatial Lotka–Volterra system

The simplest and oldest model for the interaction between predator and prey is the Lotka–Volterra model (Volterra, 1926). The model has a neutrally stable equilibrium, surrounded by neutrally stable closed orbits. The dynamics show periodic oscillations with an amplitude which depends on the initial conditions; therefore, there is no restriction on the possible amplitudes. The spatial counterpart of this model is different in that the amplitude of the oscillations can be restricted by stability, even though no long lasting spatial patterns can develop, and all solutions in the end converge to a spatially homogeneous solution (for the spatially continuous case see Murray (1975), for the spatially discrete case see Appendix). Indeed, in a two patch Lotka–Volterra model spatially homogeneous periodic solutions that oscillate with a large amplitude can be diffusively unstable (Jansen, 1994, 1995; Jansen and De Roos, 2000). This restricts the amplitude of the oscillations to those spatially homogeneous solutions that are (neutrally) stable.

We shall demonstrate how the maximum possible amplitude of the oscillation depends on the size of the spatial domain. For this, the results for the two-patch Lotka–Volterra model need to be extrapolated to general spatial models. We shall do this for a chain of identical patches for which the local dynamics are given by

$$f(x_j) = \begin{pmatrix} rH_j - H_j P_j \\ H_j P_j - \mu P_j \end{pmatrix} \tag{14}$$

where $x_j = (H_j, P_j)^T$.

In the two-patch model, the reduction in the possible amplitudes is strongest when the prey are sessile and only the predators migrate (Jansen, 1994). We shall therefore use

$$M = \begin{bmatrix} 0 & 0 \\ 0 & m_P \end{bmatrix}.$$

For a chain of two patches the matrix C, as defined by (12), has the eigenvalues 0 and -1. The subsystem of the form (3) corresponding to the eigenvalue 0 is just the linearisation of the single patch Lotka–Volterra model. Given $s(t)$, a periodic solution of the non-spatial Lotka–Volterra system (which, by definition, has $s(t + T) = s(t)$, where T is the period of the oscillation), we immediately see that the corresponding spatially homogeneous solutions of the spatial model exhibit at best neutral stability. But we shall now see that it is possible for migration to destabilise such solutions. We consider the following subsystem, corresponding to the eigenvalue -1 of C,

$$\dot{x} = (Df(s(t)) - M)\, x. \tag{15}$$

The stability properties of the above system can be established by numerically integrating the system of differential equations. If x grows away from 0 the flat solution is unstable. A more formal, but essentially similar method, is to determine the dominant Floquet multiplier of (15) (see e.g. Hartman, 1964). The values of the multipliers of subsystems (15) with $x = 0$ depend on $s(t)$. Fig. 2 shows that system (15) is unstable for solutions $s(t)$ which oscillate with a large amplitude. For solutions which oscillate with a smaller amplitude, (15) has two multipliers inside the unit circle. Between the neutrally stable and the unstable solutions, one flat solution exists for which (15) has a multiplier at -1. In Fig. 2 the minimum and maximum prey value of this solution is shown. To demonstrate the effect of the size of the spatial domain on the observable oscillations in the predator–prey model, we shall analyse the stability of spatially homogeneous solutions in longer chains.
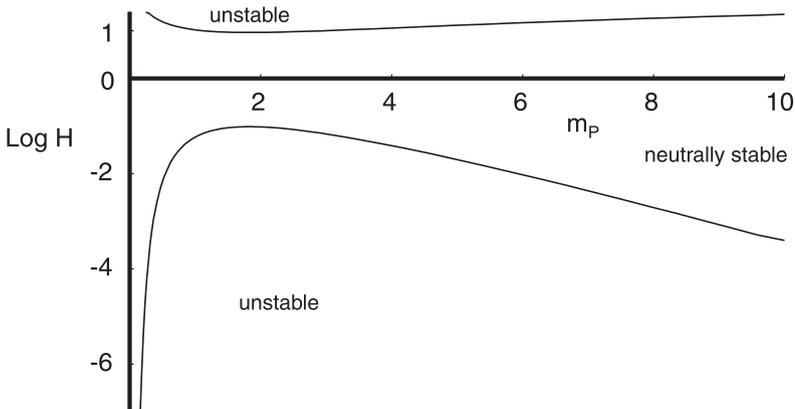

Fig. 2. A graph of the predator migration rate vs. the minimum and maximum of the prey densities of the solutions of the Lotka–Volterra model $s(t)$ for which (15) has a multiplier at -1. Flat solutions with a larger amplitude are unstable, flat solutions with a smaller amplitude are neutrally stable. Therefore this graph also gives the maximum oscillation in prey densities in a chain of two patches after transients have died out. Parameter values: $r = 1, \mu = 2$.

For a chain of n patches the stability of the flat solutions is determined by n subsystems (3). These subsystems are identical to (15) after a scaling of m with $-\lambda_i$. The stability of flat solutions of any chain can thus be derived from a chain of length two. For instance, for a chain of three patches the relevant eigenvalues of C are $-\frac{1}{2}$ and $-\frac{3}{2}$. To establish the size of possible oscillations for a given m_P the graph in Fig. 2 has to be read at $\frac{1}{2}m_P$ and $\frac{3}{2}m_P$. Since a flat solution that is unstable for any of these two values will not be observed, only the most restrictive value matters. In this way a diagram of the maximum possible oscillations versus the length of the chain can be constructed (Fig. 3).

With increasing chain length, the number of eigenvalues increases and it becomes more likely that there is an eigenvalue at or nearby the minimum of the graph in Fig. 2. Thus, the range of predator migration rates for which the oscillations will be reduced will increase with the size of the spatial domain (the number
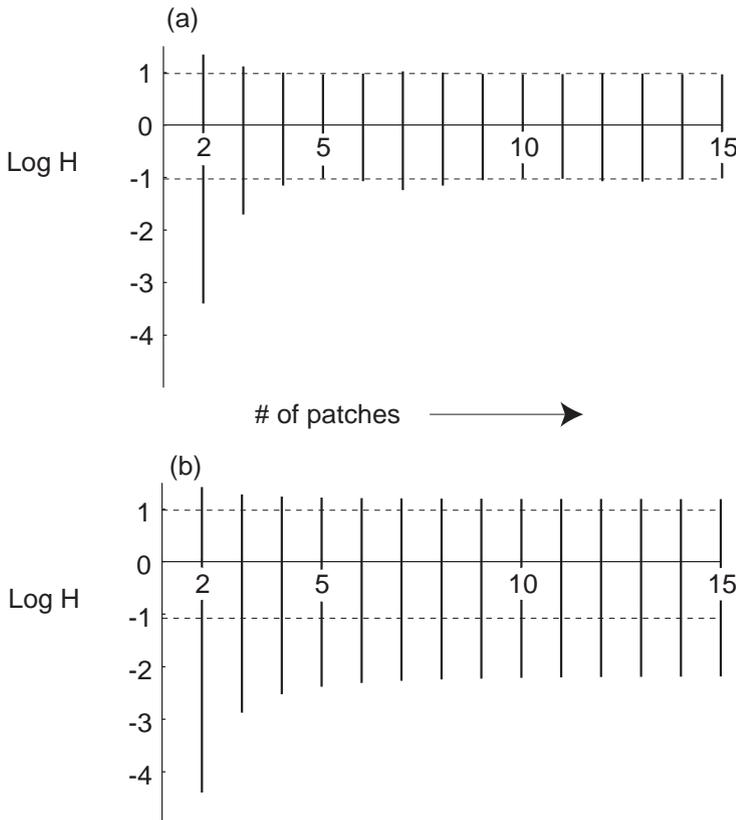

Fig. 3. Logarithm of the maximum and minimum prey densities of solutions of the non-spatial Lotka–Volterra model, for which a chain of patches is still stable vs. chain length. This also represents the maximum observable oscillation after transients have died out as a function of the size of the spatial domain. The dashed lines give the minimum of Fig. 2. Parameters: $r = 1$, $\mu = 2$ and in (a) $m_P = 10$, in (b) $m_P = 0.25$.

of patches). For migration rates larger than that for which the curve in Fig. 2 attains its minimum, the amplitude of the maximum observable oscillations will converge towards the minimum for a two patch system, as can be seen in Fig. 3a. For smaller migration rates the observable oscillations converge with increasing domain size towards either the minimum value possible or to the maximum possible oscillation in a chain of two patches with twice the migration rate (Fig. 3b). (This is again a consequence of the fact that the smallest eigenvalue of C goes towards -2 as the length of the chain goes to infinity.) Closed orbits that are neutrally stable can only become unstable, never stable. As in the previous example, the spatial interaction can only destabilise the dynamics, but in this example this comes with a little twist. As only the homogeneous oscillations with a larger amplitude can become unstable, but not the ones with a small amplitude, the spatial interactions result in dynamics which oscillate with smaller amplitudes. Thus spatial interactions result in the reduction of the amplitude of spatial predator–prey oscillations. An increase in the number of patches generally tends to decrease the observable amplitude, but this decrease is not strict.

5. Discussion

Local stability analysis of spatially homogeneous solutions in n-patch k-species systems can, once the eigenvalues of the connectivity matrix are found, be reduced to finding the stability of n corresponding k-dimensional systems. For the local stability analysis of a spatially homogeneous equilibrium this might be sufficient to make the algebra tractable, as illustrated for the predator–prey model with a pool of dispersers. For periodic or chaotic solutions, it is unlikely that the stability criteria can be derived in closed form. The results presented here can still greatly reduce the numerical effort, because the stability analysis can be reduced to that of a lower dimensional system. This is illustrated for the spatial Lotka–Volterra model.

Once the connectivity matrix is known, all that is needed for a stability analysis are the eigenvalues. For regular spatial systems, such as a chain of patches with equal spacing, the eigenvalues can be found in closed form (see also Othmer and Scriven, 1971; May, 1974, for results on eigenvalues of possible connectivity matrices). Finding the eigenvalues of connectivity matrices for irregular spatial systems in closed form might turn out to be cumbersome, if not impossible. In such cases the results presented here can be used after the eigenvalues have been established by numerical means. This approach might be useful (e.g. Adler and Nuernberger, 1994) for spatial systems in which the stability depends on the spatial arrangement of the patches. In the discussion and proofs of the stability results, we assumed that it was possible to diagonalise the connectivity matrix, but this is not always the case. In some instances when the C matrix has repeated eigenvalues there may not be n linearly independent eigenvectors. In such cases, a similarity transformation can reduce the C matrix to its Jordan canonical form, containing its eigenvalues on the diagonal, a distribution of zeroes and ones on the superdiagonal, and zeroes elsewhere. (Note that the diagonal case is simply a special case of this general form.) This can still lead to a considerable decoupling of subsystems, and thus the technique may still be useful in such cases.

Further simplifications arise if migration rates are the same for all species, most notably that the stability properties of spatially homogeneous states can be determined from those of a single uncoupled patch. When migration rates differ, diffusive instabilities can arise. The analysis is analogous to the analyses of Turing instabilities in continuous space reaction difusion models (Segel and Jackson, 1972; Kot, 1989; Murray 1989; Neubert et al., 1995).

The results presented can be applied in data analysis. When the habitat of a species consists of disjoint patches, the spatial data cannot be analysed by standard methods such as Fourier analysis. The results presented here are a starting point for the analysis of such data. We saw above that the transformation defined by the matrix A plays a similar rôle in the analysis of spatially discrete systems to that played by a Fourier transform in the analysis of continuous spatial systems. When the spatial data are described as a linear combination of the eigenvectors of the connectivity matrix, instead of a Fourier series, they might reveal a spatial pattern. This can work, for instance, in a spatial system where external noise keeps bringing the spatial system back to the spatially homogeneous state, while deterministic forces try to bring the system away from this state. Then, the eigenvectors corresponding to the eigenvalues for which the subsystems (3) or (6) are unstable, should explain a large part of the spatial variation.

Here it is assumed that the geographical arrangement determines the connectivity between patches for all species in the same way. If this assumption does not hold, it is still possible in some cases to apply an analysis similar to the one presented here if the connectivity matrices for all species all have the same eigenvectors (Othmer and Scriven, 1971; Allen, 1975). This requires that the connectivity matrices commute (Allen, 1975). Throughout this paper it is assumed that dispersal is a process in which individuals leave their patch with a fixed probability. This probability can depend on the density of other species in the patch. The framework presented here can be generalised to accommodate for this and behaviourally motivated submodels can thus be incorporated in multi-patch models and in models for aggregation.

Appendix

The main result we shall prove here is that the differences in densities between the patches disappear for all solutions with positive initial conditions of (2) with f given by (14), i.e,

$$\dot{x}_j = \begin{pmatrix} \dot{H}_j \\ \dot{P}_j \end{pmatrix} = \begin{pmatrix} r H_j - H_j P_j + m_H \sum_{i=1}^{n} c_{ij} H_i \\ H_j P_j - \mu P_j + m_P \sum_{i=1}^{n} c_{ij} P_i \end{pmatrix}. \tag{16}$$

When the movement of the individuals is undirected we shall present a complete proof. For directed movement we did not succeed in formulating a concise and precise proof and we shall only deal with a special case. For undirected movement the probability for an individual to migrate from patch i to patch j is identical to the probability to migrate from patch j to patch i hence $w_{1j} c_{ij} = w_{1i} c_{ji}$. (Notice that we do not assume that the patches are of equal sizes.)

To prove that in the spatial Lotka–Volterra system all differences between patches disappear asymptotically, the function

$$V_i = H_i - \mu \ln H_i + P_i - r \ln P_i.$$

is defined. We shall show that the function

$$V = \sum_{j=1}^{n} w_{1j} V_j$$

is a Lyapunov function for all orbits of (16) with positive initial conditions. The vector $w_1 = (w_{11}, \ldots, w_{1n})^T$ is the right eigenvector of C with eigenvalue 0, hence $\sum_{j=1}^{n} w_{1j} c_{ij} = 0$ for all $i = 1, \ldots n$. First, observe that each $V_i \geq 0$ for all $H_i \geq 0$, $P_i \geq 0$. For $m_H = 0$, the derivative of V with respect to time is

$$\frac{dV}{dt} = m_P \sum_{j=1}^{n} w_{1j} \sum_{i=1}^{n} c_{ij} P_i - r m_P \sum_{j=1}^{n} w_{1j} \sum_{i=1}^{n} c_{ij} \frac{P_i}{P_j}$$

$$= m_P \sum_{i=1}^{n} P_i \sum_{j=1}^{n} w_{1j} c_{ij} - r m_P \sum_{i=1}^{n} \sum_{j=1}^{n} w_{1j} c_{ij} \frac{P_i}{P_j}.$$

Since w_1 is an eigenvector of C with eigenvalue 0, the first of these terms is equal to zero. Turning our attention to the second term, we first split it in two equal terms, then we relabel i and j in the second of these and swap the order of summation.

$$\frac{dV}{dt} = -\frac{r m_P}{2} \left(\sum_{i=1}^{n} \sum_{j=1}^{n} w_{1j} c_{ij} \frac{P_i}{P_j} + \sum_{i=1}^{n} \sum_{j=1}^{n} w_{1j} c_{ij} \frac{P_i}{P_j} \right)$$

$$= -\frac{r m_P}{2} \left(\sum_{i=1}^{n} \sum_{j=1}^{n} w_{1j} c_{ij} \frac{P_i}{P_j} + \sum_{i=1}^{n} \sum_{j=1}^{n} w_{1i} c_{ji} \frac{P_j}{P_i} \right).$$

Now we make use of migration being undirected ($w_{1i} c_{ji} = w_{1j} c_{ij}$) to give

$$\frac{dV}{dt} = -\frac{r m_P}{2} \sum_{i=1}^{n} \sum_{j=1}^{n} w_{1j} c_{ij} \left(\frac{P_i}{P_j} + \frac{P_j}{P_i} \right)$$

$$= -\frac{r m_P}{2} \sum_{j=1}^{n} \sum_{i=1}^{n} w_{1j} c_{ij} \frac{(P_i^2 + P_j^2)}{P_i P_j}.$$

Finally, we again make use of the fact that w_1 is an eigenvector of C with eigenvalue 0 to write

$$\frac{dV}{dt} = -\frac{r m_P}{2} \sum_{j=1}^{n} \sum_{i=1}^{n} w_{1j} c_{ij} \left(\frac{(P_i^2 + P_j^2)}{P_i P_j} - 2 \right)$$

$$= -\frac{r m_P}{2} \sum_{j=1}^{n} \sum_{i=1}^{n} w_{1j} c_{ij} \frac{(P_i - P_j)^2}{P_i P_j}$$

$$\leq 0$$

All ω-limit sets of orbits of (1) with positive initial conditions are contained in the invariant subsets of the set in which $\dot{V} = 0$, which is the set for which $P_i = P_j$ for all i, j. It follows directly from (16) that only the subsets for which $P_i = P_j$, $H_i = H_j$ are invariant. Hence, when there is undirected movement and the prey are sessile, all orbits of (16) with positive initial conditions converge to the set where $P_i = P_j$ and $H_i = H_j$ for all i, j.

When the prey are mobile, i.e., $m_H \neq 0$, V is also a Lyapunov function (which can be easily shown by an argument similar to the one given above) and all differences between the patches disappear asymptotically.

One of the simplest examples of directional movement occurs in a system of 3 cells. The matrix $C = C^u + C^d$ can be seen as a sum of directed and undirected movement, where $C^u = \{c_{ij}^u\}$ and $C^d = \{c_{ij}^d\}$. The entries of these matrices are given by

$$c_{ij}^u = \frac{\min(w_{1j}c_{ij}, w_{1i}c_{ji})}{w_{1j}}, \text{ for } i \neq j, \text{ and } c_{jj}^u = -\sum_{i=1, i\neq j}^{3} c_{ij}^u,$$

and

$$c_{ij}^d = \frac{w_{1j}c_{ij} - \min(w_{1j}c_{ij}, w_{1i}c_{ji})}{w_{1j}}, \text{ for } i \neq j, \text{ and } c_{jj}^d = -\sum_{i=1, i\neq j}^{3} c_{ij}^d.$$

Note that $(1, 1, 1)$ is a left eigenvector of C^u and C^d. Directed movement can result in movement in only two possible directions, and the matrix C^d is of the form $w_{13}c_{13}^d = w_{12}c_{32}^d = w_{11}c_{21}^d$ and $c_{12}^d = c_{31}^d = c_{23}^d = 0$ while for all i, $\sum_{j=1}^{3} w_{1j}c_{ij}^d = 0$ (or $w_{11}c_{31}^d = w_{13}c_{23}^d = w_{12}c_{12}^d$ and $c_{13}^d = c_{32}^d = c_{21}^d = 0$, which can be dealt with similarly). The derivative of the Lyapunov function V then is

$$\frac{dV}{dt} = m_P \sum_{j=1}^{3} w_{1j} \sum_{i=1}^{3} c_{ij} P_i - rm_P \sum_{j=1}^{3} w_{1j} \sum_{i=1}^{3} c_{ij} \frac{P_i}{P_j}$$

$$= -rm_P \sum_{j=1}^{3} \sum_{i=1}^{3} w_{1j} c_{ij} \frac{P_i}{P_j}$$

$$= -rm_P \sum_{i=1}^{3} \sum_{j=1}^{3} w_{1j} c_{ij}^u \frac{P_i}{P_j} - rm_P \sum_{i=1}^{3} \sum_{j=1}^{3} w_{1j} c_{ij}^d \frac{P_i}{P_j}$$

$$= -\frac{rm_P}{2} \sum_{j=1}^{3} \sum_{i=1}^{3} w_{1j} c_{ij}^u \frac{(P_i - P_j)^2}{P_i P_j}$$

$$\quad - rm_P \left(w_{13}c_{13}^d \frac{P_1}{P_3} + w_{12}c_{32}^d \frac{P_3}{P_2} + w_{11}c_{21}^d \frac{P_2}{P_1} - w_{13}c_{13}^d - w_{12}c_{32}^d - w_{11}c_{21}^d \right)$$

$$\leq -\frac{rm_P}{2} \sum_{j=1}^{3} \sum_{i=1}^{3} w_{1j} c_{ij}^u \frac{(P_i - P_j)^2}{P_i P_j} - rm_P w_{11} c_{21}^d \left(2\sqrt{\frac{P_1}{P_2}} + \frac{P_2}{P_1} - 3 \right)$$

$$\leq 0$$

where the one but last step used the fact that $P_1/x + x/P_2$ has a minimum value of $2\sqrt{P_2/P_1}$. By completing the argument as above it follows that the differences between patches will disappear asymptotically in a system of 3 cells. A similar argument can be constructed for larger circular systems with directed movement.

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