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Attractivity of coherent manifolds in metapopulation models

C. Connell McCluskey · David J. D. Earn

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Abstract The likelihood that coupled dynamical systems will completely synchronize, or become "coherent", is often of great applied interest. Previous work has established conditions for local stability of coherent solutions and global attractivity of coherent manifolds in a variety of spatially explicit models. We consider models of communities coupled by dispersal and explore intermediate regimes in which it can be shown that states in phase space regions of positive measure are attracted to coherent solutions. Our methods yield rigorous and practically useful coherence criteria that facilitate useful analyses of ecological and epidemiological problems.

Keywords Synchrony · Synchronization · Local stability · Global stability · Differential equations · Invariant manifolds · Lozinskii measures

Mathematics Subject Classification (2000) 34D35 · 92D40

1 Introduction

Many coupled nonlinear systems have a tendency to oscillate synchronously, a phenomenon that was first noted by Christian Huygens in 1665. Synchronization has since attracted considerable scientific and mathematical attention (Strogatz 2003; Winfree

C. C. McCluskey (✉)
Department of Mathematics, Wilfrid Laurier University,
75 University Avenue West, Waterloo, ON N2L 3C5, Canada
e-mail: ccmcc8@gmail.com

D. J. D. Earn
Department of Mathematics and Statistics, McMaster University,
1280 Main St. West, Hamilton, ON L8S 4K1, Canada
e-mail: earn@math.mcmaster.ca

2001), especially since the discovery of synchrony in systems that exhibit deterministic chaos (Pikovsky et al. 2001).

Dynamical systems of interest in ecology often have the structure of a *metapopulation*, i.e., a collection of habitat "patches" within which individuals reproduce and among which they disperse (Hanski and Gilpin 1997). The same structure often occurs in epidemiological contexts, where cities might play the role of "patches" and travel among cities produces connectivity akin to "dispersal" (Earn et al. 1998; Grenfell and Harwood 1997). In this paper, we investigate synchrony in metapopulation models.

Intuitively, we think of oscillations of two or more systems as being synchronized if their phases coincide repeatedly (e.g., highest points and lowest points always occur simultaneously) even if the amplitudes of the oscillations are otherwise uncorrelated. This relatively weak form of synchronization is often called *phase synchronization* (Blasius et al. 1999). Most theoretical work has focussed on a much stronger form of synchronization, often called *complete synchronization* or *coherence*, meaning that the different "patches" in the coupled dynamical system have identical dynamics (i.e., at any given time, the state of the system in one patch is exactly the same as the state in all other patches). Here, we focus on coherence.

Beyond its intrinsic interest, metapopulation synchrony has potentially important practical applications. Asynchronous dynamics facilitate *rescue effects*, whereby dispersal from patches with large populations prevents local extinctions in patches with small populations (Brown and Kodric-Brown 1977). Synchrony inhibits such processes, and could therefore strongly influence the vulnerability of a species to global extinction. If the species of interest is an endangered animal then we might wish to prevent or reduce the probability of synchrony, whereas if we are concerned with a pathogen that causes an infectious disease then we might wish to promote synchronous dynamics (Earn et al. 1998). In either case, it would be helpful to have rigorous criteria for synchronization, expressed in terms of controllable parameters.

Previous work has established rigorous criteria for local stability of coherent solutions of dynamical systems in terms of transverse Lyapunov exponents (Buescu 1997; Jansen and Lloyd 2000; Pikovsky et al. 2001; Silva and Giordani 2006). These conditions determine whether asymptotic approach to any given coherent solution is *possible*, but they do not provide any information about the size of basins of attraction; moreover, transverse Lyapunov exponents are asymptotic quantities that can rarely be calculated analytically, which makes the conditions awkward to use in practice. At the other extreme, recent work has yielded conditions for *global asymptotic coherence*, i.e., absolutely certain coherence, regardless of initial conditions (Earn and Levin 2006; Earn et al. 2000). While expressible in terms of system parameters, these conditions have the considerable limitation that they are merely *sufficient* for global asymptotic coherence and they may be too strong to be useful in many situations.

Our approach in this paper is intermediate. Our methods will not typically yield the sort of sharp stability boundaries that can be obtained from the traditional local theory (Buescu 1997). However, as in the global theory (Earn and Levin 2006), we are able to show—without reference to particular coherent solutions—that regions of

Table 1 Frequently used notation

Notation	Meaning
n, k	Number of patches and species
x_i^s	Density of species s in patch i
$x_i = (x_i^1, \ldots, x_i^k)^T$	Vector of density of all species in patch i
$y^s = (x_1^s, \ldots, x_n^s)^T$	Vector of density of species s in all patches
$M^s = [m_{ij}^s]$	Matrix of dispersal rates for species s
f	Functional response for in-patch dynamics, Eq. 2.1
$\mathbf{1}$	$(1, \ldots, 1)^T$
$\mathbf{0}$	$(0, \ldots, 0)^T$
$\widetilde{M} = [\widetilde{m}_{ij}] = [m_{ij} - m_{nj}]$	Modified dispersal matrix
$J_{\mathbb{C}}, \widetilde{J}_{\mathbb{C}}, J_{\mathbb{R}}, \widetilde{J}_{\mathbb{R}}$	Complex and real Jordan forms of M and $\widetilde{M}$
λ_j	Eigenvalue of M
$H_j^s = x_j^s - x_n^s$	Density of species s in patch j relative to patch n
$H_j = (H_j^1, \ldots, H_j^k)^T$	Densities in patch j relative to those in patch n
$z = x_n, H = (H_1^T, \ldots, H_{n-1}^T)^T$	Coordinates using patch n as a reference
$\Gamma = \{(z, H) : H = \mathbf{0}\}$	Coherent manifold
$\mathrm{coh}(A)$	Coherent image of a set A
$D(z, H)$	Normal flow coefficient matrix
$\bar{D}(z) = \lim_{H \to \mathbf{0}} D(z, H)$	Normal flow coefficient matrix in the coherent limit
$\bar{D}_{\mathrm{sp}}$	$\bar{D}(z)$ with entries ordered by species rather than by patch
ρ^s	Special case dispersal coefficient for species s
$M^s = \rho^s M$	Special case dispersal matrix for species s
$\Upsilon = \mathrm{diag}(\rho^1, \ldots, \rho^k)$	Matrix of dispersal coefficients
$\mu(M)$	Lozinskii measure of a matrix M
Φ, φ	Flows associated with Eqs. 4.8 and 7.1
$\mathcal{A}, \mathrm{B}(\mathcal{A})$	Attractor and its basin of attraction
$\mathcal{N}_\epsilon$	Neighbourhood of $H = \mathbf{0}$
$\mathcal{A}_\delta$	Neighbourhood of $\mathcal{A}$

phase space are attracted to the coherent manifold. In addition, the conditions will be expressible in terms of system parameters.

We begin in Sect. 2 with a description of the class of models that we will investigate. In Sect. 3, we give a formal definition of coherence and establish a number of algebraic facts that facilitate analyses in subsequent sections. A change of variables that greatly simplifies our work is presented in Sect. 4, and a fundamental quantity for our analysis is discussed in Sect. 5. Section 6 reviews the notion of Lozinskii measure (which plays a key role in our results). Our main results are presented in Sect. 7 and proved in Sect. 8. We apply our results to a few specific metapopulation models in Sect. 9 and discuss avenues for further developments in Sect. 10. Our notation is summarized in Table 1.

2 Constructing the model equations

Consider the interaction of k species that live in an environment that is fragmented into n patches. Let x_i^s be the density of species s on patch i and let $x_i = (x_i^1, \ldots, x_i^k)^T$. Then the vector x_i gives the densities of all species on patch i. Assume that the population dynamics within each patch are determined by the same density dependent processes in continuous time. Thus, in the absence of dispersal,

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = f(x_i) \tag{2.1}$$

for $i = 1, \ldots, n$. Since x_i describes population densities, the set of biologically meaningful values is the non-negative orthant $\mathbb{R}^k_{\geq 0}$. Thus, we assume that the non-negative orthant is positively invariant under the reproduction function f. Furthermore, we assume that f is C^1 on $\mathbb{R}^k_{\geq 0}$.

For each species, the rate of dispersal from patch j to patch i is assumed to be proportional to the density of that species in patch j. Thus, for $j \neq i$, the rate at which individuals of species s originating in patch j arrive in patch i can be written as $m_{ij}^s x_j^s$, where $m_{ij}^s \geq 0$. Also, the total flow of species s out of patch i can be written as $m_{ii}^s x_i^s$, where $m_{ii}^s \leq 0$. In the absence of in-patch dynamics

$$\begin{aligned}\frac{\mathrm{d}x_i^s}{\mathrm{d}t} &= \left(\sum_{j \neq i} m_{ij}^s x_j^s\right) + m_{ii}^s x_i^s \\ &= \sum_{j=1}^{n} m_{ij}^s x_j^s. \end{aligned}\tag{2.2}$$

Let $y^s = (x_1^s, \ldots, x_n^s)^T$; i.e., the vector y^s gives the density of species s in each of the n patches. Letting $M^s = [m_{ij}^s]_{n \times n}$, Eq. 2.2 gives

$$\frac{\mathrm{d}y^s}{\mathrm{d}t} = M^s y^s. \tag{2.3}$$

Note that if a component of y^s is zero (say $x_i^s = 0$), then the derivative of that component (Eq. 2.2) is greater than or equal to zero. Hence the non-negative orthant $\mathbb{R}^n_{\geq 0}$ is positively invariant under Eq. 2.3.

The species-specific dispersal matrix M^s has non-positive diagonal entries ($m_{ii}^s \leq 0$, reflecting outflow) and non-negative off-diagonal entries ($m_{ij}^s \geq 0$, reflecting inflow). We assume that dispersal between patches is instantaneous, and that no individuals are lost as they disperse, i.e., for each species, inflow balances outflow. Consequently, the rate at which species s leaves a particular patch (say i) for other patches (described by the diagonal term in column i of M^s) must equal the sum of the rates at which the species arrives in other patches from patch i (given by the off-diagonal terms in column i). Thus, summing over a column of M^s must yield zero.

If instead, dispersal time were taken into account, then the terms in Eq. 2.3 that correspond to off-diagonal entries of M^s would require a delay. If it is assumed that there is loss during dispersal, then the sign pattern of M^s would remain the same, but the column sums could be negative, indicating that not all individuals that leave a patch, necessarily make it to another patch.

We now complete the model by combining reproduction and dispersal. Denote the components of f by

$$f(x) = (f^1(x), \ldots, f^k(x))^T. \tag{2.4}$$

Then, combining the in-patch interactions between the species with the dispersal between the patches, we get the full multi-species multi-patch dynamics

$$\frac{\mathrm{d}x_i^s}{\mathrm{d}t} = f^s(x_i) + \sum_{j=1}^{n} m_{ij}^s x_j^s \quad \text{for } i = 1, \ldots, n \quad \text{and} \quad s = 1, \ldots, k. \tag{2.5}$$

Thus the behaviour is described by an nk-dimensional system of ordinary differential equations. The biologically relevant region is the non-negative orthant $\mathbb{R}^{nk}_{\geq 0}$. Note that the positive invariance of $\mathbb{R}^{nk}_{\geq 0}$ under the dynamics described by Eq. 2.5 follows from the invariance of $\mathbb{R}^{k}_{\geq 0}$ and $\mathbb{R}^{n}_{\geq 0}$ under Eqs. 2.1 and 2.3, respectively.

3 Coherence and related algebraic properties

One way to denote the state variable for system (2.5) is $x = (x_1, \ldots, x_n)$, where each $x_i \in \mathbb{R}^{k}_{\geq 0}$.

Definition 3.1 (*Coherence*) A point x is said to be *coherent* if $x_1 = \cdots = x_n$. A solution $x(t)$ of (2.5) is coherent if $x_1(t) = \cdots = x_n(t)$ for all $t \in \mathbb{R}$.

Not all systems of the form (2.5) admit coherent solutions. The purpose of this study is to determine how dispersal over a network of patches affects the spatial structure of populations. In particular, we are interested in conditions on the dispersal pattern that will make coherence stable. A precondition for this is that coherence is possible. More precisely, we assume that any coherent initial condition for Eq. 2.5 yields a coherent solution.

Consider a coherent solution $x(t)$. Since $x_1(t) = \cdots = x_n(t)$ for all t, it follows that $\frac{\mathrm{d}x_1}{\mathrm{d}t}(t) = \cdots = \frac{\mathrm{d}x_n}{\mathrm{d}t}(t)$ for all t and, hence, we must have $\frac{\mathrm{d}x_i^s}{\mathrm{d}t} - \frac{\mathrm{d}x_n^s}{\mathrm{d}t} = 0$ for $i = 1, \ldots, n-1$ and for $s = 1, \ldots, k$. Therefore, along any coherent solution,

$$0 = \left(f^s(x_i) + \sum_{j=1}^{n} m_{ij}^s x_j^s \right) - \left(f^s(x_n) + \sum_{j=1}^{n} m_{nj}^s x_j^s \right).$$

Since $x_i = x_n$, this becomes

$$0 = \sum_{j=1}^{n} m_{ij}^s x_j^s - \sum_{j=1}^{n} m_{nj}^s x_j^s. \tag{3.1}$$

Noting that, at a coherent point, $y^s = (x_1^s, \ldots, x_n^s)^T$ is a scalar multiple of $\mathbf{1} = (1, \ldots, 1)^T$, it follows that Eq. 3.1 can be rewritten as

$$0 = x_1^s \left(\sum_{j=1}^{n} m_{ij}^s - \sum_{j=1}^{n} m_{nj}^s \right). \tag{3.2}$$

Since this is to hold for any coherent initial value, we may assume that x_1^s is non-zero and, hence,

$$\sum_{j=1}^{n} m_{ij}^s = \sum_{j=1}^{n} m_{nj}^s, \qquad i = 1, \ldots, n-1. \tag{3.3}$$

This means that all row sums of M^s are equal, which is the motivation for the following definition.

Definition 3.2 (*CD-Matrix*) A square matrix is a *coherent dispersal matrix*, or *CD-matrix*, if the off-diagonal entries are non-negative and all row sums are equal.

As discussed in Sect. 2, for a continuous-time model with no loss and no delay (i.e., each individual that leaves one patch arrives instantaneously in another patch), the column sums of the dispersal matrix are zero. This implies that the row sums are also zero. To see this, suppose that the row sum for each row is α. Then we have $M^s\mathbf{1} = \alpha\mathbf{1}$. Thus, $\mathbf{1}^T M^s \mathbf{1} = n\alpha$. However, $\mathbf{1}^T M^s = \mathbf{0}^T$ (where $\mathbf{0} = (0, \ldots, 0)^T$) so we must have $\mathbf{1}^T M^s \mathbf{1} = 0$. Thus, $\alpha = 0$. Hence, we see that coherent solutions are possible in a continuous-time, no-loss, no-delay model, if and only if the row sums of M^s are zero for each s.

Definition 3.3 (*CNCD-Matrix*) A *continuous-time, no-loss coherent dispersal matrix*, or *CNCD-matrix*, is a CD-matrix for which the row sums and column sums are zero. The off-diagonal entries of such a matrix are non-negative and the diagonal entries are non-positive.

Remark 1 For a continuous time model with loss, the column sums of the dispersal matrix are non-positive but not necessarily equal, and the row sums are all negative and equal. If travel time between patches is accounted for, then the system is modelled by delay differential equations or integro-differential equations rather than ordinary differential equations.

A discrete time model is represented by difference equations. If there is no loss, as in the case studied in Earn and Levin (2006) and Earn et al. (2000), then the column sums and row sums of the dispersal matrix are equal to one rather than zero. For a discrete time model with loss, the column sums are non-negative but may be less than one, though not necessarily equal, and the row sums are positive, less than one, and equal.

For the remainder of this paper, we deal exclusively with continuous-time, no-loss coherent dispersal matrices. The rest of the present section is a catalogue of useful algebraic properties of CNCD-matrices.

Proposition 3.1 *If M is a CNCD-matrix, then each eigenvalue of M has real part less than or equal to zero. Furthermore, zero is an eigenvalue and M has no non-zero eigenvalues that are purely imaginary.*

Proof Due to the sign pattern of a CNCD-matrix M, and the fact that the row sums are zero, the Gersgorin discs (Lancaster and Tismenetsky 1985, Sect. 10.6) all lie in the closed left half-plane. Furthermore, the Gersgorin discs only intersect the imaginary axis at the origin. Thus each eigenvalue of M has non-positive real part, and has real part zero only if the eigenvalue is zero, i.e., M has no eigenvalues of the form $\beta\mathbf{i}$ with $\beta \neq 0$. Additionally since $M\mathbf{1} = \mathbf{0}$, zero is an eigenvalue of M. □

Definition 3.4 ($\widetilde{M}$) For an $n \times n$ CNCD-matrix $M = [m_{ij}]$, the *modified dispersal matrix* associated with M is the $(n-1) \times (n-1)$ matrix $\widetilde{M} = [\widetilde{m}_{ij}]$, where $\widetilde{m}_{ij} = m_{ij} - m_{nj}$ for $i, j = 1, \ldots, n-1$.

As will be shown in Sect. 4, employing $\widetilde{M}$ allows us to simplify our analysis of system (2.5). In preparation for that development, we now establish some useful algebraic relationships between M and $\widetilde{M}$.

The next proposition is useful for characterizing when a CNCD-matrix describes a system that is better considered as two or more distinct subsystems (among which there is no dispersal). In such a case, the graph representing the dispersal pattern has two or more components.

Proposition 3.2 *If zero is an eigenvalue of $\widetilde{M}$, then M is reducible and, by reordering the basis, can be written in block diagonal form.*

Proof Suppose zero is an eigenvalue of $\widetilde{M}$. Then there exists a non-zero vector $\widetilde{v} = (\widetilde{v}_1, \ldots, \widetilde{v}_{n-1})^T$ such that

$$\begin{aligned} 0 &= \sum_{j=1}^{n-1} \widetilde{m}_{ij}\widetilde{v}_j \quad \text{for each} \quad i = 1, \ldots, n-1 \\ &= \sum_{j=1}^{n-1} (m_{ij} - m_{nj})\widetilde{v}_j. \end{aligned} \tag{3.4}$$

Let $v = (\widetilde{v}_1, \ldots, \widetilde{v}_{n-1}, 0)^T$. Then Eq. 3.4 implies that for each $i = 1, \ldots, n-1$, the dot product of the ith row of M with v is equal to the dot product of the nth row of M with v. Call this product β. Then $Mv = \beta\mathbf{1}$. Multiplying by $\mathbf{1}^T$ on the left, and using the fact that the columns of M sum to zero we see that $0 = \beta n$ and so $\beta = 0$. Thus,

$Mv = \mathbf{0}$. Clearly v is linearly independent of $\mathbf{1}$, and hence, 0 is a repeated eigenvalue of M with eigenvectors v and $\mathbf{1}$.

Note that there exists $\gamma > 0$ such that $M + \gamma I$ is a non-negative matrix with spectral radius γ. This follows from Proposition 3.1 and the fact that the eigenvalues of $M + \gamma I$ are found by adding γ to the eigenvalues of M. Hence, by Theorem 8.4.4.d of Horn and Johnson (1985), $M + \gamma I$ is irreducible only if γ is a simple eigenvalue of $M + \gamma I$. Since v and $\mathbf{1}$ are eigenvectors of M with eigenvalue 0, they are also both eigenvectors of $M + \gamma I$ with eigenvalue γ. Hence $\lambda = \gamma$ has multiplicity greater than or equal to two, and therefore $M + \gamma I$ is reducible. Thus, M is reducible.

This means that the basis can be reordered so that M can be expressed in block form as

$$M = \begin{bmatrix} A & B \\ 0 & C \end{bmatrix}.$$

It remains to be shown that the off-diagonal block B is a block of zeros. Note that the column sums for the columns involving A are each zero and so the sum of these column sums is zero. But, the sum of these column sums is the same as the sum of all entries in A. Similarly each row sum involving A and B is zero, and so the sum of these row sums is zero. This implies that the sum of all entries of A and of B is zero. Since the sum of all entries of A is zero, the same must be true for the sum of all entries of B. However, since B is an off-diagonal block, each entry is non-negative. Thus, each entry of B is in fact zero. □

In the Jordan canonical form of a matrix M, a real eigenvalue λ with corresponding eigenvector v appears in a 1×1 Jordan block only if there is no generalized eigenvector u such that $(M - \lambda I)u = v$. If M is a CNCD-matrix then, as we have seen, $\lambda = 0$ is an eigenvalue of M with eigenvector $\mathbf{1}$. The next proposition implies that in the Jordan form of M, $\lambda = 0$ appears as a 1×1 block.

Proposition 3.3 *If M is a CNCD-matrix, then there is no vector $u \in \mathbb{R}^n$ such that $Mu = \mathbf{1}$.*

Proof Suppose to the contrary that $Mu = \mathbf{1}$, where $u = (u^1, \dots, u^n)$. Then for $i = 1, \dots, n$,

$$\begin{aligned} 1 &= \sum_{j=1}^{n} m_{ij} u^j \\ &= \sum_{j \neq i} m_{ij} (u^j - u^i) \end{aligned} \tag{3.5}$$

since $m_{ii} = -\sum_{j \neq i} m_{ij}$. Choose i such that $u^i \geq u^j$ for $j \neq i$. Then the right-hand side of (3.5) is non-positive and cannot equal the left-hand side. Thus, no such vector u exists. □

Remark 2 In fact, a similar argument shows that for any $u \in \mathbb{R}^n$, at least one component of Mu is less than or equal to zero, i.e., the positive orthant has no preimage under multiplication by M.

Let $J_{\mathbb{C}}$ be the complex Jordan form of M. Then there is a complex matrix $P = [v_1|\cdots|v_n]$ such that $J_{\mathbb{C}} = P^{-1}MP$, where each column of P is a generalized eigenvector of M (Horn and Johnson 1985). By Proposition 3.3, $\lambda = 0$ appears as a 1×1 block in $J_{\mathbb{C}}$ and hence the row and column of $J_{\mathbb{C}}$ containing $\lambda = 0$ consist entirely of zeros. Without loss of generality, we can choose $v_n = \mathbf{1}$ so that $\lambda = 0$ appears in the bottom right corner of $J_{\mathbb{C}}$.

For $j = 1, \dots, n-1$, write $v_j = [v_j^1, \dots, v_j^n]^T$. Define $\widetilde{v}_j = [\widetilde{v}_j^1, \dots, \widetilde{v}_j^{n-1}]^T \in \mathbb{R}^{n-1}$ where $\widetilde{v}_j^l = v_j^l - v_j^n$ for $l, j = 1, \dots, n-1$, and let $\widetilde{P} = [\widetilde{v}_1|\cdots|\widetilde{v}_{n-1}] \in \mathbb{M}_{(n-1)\times(n-1)}$.

Proposition 3.4 *The complex Jordan form* $\widetilde{J}_{\mathbb{C}}$ *of* $\widetilde{M}$ *is given by* $\widetilde{J}_{\mathbb{C}} = \widetilde{P}^{-1}\widetilde{M}\widetilde{P}$. *Furthermore,* $\widetilde{J}_{\mathbb{C}}$ *consists of the first* $(n-1)$ *rows and columns of* $J_{\mathbb{C}}$.

Proof We first establish the fact that $\widetilde{P}$ is invertible. Since P is invertible, the determinant of P must be non-zero. Hence,

$$0 \neq \det P = \det \begin{bmatrix} v_1^1 & \cdots & v_{n-1}^1 & 1 \\ \vdots & & \vdots & \vdots \\ v_1^{n-1} & \cdots & v_{n-1}^{n-1} & 1 \\ v_1^n & \cdots & v_{n-1}^n & 1 \end{bmatrix}.$$

By subtracting v_j^n times the nth column from the jth column, for $j = 1, \dots, n-1$ we see that $\det P = \det \widetilde{P}$ and so $\widetilde{P}$ is also invertible.

Let $\lambda_1, \dots, \lambda_n$ be the eigenvalues of M corresponding to the generalized eigenvectors $v_1, \dots, v_n$, respectively. Then

$$\left(M - \lambda_j I\right) v_j = \begin{cases} 0 & \text{if } v_j \text{ is an eigenvector of } M \\ v_{j-1} & \text{if } v_j \text{ is a generalized eigenvector, but not an eigenvector.} \end{cases}$$

Equivalently, $Mv_j = \lambda_j v_j + \alpha_j v_{j-1}$, where $\alpha_j \in \{0, 1\}$. Thus,

$$(\text{Row } i \text{ of } M) \cdot v_j = \lambda_j v_j^i + \alpha_j v_{j-1}^i. \tag{3.6}$$

Since $P^{-1}P$ is the identity and $P = [v_1|\cdots|v_n]$, we have $P^{-1}v_j = e_j$, where e_j is the jth standard basis vector in $\mathbb{R}^n$ for $j = 1, \dots, n$. Thus, $P^{-1}Mv_j = P^{-1}\left(\lambda_j v_j + \alpha_j v_{j-1}\right) = \lambda_j e_j + \alpha_j e_{j-1}$. Hence, the jth column of $J_{\mathbb{C}} = P^{-1}MP$ is given by $\lambda_j e_j + \alpha_j e_{j-1}$

We now work towards finding $\widetilde{M}\widetilde{v}_j$ by first calculating $\widetilde{u}_j^i$, the ith entry of $\widetilde{M}\widetilde{v}_j$ for $i, j = 1, \dots, n-1$.

$$\begin{aligned} \widetilde{u}_j^i &= \left(\text{Row } i \text{ of } \widetilde{M}\right) \cdot \widetilde{v}_j \\ &= \sum_{l=1}^{n-1} (m_{il} - m_{nl})(v_j^l - v_j^n). \end{aligned}$$

Noting that $v_j^l - v_j^n$ is zero if $l = n$, it is clear that the above summation can be extended to terminate at $l = n$, giving

$$\begin{aligned}
\widetilde{u}_j^i &= \sum_{l=1}^{n} (m_{il} - m_{nl})(v_j^l - v_j^n) \\
&= \sum_{l=1}^{n} (m_{il} - m_{nl}) v_j^l \; - \; v_j^n \sum_{l=1}^{n} (m_{il} - m_{nl}) \\
&= (\text{Row } i \text{ of } M) \cdot v_j - (\text{Row } n \text{ of } M) \cdot v_j \\
&\quad - v_j^n \left((i\text{th row sum of } M) - (n\text{th row sum of } M) \right).
\end{aligned}$$

Recalling that the row sums of M are equal and then using Eq. 3.6, we obtain

$$\begin{aligned}
\widetilde{u}_j^i &= (\text{Row } i \text{ of } M) \cdot v_j - (\text{Row } n \text{ of } M) \cdot v_j \\
&= \left(\lambda_j v_j^i + \alpha_j v_{j-1}^i \right) - \left(\lambda_j v_j^n + \alpha_j v_{j-1}^n \right) \\
&= \lambda_j \widetilde{v}_j^i + \alpha_j \widetilde{v}_{j-1}^i.
\end{aligned}$$

Thus,

$$\widetilde{M} \widetilde{v}_j = \lambda_j \widetilde{v}_j + \alpha_j \widetilde{v}_{j-1}.$$

Since $\widetilde{P}^{-1} \widetilde{P} = I$, we have $\widetilde{P}^{-1} \widetilde{v}_j = \widetilde{e}_j$, where $\widetilde{e}_j$ is the jth standard basis vector in $\mathbb{R}^{n-1}$ for $j = 1, \ldots, n-1$. Thus, $\widetilde{P}^{-1} \widetilde{M} \widetilde{v}_j = \lambda_j \widetilde{e}_j + \alpha_j \widetilde{e}_{j-1}$. This means that the jth column of $\widetilde{P}^{-1} \widetilde{M} \widetilde{P} = \widetilde{J}_{\mathbb{C}}$ is given by $\lambda_j \widetilde{e}_j + \alpha_j \widetilde{e}_{j-1}$. Therefore, $\widetilde{J}_{\mathbb{C}}$ is the matrix $J_{\mathbb{C}}$ with the last column and row (all zeroes) omitted. □

By working with real Jordan forms rather than complex Jordan forms (Horn and Johnson 1985, Section 3.4), the following can be obtained.

Corollary 3.5 *The real Jordan form $\widetilde{J}_{\mathbb{R}}$ of $\widetilde{M}$ consists of the first $(n-1)$ rows and columns of $J_{\mathbb{R}}$, the real Jordan form of M.*

Note that if all eigenvalues of a matrix are real, then the real and complex Jordan forms are the same.

Corollary 3.6 *If the eigenvalues of $\widetilde{M}$ are $\lambda_1, \ldots, \lambda_{n-1}$, then the eigenvalues of M are $\lambda_1, \ldots, \lambda_{n-1}, 0$.*

The following theorem follows from Propositions 3.1, 3.2 and Corollary 3.6.

Theorem 3.7 *If a CNCD-matrix M is irreducible, then $\widetilde{M}$ is non-singular and all of the eigenvalues of $\widetilde{M}$ have negative real part.*

4 A useful change of coordinates

For $j = 1, \dots, n$, let $H_j = x_j - x_n$. Then $H_j = (H_j^1, \dots, H_j^k)^T$, where $H_j^s = x_j^s - x_n^s$ for $s = 1, \dots, k$. Note that $H_n = \mathbf{0}$. A point $x \in \mathbb{R}^{nk}_{\geq 0}$ can be expressed as (z, H), where $H = (H_1^T, \dots, H_{n-1}^T)^T \in \mathbb{R}^{k(n-1)}$, $z = (z^1, \dots, z^k) \in \mathbb{R}^k_{\geq 0}$ and $H_j + z \in \mathbb{R}^k_{\geq 0}$ for $j = 1, \dots, n-1$. Here, z represents the population densities on patch n ($z^s = x_n^s$ for each s) and H represents the population densities on all other patches, relative to the densities on patch n. A point is coherent if and only if it satisfies $H_1 = \dots = H_{n-1} = \mathbf{0}$.

Definition 4.1 The *coherent manifold* Γ is given by

$$\Gamma = \{(z, H) : H = \mathbf{0}\}. \tag{4.1}$$

Definition 4.2 The *coherent image* $\mathrm{coh}(A)$ of a set $A \subseteq \mathbb{R}^k$, is defined by $\mathrm{coh}(A) = \{(z, H) \in \mathbb{R}^k \times \mathbb{R}^{k(n-1)} : z \in A, H = \mathbf{0}\}$.

The goal of this paper is to give conditions under which the coherent manifold has some form of local stability under the flow associated with (2.5). In other words we want to develop conditions which, when satisfied, imply that solutions starting near Γ tend to a subset of Γ. In order to do this, we will rewrite system (2.5) in terms of z and H.

Since $z = x_n$, we have

$$\begin{aligned}
\frac{\mathrm{d}z^s}{\mathrm{d}t} &= f^s(x_n) + \sum_{j=1}^{n} m_{nj}^s x_j^s \\
&= f^s(z) + \sum_{j=1}^{n} m_{nj}^s \left(z^s + H_j^s\right) \\
&= f^s(z) + \sum_{j=1}^{n-1} m_{nj}^s H_j^s,
\end{aligned} \tag{4.2}$$

since $\sum_{j=1}^n m_{nj}^s z^s = z^s \sum_{j=1}^n m_{nj}^s = 0$ and $H_n^s = 0$. We now work towards finding a convenient expression for the time-derivative of H.

$$\begin{aligned}
\frac{\mathrm{d}H_i^s}{\mathrm{d}t} &= \frac{\mathrm{d}(x_i^s - z^s)}{\mathrm{d}t} \\
&= \left(f^s(x_i) + \sum_{j=1}^{n} m_{ij}^s x_j^s\right) - \frac{\mathrm{d}z^s}{\mathrm{d}t} \\
&= \left(f^s(z + H_i) + \sum_{j=1}^{n} m_{ij}^s \left(z^s + H_j^s\right)\right) - \left(f^s(z) + \sum_{j=1}^{n} m_{nj}^s H_j^s\right).
\end{aligned} \tag{4.3}$$

Again, $\sum_{j=1}^{n} m_{ij}^{s} z^{s} = 0$, so

$$\begin{aligned}\frac{\mathrm{d}H_i^s}{\mathrm{d}t} &= \left(f^s(z+H_i) + \sum_{j=1}^{n} m_{ij}^s H_j^s\right) - \left(f^s(z) + \sum_{j=1}^{n} m_{nj}^s H_j^s\right)\\ &= \left(f^s(z+H_i) - f^s(z)\right) + \sum_{j=1}^{n-1}\left(m_{ij}^s - m_{nj}^s\right) H_j^s. \end{aligned} \tag{4.4}$$

Note that if each component of H_i is non-zero, then

$$\begin{aligned} & f^s(z+H_i) - f^s(z)\\ &\quad = f^s(z^1+H_i^1,\ldots,z^k+H_i^k) - f^s(z^1,\ldots,z^k)\\ &\quad = f^s(z^1+H_i^1,\ldots,z^k+H_i^k) - f^s(z^1+H_i^1,\ldots,z^{k-1}+H_i^{k-1},z^k)\\ &\qquad + f^s(z^1+H_i^1,\ldots,z^{k-1}+H_i^{k-1},z^k) - \cdots - f^s(z^1+H_i^1,z^2,\ldots,z^k)\\ &\qquad + f^s(z^1+H_i^1,z^2,\ldots,z^k) - f^s(z^1,\ldots,z^k)\\ &\quad = \frac{f^s(z^1+H_i^1,\ldots,z^k+H_i^k) - f^s(z^1+H_i^1,\ldots,z^{k-1}+H_i^{k-1},z^k)}{H_i^k} H_i^k\\ &\qquad + \cdots + \frac{f^s(z^1+H_i^1,z^2,\ldots,z^k) - f^s(z^1,\ldots,z^k)}{H_i^1} H_i^1\\ &\quad = Q^{sk}(z,H_i)H_i^k + \cdots + Q^{s1}(z,H_i)H_i^1, \end{aligned} \tag{4.5}$$

where for $r = 1,\ldots,k$, $Q^{sr}(z,H_i)$ is the difference quotient defined by the above equation. Filling (4.5) into (4.4) gives

$$\begin{aligned}\frac{\mathrm{d}H_i^s}{\mathrm{d}t} &= \sum_{r=1}^{k} Q^{sr}(z,H_i)H_i^r + \sum_{j=1}^{n-1}\left(m_{ij}^s - m_{nj}^s\right) H_j^s\\ &= \sum_{r=1}^{k} Q^{sr}(z,H_i)H_i^r + \sum_{j=1}^{n-1} \widetilde{m}_{ij}^s H_j^s. \end{aligned} \tag{4.6}$$

Since the components of H are given by the various H_i^s, we see that it is possible to write

$$\frac{\mathrm{d}H}{\mathrm{d}t} = D(z,H)H, \tag{4.7}$$

where $D(z,H)$ is a matrix of size $k(n-1) \times k(n-1)$, which we shall refer to as the *normal flow coefficient matrix*.[1] For one species on n patches (dropping the

[1] In the case that H_i^r is zero, the difference quotients Q^{sr}, $s = 1,\ldots,k$ are replaced in $D(z,H)$ by the partial derivatives which are their limits as H_i^r goes to zero.

superscripts related to the species, since they must all be one), we get the $(n-1)\times(n-1)$ matrix

$$D(z, H) = \operatorname{diag}\left(Q(z, H_1), \ldots, Q(z, H_{n-1})\right) + \widetilde{M}.$$

For k species on n patches, $D(z, H)$ has the block form

$$D(z, H) = \begin{bmatrix} \mathcal{Q}_1 & 0 & \cdots & 0 \\ 0 & \ddots & & \vdots \\ \vdots & & \ddots & 0 \\ 0 & \cdots & 0 & \mathcal{Q}_{n-1} \end{bmatrix} + \begin{bmatrix} \widetilde{M}_{11} & \cdots & \widetilde{M}_{1(n-1)} \\ \vdots & & \vdots \\ \widetilde{M}_{(n-1)1} & \cdots & \widetilde{M}_{(n-1)(n-1)} \end{bmatrix},$$

where

$$\mathcal{Q}_i = \begin{bmatrix} Q^{11}(z, H_i) & \cdots & Q^{1k}(z, H_i) \\ \vdots & & \vdots \\ Q^{k1}(z, H_i) & \cdots & Q^{kk}(z, H_i) \end{bmatrix}$$

and

$$\widetilde{M}_{ij} = \operatorname{diag}\left(\widetilde{m}^1_{ij}, \ldots, \widetilde{m}^k_{ij}\right).$$

Combining Eqs. 4.2 and 4.7 we are able to rewrite Eq. 2.5 in the new variables, getting

$$\begin{aligned} \frac{\mathrm{d}z^s}{\mathrm{d}t} &= f^s(z) + \sum_{j=1}^{n-1} m^s_{nj} H^s_j, \quad \text{for } s = 1, \ldots, k \\ \frac{\mathrm{d}H}{\mathrm{d}t} &= D(z, H)H. \end{aligned} \tag{4.8}$$

5 The normal flow coefficient matrix in the coherent limit: $\bar{D}$

In the limit as H_i goes to zero,

$$\lim_{H_i \to \mathbf{0}} Q^{sr}(z, H_i) = \frac{\partial f^s}{\partial z^r}(z). \tag{5.1}$$

Thus, for H near $\mathbf{0}$, we get $D(z, H)$ to be approximately $\bar{D}(z)$, where

$$\bar{D}(z) = \lim_{H \to \mathbf{0}} D(z, H) = \begin{bmatrix} \frac{\partial f}{\partial z}(z) & 0 & \cdots & 0 \\ 0 & \ddots & & \vdots \\ \vdots & & \ddots & 0 \\ 0 & \cdots & 0 & \frac{\partial f}{\partial z}(z) \end{bmatrix} + \begin{bmatrix} \widetilde{M}_{11} & \cdots & \widetilde{M}_{1(n-1)} \\ \vdots & & \vdots \\ \widetilde{M}_{(n-1)1} & \cdots & \widetilde{M}_{(n-1)(n-1)} \end{bmatrix} \tag{5.2}$$

and $\frac{\partial f}{\partial z}$ is the $k \times k$ Jacobian matrix.

At this point, it is useful to consider a reordering of the basis. The basis ordering that is used for Eq. 5.2 involves grouping the variables by patch, and then ordering them within each group by species. Thus, $H = (H_1^1, \ldots, H_1^k, \ldots, H_{n-1}^1, \ldots, H_{n-1}^k)^T$. If, instead, the variables are grouped first by species, and then ordered by patch, i.e., $H = (H_1^1, \ldots, H_{n-1}^1, \ldots, H_1^k, \ldots, H_{n-1}^k)^T$, then the right-hand side of (5.2) becomes

$$\bar{D}_{\mathrm{sp}} = \begin{bmatrix} \frac{\partial f^1}{\partial z^1}(z)I & \cdots & \frac{\partial f^1}{\partial z^k}(z)I \\ \vdots & & \vdots \\ \frac{\partial f^k}{\partial z^1}(z)I & \cdots & \frac{\partial f^k}{\partial z^k}(z)I \end{bmatrix} + \begin{bmatrix} \widetilde{M}^1 & 0 & \cdots & 0 \\ 0 & \ddots & & \vdots \\ \vdots & & \ddots & 0 \\ 0 & \cdots & 0 & \widetilde{M}^k \end{bmatrix}, \tag{5.3}$$

where I is the $(n-1) \times (n-1)$ identity matrix and $\widetilde{M}^s$ is given by Definition 3.4. We note that for $\bar{D}$, the Jacobian terms are nicely grouped, but the dispersal terms are not, whereas in $\bar{D}_{\mathrm{sp}}$, the dispersal terms are nicely grouped, but the Jacobian terms are not.

An important special case. We now consider the case where all species have the same dispersal pattern, but potentially different dispersal rates; this framework was used in Jansen and Lloyd (2000). Let $\rho = (\rho^1, \ldots, \rho^k) \in \mathbb{R}^k_{\geq 0}$ and suppose

$$M^s = \rho^s M, \quad s = 1, \ldots, k, \tag{5.4}$$

where $M = [m_{ij}]$ is a CNCD-matrix with eigenvalues $\lambda_1, \ldots, \lambda_{n-1}, 0$. Define the matrix of dispersal coefficients

$$\Upsilon = \mathrm{diag}(\rho^1, \ldots, \rho^k).$$

Let J be the complex Jordan form of M with $J = P^{-1}MP$. Without loss of generality, we may assume that a Jordan block containing the eigenvalue 0 is in the (n, n)

position. Let $\widetilde{M}$ be the modified dispersal matrix associated with M. Then by Proposition 3.4, $\widetilde{J}$, the Jordan form of $\widetilde{M}$, consists of the first $n-1$ rows and columns of J. Let $\widetilde{P}$ be a matrix such that $\widetilde{J} = \widetilde{P}^{-1}\widetilde{M}\widetilde{P}$. Then $\widetilde{M}^s = \rho^s\widetilde{M}$ and $\widetilde{P}^{-1}\widetilde{M}^s\widetilde{P} = \rho^s\widetilde{J}$ for $s = 1, \ldots, k$.

Let $\mathbb{P}$ be the block diagonal matrix consisting of k copies of $\widetilde{P}$ on the diagonal. Then

$$\mathbb{P}^{-1}\bar{D}_{\rm sp}\mathbb{P} = \begin{bmatrix} \widetilde{P}^{-1} & & 0 \\ & \ddots & \\ 0 & & \widetilde{P}^{-1} \end{bmatrix} \begin{bmatrix} \frac{\partial f^1}{\partial z^1}(z)I & \cdots & \frac{\partial f^1}{\partial z^k}(z)I \\ \vdots & & \vdots \\ \frac{\partial f^k}{\partial z^1}(z)I & \cdots & \frac{\partial f^k}{\partial z^k}(z)I \end{bmatrix} \begin{bmatrix} \widetilde{P} & & 0 \\ & \ddots & \\ 0 & & \widetilde{P} \end{bmatrix}$$
$$+ \begin{bmatrix} \widetilde{P}^{-1} & & 0 \\ & \ddots & \\ 0 & & \widetilde{P}^{-1} \end{bmatrix} \begin{bmatrix} \rho^1\widetilde{M} & & 0 \\ & \ddots & \\ 0 & & \rho^k\widetilde{M} \end{bmatrix} \begin{bmatrix} \widetilde{P} & & 0 \\ & \ddots & \\ 0 & & \widetilde{P} \end{bmatrix}$$
$$= \begin{bmatrix} \frac{\partial f^1}{\partial z^1}(z)I & \cdots & \frac{\partial f^1}{\partial z^k}(z)I \\ \vdots & & \vdots \\ \frac{\partial f^k}{\partial z^1}(z)I & \cdots & \frac{\partial f^k}{\partial z^k}(z)I \end{bmatrix} + \begin{bmatrix} \rho^1\widetilde{J} & & 0 \\ & \ddots & \\ 0 & & \rho^k\widetilde{J} \end{bmatrix}. \tag{5.5}$$

By reverting to the original basis order, it is clear that $\mathbb{P}^{-1}\bar{D}_{\rm sp}\mathbb{P}$, and therefore $\bar{D}_{\rm sp}$, is similar to the $k(n-1) \times k(n-1)$ matrix

$$\bar{D}_{\rm J} = \operatorname{diag}\left(\frac{\partial f}{\partial z}, \ldots, \frac{\partial f}{\partial z}\right) + \mathbb{J}, \tag{5.6}$$

where $\mathbb{J}$ is the block matrix where each block is of size $k \times k$, and the ij block is given by the ij entry of matrix $\widetilde{J}$ times the matrix Υ. The matrix $\bar{D}_{\rm J}$ is similar to $\bar{D}$, but with a change of basis that puts the dispersal terms into a canonical form.

If $\widetilde{J}$ is a diagonal matrix (i.e., the original dispersal matrix M is diagonalizable), then $\bar{D}_{\rm J}$ is given by

$$\begin{bmatrix} \frac{\partial f}{\partial z}(z) + \lambda_1\Upsilon & & 0 \\ & \ddots & \\ 0 & & \frac{\partial f}{\partial z}(z) + \lambda_{n-1}\Upsilon \end{bmatrix}. \tag{5.7}$$

If $\widetilde{J}$ is upper-triangular, but not diagonal (i.e., some eigenvalues require generalized eigenvectors), then $\bar{D}_{\rm J}$ has similar structure to (5.7), but with some zero-blocks above the main diagonal replaced by Υ (corresponding to off-diagonal one's in $\widetilde{J}$).

Table 2 The Lozinskii measures associated with the l_1, l_2 and l_∞ norms, where $w = (w_1, \ldots, w_n)^T$, $M = [m_{ij}] \in \mathbb{M}_{n\times n}$ and λ is the largest eigenvalue of $\frac{1}{2}(M^T + M)$

Norm	$\|w\|$	$\mu(M)$
l_1	$\sum_{j=1}^{n} \|w_j\|$	$\max_j \left\{\Re(m_{jj}) + \sum_{i\neq j} \|m_{ij}\|\right\}$
l_2	$\sqrt{\sum_{j=1}^{n} w_j^2}$	λ
l_∞	$\max_j \|w_j\|$	$\max_i \left\{\Re(m_{ii}) + \sum_{j\neq i} \|m_{ij}\|\right\}$

A similar table can be found in Coppel (1965, p. 41)

6 Lozinskii measures

Let $\|\cdot\|$ be a norm on $\mathbb{R}^N$. Associated with $\|\cdot\|$ is a function $\mu : \mathbb{M}_{N\times N} \to \mathbb{R}$, called the Lozinskii measure, defined by

$$\mu(M) = \inf\left\{c : \mathcal{D}_+\|w\| \leq c\|w\| \text{ for all solutions to } \frac{dw}{dt} = Mw\right\},$$

where $\mathcal{D}_+$ is the right-hand derivative: $\mathcal{D}_+\|w(t)\| = \limsup_{h\to 0^+} \frac{1}{h}\left(\|w(t+h)\| - \|w(t)\|\right)$. The Lozinskii measures for some common norms are given in Table 2.

The Lozinskii measure $\mu(M)$ gives an upper bound on the exponential growth of the magnitude of solutions to the linear differential equation which has coefficient matrix M. In particular, if $\mu(M) < 0$ then solutions are decaying in magnitude exponentially. If M is a constant matrix, then Lozinskii measures are unnecessary, as the largest real part of an eigenvalue of M gives a sharp bound on the exponential behaviour. However, if M is non-constant, then it is no longer sufficient to consider the eigenvalues of M (see Markus and Yamabe 1960, p. 310 or Hale 1969, p. 121). For this reason, we consider Lozinskii measures here.

Consider the differential equation

$$\frac{dw}{dt} = M(t)\, w.$$

Then $\mathcal{D}_+\|w(t)\| \leq \mu\left(M(t)\right)\|w(t)\|$, and so

$$\|w(t)\| \leq \|w(t_0)\| \;\exp\left(\int_{t_0}^{t} \mu(M(s))\, ds\right).$$

Suppose $\mu(M(t)) \leq -\delta < 0$ for all $t > t_0$. Then

$$\|w(t)\| \leq \|w(t_0)\| \;\exp\left(-\,\delta(t - t_0)\right). \tag{6.1}$$

As t approaches infinity, the norm of $w(t)$, and therefore $w(t)$ itself, approaches zero.

The first three points in the following theorem can be found in (Coppel, 1965, p. 41). The final statement is due to Pao (1973).

Proposition 6.1 *A Lozinskii measure μ satisfies the following properties.*

(1) *If λ is an eigenvalue of A, then $\Re(\lambda) \leq \mu(A)$.*
(2) $\mu(\alpha A) = \alpha\mu(A)$ *for* $\alpha \geq 0$.
(3) $\mu(A_1 + A_2) \leq \mu(A_1) + \mu(A_2)$.

Furthermore, $\inf \mu(A) = \max \Re(\lambda)$, *where the infimum is taken over all Lozinskii measures μ and the maximum is taken over all eigenvalues λ of A.*

Proposition 6.2 *Let μ and μ_P be the Lozinskii measures associated with the norms $\|\cdot\|$ and $\|\cdot\|_P$, respectively, where P is an invertible $n \times n$ matrix and $\|w\|_P = \|Pw\|$. Then $\mu_P(M) = \mu(PMP^{-1})$.*

Proof Suppose $\frac{\mathrm{d}w}{\mathrm{d}t} = Mw$. Let $u = Pw$. Then $\frac{\mathrm{d}u}{\mathrm{d}t} = PMP^{-1}u$. Thus,

$$D_+\|w\|_P = D_+\|Pw\| = D_+\|u\| \leq \mu(PMP^{-1})\|u\| = \mu(PMP^{-1})\|w\|_P.$$

Furthermore, the inequality is sharp, and so the result follows from the definition of the Lozinskii measure. □

A consequence of the previous result is that it is sufficient to show, for example, that there exists a Lozinskii measure μ such that $\mu(\bar{D}_{\mathrm{sp}})$ is negative, in order to achieve the same result for $\bar{D}$ since the two matrices are similar.

Remark 3 The Lozinskii measure μ_1, associated with the l_1 norm, is calculated for a particular matrix as follows. For each column, add the real part of the diagonal entry to the sum of the moduli of the off-diagonal entries in the same column. Taking the maximum over all columns gives the Lozinskii measure. The Lozinskii measure μ_∞, associated with the l_∞ norm, is calculated similarly, but by using the rows rather than the columns. Formulas to this effect are given in Table 2.

7 The main results

The dynamics for a single isolated patch are given by

$$\frac{\mathrm{d}z}{\mathrm{d}t} = f(z), \tag{7.1}$$

where $z = (z^1, \ldots, z^k)$ gives the population densities in the patch. Let φ be the flow associated with (7.1) and let Φ be the flow associated with Eq. 4.8.

Definition 7.1 (*Attractor*) Given a differential equation, a compact set $\mathcal{A}$ is called an attractor if $\mathcal{A}$ is invariant under the flow associated with the differential equation and there is an open set $\mathcal{O}$ containing $\mathcal{A}$ such that the omega limit set of any trajectory that intersects $\mathcal{O}$, is a subset of $\mathcal{A}$. The union $\mathrm{B}(\mathcal{A})$ of all trajectories that tend to $\mathcal{A}$ is an open set which is called the basin of attraction. We note that $\mathrm{B}(\mathcal{A})$ is invariant under the flow.

Definition 7.2 (*Coherent attractor*) An attractor for Eq. 4.8 that is contained in the coherent manifold is called a coherent attractor.

We note that if a set is a coherent attractor for (4.8), then it is an attractor for the dynamics within the invariant manifold, and therefore is the coherent image of an attractor for the one-patch system (7.1).

We now introduce notation that will be useful for referring to solutions that are close to a given set in the coherent manifold Γ. Given a norm $\|\cdot\|$ on $\mathbb{R}^{k(n-1)}$ and $\epsilon > 0$, let

$$\mathcal{N}_\epsilon = \{H \in \mathbb{R}^{k(n-1)} : \|H\| \leq \epsilon\}. \tag{7.2}$$

Also, given $\delta > 0$ and a set $\mathcal{A} \in \mathbb{R}^k$, we define the set $\mathcal{A}_\delta$ by

$$\mathcal{A}_\delta = \{z \in \mathbb{R}^k : d(z, \mathcal{A}) \leq \delta\}. \tag{7.3}$$

The following definition makes precise the kind of stability that we will be investigating.

Definition 7.3 (*CLAC*) Suppose Eq. 7.1 has a compact attractor $\mathcal{A}$. We say $\mathcal{A}$ is *compactly, locally asymptotically coherent*, or *CLAC*, under Eq. 4.8, if for each compact set $C \subset \mathrm{B}(\mathcal{A})$ there exists $\epsilon > 0$ such that $(z(0), H(0)) \in C \times \mathcal{N}_\epsilon$ implies $\|H(t)\| \to 0$ and $d(z(t), \mathcal{A}) \to 0$ as $t \to \infty$, where $(z(t), H(t))$ is a solution to Eq. 4.8.

Theorem 7.1 *Suppose $\mathcal{A}$ is an attractor for Eq.* 7.1. *The coherent image of $\mathcal{A}$ is an attractor for* (4.8) *if and only if $\mathcal{A}$ is CLAC.*

Proof It follows immediately from the definitions that if $\mathcal{A}$ is CLAC, then $\mathrm{coh}(\mathcal{A})$ is an attractor.

Suppose that $\mathrm{coh}(\mathcal{A})$ is an attractor for (4.8). Then the coherent image $\mathrm{coh}(\mathrm{B}(\mathcal{A}))$ is the intersection of $\mathrm{B}(\mathrm{coh}(\mathcal{A}))$ with the coherent manifold Γ. Let $\mathcal{O}$ be an open neighbourhood of $\mathrm{coh}(\mathcal{A})$ which lies in $\mathrm{B}(\mathrm{coh}(\mathcal{A}))$.

Let $\mathcal{C} \subseteq \mathrm{B}(\mathcal{A})$ be a compact set. Then $\mathrm{coh}(\mathcal{C})$ is a compact subset of $\mathrm{B}(\mathrm{coh}(\mathcal{A}))$. Thus, there exists t_1 such that Φ_{t_1} maps $\mathrm{coh}(\mathcal{C})$ into $\mathcal{O}$. Since $\mathcal{O}$ is open and $\mathrm{coh}(\mathcal{C})$ is compact, there is an open neighbourhood $\mathcal{O}_0$ of $\mathrm{coh}(\mathcal{C})$ such that Φ_{t_1} maps $\mathcal{O}_0$ into $\mathcal{O}$, and therefore into $\mathrm{B}(\mathrm{coh}(\mathcal{A}))$. Thus, $\mathcal{O}_0$ is itself in the basin of attraction of $\mathrm{coh}(\mathcal{A})$.

Choose $\epsilon > 0$ such that $\mathrm{coh}(\mathcal{C}) \times \mathcal{N}_\epsilon \subseteq \mathcal{O}_0$. Then $\mathrm{coh}(\mathcal{C}) \times \mathcal{N}_\epsilon \subseteq \mathrm{B}(\mathrm{coh}(\mathcal{A}))$ and it follows that $\mathcal{A}$ is CLAC. □

Remark 4 The fact that $\mathrm{coh}(\mathcal{A})$ is an attractor if and only if $\mathcal{A}$ is CLAC, gives important information about $\mathrm{B}(\mathrm{coh}(\mathcal{A}))$. First, $\mathrm{coh}(\mathrm{B}(\mathcal{A})) \subseteq \Gamma$ is a subset of $\mathrm{B}(\mathrm{coh}(\mathcal{A}))$. Furthermore, the coherent image of each interior point of $\mathrm{B}(\mathcal{A})$ is an interior point of $\mathrm{B}(\mathrm{coh}(\mathcal{A}))$. Thus, $\mathrm{B}(\mathrm{coh}(\mathcal{A}))$ contains a neighbourhood of $\mathrm{coh}(\mathrm{B}(\mathcal{A}))$. On the other hand, no information about the "thickness" of $\mathrm{B}(\mathrm{coh}(\mathcal{A}))$ is given.

Remark 5 In the special case that the one-patch attractor is a single equilibrium point $\bar{z}$, the condition that it be CLAC implies $\lim_{t\to\infty}(z(t), H(t)) = (\bar{z}, \mathbf{0})$ (for appropriate initial conditions).

Definition 7.4 (*Asymptotically Stable Behaviour*) Given $\delta, \epsilon > 0$, we say that H behaves *asymptotically stably* in $\mathcal{A}_\delta \times \mathcal{N}_\epsilon$ if there exists $L, \nu > 0$ such that $(z(\tau), H(\tau)) \in \mathcal{A}_\delta \times \mathcal{N}_\epsilon$ for all $\tau \in [s, t]$ implies $\|H(t)\| \leq \|H(s)\| L\mathrm{e}^{-\nu(t-s)}$.

We have defined asymptotically stable behaviour to mean that there is a decaying exponential $L\mathrm{e}^{-\nu t}$ such that whenever a solution lies in the set $\mathcal{A}_\delta \times \mathcal{N}_\epsilon$ for an interval of time, the magnitude of the H component of the solution decays at least as quickly as the exponential. The next lemma shows that if the growth of the H component is bounded by an exponential $\mathrm{e}^{\alpha t}$ on some interval $[0, T]$, and contracts from $t = 0$ to $t = T$, then we have asymptotically stable behaviour as long as the solution remains in $\mathcal{A}_\delta \times \mathcal{N}_\epsilon$.

Lemma 7.2 *If there exist $T > 0$, $\alpha \in \mathbb{R}$ and $q \in (0, 1)$, such that $(z(\tau), H(\tau)) \in \mathcal{A}_\delta \times \mathcal{N}_\epsilon$ for all $\tau \in [0, T]$ implies $\|H(\tau)\| \leq \|H(0)\| e^{\alpha\tau}$ and $\|H(T)\| \leq q\|H(0)\|$, then H behaves asymptotically stably in $\mathcal{A}_\delta \times \mathcal{N}_\epsilon$.*

Proof Suppose $(z(\tau), H(\tau)) \in \mathcal{A}_\delta \times \mathcal{N}_\epsilon$ for all $\tau \in [0, t]$. Write $t = \sigma + kT$ where $0 \leq \sigma < T$ and k is a non-negative integer. Then

$$\|H(t)\| \;\leq\; q^k \|H(\sigma)\| \;\leq\; q^k \mathrm{e}^{\alpha\sigma} \|H(0)\|.$$

Choose $\nu > 0$ such that $q = \mathrm{e}^{-T\nu}$. Then

$$\begin{aligned} \|H(t)\| &\leq \mathrm{e}^{-kT\nu+\alpha\sigma} \|H(0)\| \\ &= \mathrm{e}^{-(\sigma+kT)\nu} \mathrm{e}^{(\nu+\alpha)\sigma} \|H(0)\| \\ &\leq \mathrm{e}^{-t\nu} L \|H(0)\| \end{aligned}$$

where $L = \mathrm{e}^{(\nu+\alpha)T}$. This shows that the condition for asymptotically stable behaviour is satisfied for the case where $s = 0$. Since the flow is autonomous, the result holds for all s, completing the proof. □

The condition that H behave asymptotically stably is geometric in nature, but, in practice, must be checked through algebraic means. Thus, we introduce the following proposition which shows how this can be done by using Lozinskii measures.

Proposition 7.3 *Let $\|\cdot\|$ be a norm on $\mathbb{R}^{k(n-1)}$ with Lozinskii measure μ. If $\mu\left(\bar{D}(z)\right) < 0$ for all $z \in \mathcal{A}$, then there exist $\epsilon, \delta > 0$ such that H behaves asymptotically stably in $\mathcal{A}_\delta \times \mathcal{N}_\epsilon$.*

Proof Suppose $\mu(\bar{D}(z))$ is negative on $\mathcal{A}$. Since $\mathcal{A}$ is compact, there exists $\nu > 0$ such that $\mu(\bar{D}(z)) \leq -2\nu$ for all $z \in \mathcal{A}$. Also, there exist $\epsilon, \delta > 0$ such that $\mu(D(z, H)) \leq -\nu$ for all $(z, H) \in \mathcal{A}_\delta \times \mathcal{N}_\epsilon$. Since $\frac{\mathrm{d}H}{\mathrm{d}t} = D(z, H)H$, the result then follows from Eq. 6.1. □

Theorem 7.4 *Suppose that $\mathcal{A}$ is an attractor for Eq. 7.1 and that there exist $\delta, \epsilon > 0$ such that H behaves asymptotically stably in $\mathcal{A}_\delta \times \mathcal{N}_\epsilon$. Then* $\mathrm{coh}(\mathcal{A})$ *is a coherent attractor for Eq. 4.8.*

The proof of Theorem 7.4 is deferred to Sect. 8. Combining Proposition 7.3 with Theorem 7.4 gives the following result.

Theorem 7.5 *Suppose that $\mathcal{A}$ is an attractor for Eq. 7.1. If there exists a Lozinskii measure μ such that $\mu\left(\bar{D}(z)\right) < 0$ for all $z \in \mathcal{A}$, then* $\mathrm{coh}(\mathcal{A})$ *is a coherent attractor for Eq. 4.8.*

Remark 6 It follows, in particular, that if $\mu\left(\bar{D}(z)\right) < 0$ for all $z \in \mathbb{R}^k_{\geq 0}$ then all attractors for Eq. 7.1 yield coherent attractors for Eq. 4.8. This observation provides a way to prove that the entire coherent manifold is attracting, even if we know nothing about the structure or dynamical nature of the attractors within it. Also, if an attractor $\mathcal{A}$ for Eq. 7.1 is known to lie in a given subset of $\mathbb{R}^k$, and $\mu(\bar{D})$ is negative on this subset, then $\mathrm{coh}(\mathcal{A})$ is a coherent attractor for Eq. 4.8. This approach is used in Example 9.4 for which there is a strange attractor.

In order to provide insight, we first state and prove a special case of Theorem 7.5. Recalling from Proposition 6.1 that if σ is the largest real part of an eigenvalue of a constant matrix M, then given any $\epsilon > 0$, there exists a Lozinskii measure μ such that $\mu(M) < \sigma + \epsilon$, we get the following result, which avoids the language of Lozinskii measures.

Corollary 7.6 *Suppose that Eq. 7.1 has a locally asymptotically stable equilibrium $\bar{z}$. If all eigenvalues of $\bar{D}(\bar{z})$ have negative real part, then $\{\bar{z}\}$ is CLAC, and hence* $\mathrm{coh}(\{\bar{z}\})$ *is a coherent attractor.*

Proof The full system is given by Eq. 4.8, which has the point $\bar{Z} = (\bar{z}, \mathbf{0})$ as an equilibrium. The Jacobian matrix for this system at $\bar{Z}$ is

$$J = \begin{bmatrix} \frac{\partial f}{\partial z}(\bar{z}) & M^* \\ 0 & \bar{D}(\bar{z}) \end{bmatrix}, \tag{7.4}$$

where M^* is a $k \times k(n-1)$ matrix. The eigenvalues of J are the eigenvalues of $\frac{\partial f}{\partial z}(\bar{z})$, which have negative real part since $\bar{z}$ is locally asymptotically stable for Eq. 7.1, and the eigenvalues of $\bar{D}(\bar{z})$, which have real part less than zero by assumption. Hence, $\bar{Z}$ is locally asymptotically stable for (4.8).

Thus, there is an open neighbourhood $\mathcal{O}_1$ of $\bar{Z}$ such that $\Phi_t(\mathcal{O}_1) \to \bar{Z}$. Let $\mathcal{C}$ be a compact subset of $\mathrm{B}(\{\bar{z}\})$. Then $\varphi_t(\mathcal{C}) \to \bar{z}$. Thus $\Phi_t(\mathcal{C}, \mathbf{0}) \to \bar{Z}$. By continuity, there is an open neighbourhood $\mathcal{O}_2$ of $(\mathcal{C}, \mathbf{0})$ such that $\Phi_t(\mathcal{O}_2) \subseteq \mathcal{O}_1$ for large enough t. Then, since $\mathcal{O}_1$ is attracted to $\bar{Z}$ we see that $\Phi_t(\mathcal{O}_2) \to \bar{Z}$.

By picking $\epsilon > 0$ so that $\mathcal{C} \times \mathcal{N}_\epsilon \subseteq \mathcal{O}_2$, we see that $\{\bar{z}\}$ is CLAC. Then, by Theorem 7.1, $\mathrm{coh}(\{\bar{z}\})$ is a coherent attractor. □

The next result deals with the case where the dispersal matrices are of the type described in Eq. 5.4 and used in Jansen and Lloyd (2000). In this case, we can weaken the main hypothesis of the theorem, allowing a different Lozinskii measure to be associated with each of the $n-1$ eigenvalues of $\widetilde{M}$.

Proposition 7.7 *Suppose that Eq. 7.1 has an attractor $\mathcal{A}$ and that the dispersal matrices satisfy* (5.4). *For each $i = 1, \dots, n-1$, let $\|\cdot\|_i$ be a norm on $\mathbb{R}^k$ with Lozinskii measure μ_i. If $\mu_i\left(\frac{\partial f}{\partial z}(z) + \lambda_i \Upsilon\right) < 0$ for all $z \in \mathcal{A}$, for each $i = 1, \dots, n-1$, then* $\mathrm{coh}(\mathcal{A})$ *is a coherent attractor.*

Proof Recall that $\bar{D}_{\mathrm{J}}$ has block upper triangular form with the diagonal blocks given by $\frac{\partial f}{\partial z}(z)+\lambda_j\Upsilon$, $j = 1, \dots, n-1$. Since $\mu_{n-1}\left(\frac{\partial f}{\partial z}(z) + \lambda_{n-1}\Upsilon\right) < 0$, the k variables associated with the $(n-1)$st diagonal block go to zero. Thus, any dependence that the other variables have on these k variables can be ignored. By continuing in sequence from $n-1$ to 1, each k-dimensional subsystem can be shown to go to zero. □

The next result combines Corollary 7.6 and Proposition 7.7, and deals with a situation that commonly arises.

Corollary 7.8 *Suppose that under the dynamics described by Eq. 7.1, $\bar{z}$ is a locally asymptotically stable equilibrium, and that the dispersal matrices satisfy* (5.4). *If for each $i = 1, \dots, n-1$, all eigenvalues of $\frac{\partial f}{\partial z}(\bar{z}) + \lambda_i \Upsilon$ have negative real part, then* $\mathrm{coh}(\{\bar{z}\})$ *is a coherent attractor.*

Theorem 7.9 *Suppose that an attractor $\mathcal{A}$ for Eq. 7.1 consists entirely of hyperbolic equilibria and connecting orbits. If the eigenvalues of $\bar{D}$ all have negative real part at each equilibrium in $\mathcal{A}$, then* $\mathrm{coh}(\mathcal{A})$ *is a coherent attractor for Eq. 4.8.*

Proof Recall that the definition of an attractor requires that $\mathcal{A}$ be compact. Since all equilibria in $\mathcal{A}$ are hyperbolic, there are a finite number of such equilibria; if there were an infinite number, then there would be an accumulation point which would be a non-hyperbolic equilibrium.

Denote the equilibria by $\bar{z}_i$ for $i = 1, \dots, p$. Since the eigenvalues of $\bar{D}(z_i)$ all have negative real part for each i, Proposition 6.1 implies there exist Lozinskii measures μ_i, $i = 1, \dots, p$ such that $\mu_i\left(\bar{D}(\bar{z}_i)\right) < 0$ for each i. Since D depends continuously on (z, H) and a Lozinskii measure depends continuously on its matrix argument, it follows that there exist $\nu, \epsilon > 0$ such that $\mu_i\left(D(z, H)\right) \le -\nu < 0$ whenever $(z, H) \in \{\bar{z}_i\}_\epsilon \times \mathcal{N}_\epsilon$. We may assume that ϵ is sufficiently small that $\mathcal{A}_\epsilon$ contains no equilibria except those in the attractor $\mathcal{A}$.

Let $E = \cup_{i=1}^n E_i$, where $E_i = \mathrm{int}\left(\{\bar{z}_i\}_\epsilon\right)$, and let $C^Q = \mathcal{A} \backslash E$. Then C^Q is the compact set consisting of the attractor $\mathcal{A}$ with an open neighbourhood of each equilibrium deleted. (We may assume that ϵ is small enough that C^Q is non-empty.) Note that C^Q is a compact set composed entirely of segments of saddle connectors whose limit points are a positive distance away from C^Q. Thus, there exists $T_1 > 0$ such that $z \in C^Q$ implies $\varphi_{T_1}(z) \notin C^Q$. Of particular importance is the fact that $z \in C^Q$ implies $\varphi_{T_1}(z) \in E$, where E is open.

Let μ_0 be an arbitrary Lozinskii measure and let $\|\cdot\|_i$ be the norm associated with μ_i for $i = 0, \dots, p$. We define

$$\beta_1 = \max_{i=1,\dots,p} \max_{H \ne 0} \frac{\|H\|_0}{\|H\|_i} \qquad \text{and} \qquad \beta_2 = \max_{i=1,\dots,p} \max_{H \ne 0} \frac{\|H\|_i}{\|H\|_0}.$$

Let

$$\alpha_0 = \max_{z \in \mathcal{A}} \mu_0 \left(\bar{D}(z) \right) \qquad \text{and} \qquad \alpha = 1 + \max \{\alpha_0, 0\}.$$

Fix $q \in (0, 1)$. We now choose $\delta \in (0, \epsilon)$ sufficiently small that three conditions are satisfied. First, we require that $(z, H) \in \mathcal{A}_\delta \times \mathcal{N}_\delta$ implies $\mu_0 (D(z, H)) \leq \alpha$. Second, we require that solutions intersecting $(\mathcal{A}_\delta \setminus E) \times \mathcal{N}_\delta$ enter $E \times \mathcal{N}_\epsilon$ within time $2T_1$. Third, noting that solutions intersect $\mathcal{A} \cap E$ for unbounded duration, we require that solutions intersecting $(\mathcal{A}_\delta \cap E) \times \mathcal{N}_\delta$ do so for at least duration T^*, where

$$T^* = \frac{1}{\nu} \left(2\alpha T_1 + \ln \frac{\beta_1 \beta_2}{q} \right).$$

We now consider a solution which remains in $\mathcal{A}_\delta \times \mathcal{N}_\delta$ for $t \in [0, 2T_1 + T^*]$. Without loss of generality, we may assume the solution intersects $(\mathcal{A}_\delta \cap E_i) \times \mathcal{N}_\delta$ for the final duration T^* of the interval. Then for any $\tau \in [0, 2T_1 + T^*]$, we have $\|H(\tau)\|_0 \leq \mathrm{e}^{\alpha\tau} \|H(0)\|_0$. Also,

$$\begin{aligned} \|H(2T_1 + T^*)\|_0 &\leq \beta_1 \|H(2T_1 + T^*)\|_i \\ &\leq \beta_1 \mathrm{e}^{-\nu T^*} \|H(2T_1)\|_i \\ &\leq \beta_1 \beta_2 \mathrm{e}^{-\nu T^*} \|H(2T_1)\|_0 \\ &\leq \beta_1 \beta_2 \mathrm{e}^{2\alpha T_1 - \nu T^*} \|H(0)\|_0 \\ &= q \|H(0)\|_0. \end{aligned}$$

Thus, letting $T = 2T_1 + T^*$, we see that Lemma 7.2 implies H behaves asymptotically stably in $\mathcal{A}_\delta \times \mathcal{N}_\delta$, and so Theorem 7.4 implies $\operatorname{coh}(\mathcal{A})$ is a coherent attractor. □

The significance of the following theorem is that it states that dispersal is always stabilizing if it occurs at a fast enough rate. On the other hand, Example 9.3 shows that dispersal can be destabilizing at intermediate levels.

Theorem 7.10 *Suppose that $\mathcal{A}$ is an attractor for Eq. 7.1. If $M^1, \ldots, M^k$ are each irreducible, then there exists $\bar{\rho} > 0$ such that for any $\rho > \bar{\rho}$, replacing each M^s in Eq. 4.8 with ρM^s, yields a system for which* $\operatorname{coh}(\mathcal{A})$ *is a coherent attractor.*

Proof We show that a Lozinskii measure μ exists for which $\mu(\bar{D}_{\mathrm{sp}}) < 0$. It then follows from Proposition 6.2, that there is a Lozinskii measure μ_P such that $\mu_P(\bar{D}) < 0$. Then, the result follows from Theorem 7.5.

Since each M^s is irreducible, Theorem 3.7 implies that all of the eigenvalues of each $\widetilde{M}^s$ have negative real part and, hence, the same is true for the matrix

$$M_{\mathrm{sp}} = \begin{bmatrix} \widetilde{M}^1 & 0 & \cdots & 0 \\ 0 & \ddots & & \vdots \\ \vdots & & \ddots & 0 \\ 0 & \cdots & 0 & \widetilde{M}^k \end{bmatrix}.$$

Thus, by Proposition 6.1, there is a Lozinskii measure μ such that $\mu(M_{\text{sp}}) < 0$. Let $\alpha = -\mu(M_{\text{sp}}) > 0$. For any positive ρ, replacing each M^s with ρM^s gives $\mu(M_{\text{sp}}) = -\rho\alpha < 0$. Let

$$F_{\text{sp}} = \begin{bmatrix} \frac{\partial f^1}{\partial z^1}(z)I & \cdots & \frac{\partial f^1}{\partial z^k}(z)I \\ \vdots & & \vdots \\ \frac{\partial f^k}{\partial z^1}(z)I & \cdots & \frac{\partial f^k}{\partial z^k}(z)I \end{bmatrix}.$$

Then $\bar{D}_{\text{sp}} = F_{\text{sp}} + M_{\text{sp}}$, and so, by Proposition 6.1,

$$\begin{aligned} \mu(\bar{D}_{\text{sp}}) &\leq \mu(F_{\text{sp}}) + \mu(M_{\text{sp}}) \\ &= \mu(F_{\text{sp}}) - \rho\alpha. \end{aligned}$$

Clearly, ρ can be chosen sufficiently large such that the final expression is negative. Furthermore, it is sufficient to choose, $\rho > \bar{\rho}$, where $\bar{\rho} = \mu(F_{\text{sp}})/\alpha$. □

8 Proof of Theorem 7.4

Proof Let $\mathcal{A} \subseteq \mathbb{R}^k$ be a compact attractor for Eq. 7.1. Then given any open set $\mathcal{O}$ containing $\mathcal{A}$, and any compact set $\mathcal{C} \subseteq \mathrm{B}(\mathcal{A})$, there exists $\tau > 0$ such that $\varphi_t(\mathcal{C}) \subseteq \mathcal{O}$ for all $t \geq \tau$.

Suppose there exist $\delta, \epsilon > 0$ such that H behaves asymptotically stably in $\mathcal{A}_\delta \times \mathcal{N}_\epsilon$. Then there exist $L, \nu > 0$ such that $(z(\tau), H(\tau)) \in \mathcal{A}_\delta \times \mathcal{N}_\epsilon$ for all $\tau \in [s, t]$ implies $\|H(t)\| \leq \|H(s)\| L \mathrm{e}^{-\nu(t-s)}$. We may assume that δ is sufficiently small that $\mathcal{A}_\delta \subseteq \mathrm{B}(\mathcal{A})$.

Let $\mathcal{O}_0 \subseteq \mathcal{A}_\delta$ be open. Let $\mathcal{O} = \cup_{t\geq 0}\varphi_t(\mathcal{O}_0)$. Then $\mathcal{O}$ is open and positively invariant. We may assume that $\mathcal{O}_0$ was chosen so that $\mathcal{O} \subseteq \mathcal{A}_\delta$.

Let $\mathcal{O}_1$ be an open set such that $\mathcal{A}_\delta \subseteq \mathcal{O}_1$ and $\mathrm{cl}\,(\mathcal{O}_1) \subseteq \mathrm{B}(\mathcal{A})$, and let $\mathcal{C} = \cup_{t\geq 0}\varphi_t\,(\mathrm{cl}\,(\mathcal{O}_1))$. Then $\mathcal{C}$ is a positively invariant compact subset of $\mathrm{B}(\mathcal{A})$. Furthermore, $\mathcal{A}_\delta$ is contained in the interior of $\mathcal{C}$. Note that there exists t_1 such that $\varphi_t(\mathcal{C}) \subseteq \mathcal{O}$ for all $t \geq t_1$, which also implies $\varphi_t(\mathcal{A}_\delta) \subseteq \mathcal{O}$ for all $t \geq t_1$.

We note that $\mathcal{O} \subset \mathcal{A}_\delta \subset \mathcal{C} \subset \mathrm{B}(\mathcal{A}) \subseteq \mathbb{R}^k$.

Fix $\epsilon_1 \in (0, \epsilon]$ such that $\Phi_t(\mathcal{A}_\delta \times \mathcal{N}_{\epsilon_1}) \subseteq \mathcal{C} \times \mathcal{N}_\epsilon$ for all $t \in [0, t_2]$ and such that $\Phi_t(\mathcal{A}_\delta \times \mathcal{N}_{\epsilon_1}) \subseteq \mathcal{O} \times \mathcal{N}_\epsilon$ for all $t \in [t_1, t_2]$, where $t_2 > t_1$ is yet to be determined. Of course, the choice of t_2 will affect the choice of ϵ_1.

Let $q = \max\{\mu(D(z, H)) : (z, H) \in \mathcal{C} \times \mathcal{N}_{\epsilon_1}\}$. Suppose $(z(0), H(0)) \in \mathcal{A}_\delta \times \mathcal{N}_{\epsilon_1}$. Recalling that $\mathcal{O} \times \mathcal{N}_\epsilon \subseteq \mathcal{A}_\delta \times \mathcal{N}_\epsilon$ it follows that H behaves asymptotically stably for $t \geq t_1$. Thus,

$$\begin{aligned} \|H(t_2)\| &\leq \|H(t_1)\|\ L\mathrm{e}^{-\nu(t_2-t_1)} \\ &\leq \|H(0)\|\ L\mathrm{e}^{qt_1}\mathrm{e}^{-\nu(t_2-t_1)} \\ &\leq \epsilon_1 \mathrm{e}^{\bar{\beta}}, \end{aligned}$$

where $\bar{\beta} = \ln(L) + (q + \nu)t_1 - \nu t_2$. Now, choose t_2 large enough so that $\bar{\beta} < 0$ and let $\beta = \mathrm{e}^{\bar{\beta}}$. Then $\beta \in (0, 1)$ and $\|H(t_2)\| \leq \epsilon_1 \beta$.

We have now shown that $\Phi_{t_2}(\mathcal{A}_\delta \times \mathcal{N}_{\epsilon_1}) \subseteq \mathcal{O} \times \mathcal{N}_{\epsilon_1 \beta}$, which is in turn a subset of $\mathcal{A}_\delta \times \mathcal{N}_{\epsilon_1}$. Similarly, $\Phi_{2t_2}(\mathcal{A}_\delta \times \mathcal{N}_{\epsilon_1}) \subseteq \mathcal{O} \times \mathcal{N}_{\epsilon_1 \beta^2}$ and, in fact for $p = 1, 2, \ldots$, we have $\Phi_{pt_2}(\mathcal{A}_\delta \times \mathcal{N}_{\epsilon_1}) \subseteq \mathcal{O} \times \mathcal{N}_{\epsilon_1 \beta^p}$; that is, $z(pt_2) \in \mathcal{O} \subseteq \mathcal{A}_\delta$ and $\|H(pt_2)\| \leq \epsilon_1 \beta^p$. Thus, the omega limit set intersects $\mathrm{coh}(\mathcal{O})$. By continuity of Φ_t and the fact that $\mathrm{coh}(\mathcal{O})$ is positively invariant under Φ, it follows that the omega limit set is completely contained in $\mathrm{coh}(\mathcal{O})$.

Recalling that $\mathcal{O} \subseteq \mathrm{B}(\mathcal{A})$, we may conclude that the omega limit set is contained in $\mathrm{coh}(\mathcal{A})$. This completes the proof. □

9 Examples

We consider four examples that illustrate how to use the results of this paper to establish local asymptotic coherence in particular systems. In the first example, we consider a spatially distributed version of a classical predator–prey model that has a globally asymptotically stable equilibrium (in the absence of spatial structure). We then consider a spatially extended version of an epidemic model that has a more complex attractor in the non-spatial case. Then, we use the ideas of this paper to explore dispersal-induced instabilities (i.e., instability of coherence) in a class of two-species metapopulations, demonstrating that, at low levels, dispersal can be a destabilizing influence. Finally, we demonstrate that dispersal can cause solutions to limit to a coherent version of a strange attractor, by considering coupled Lorenz equations. We emphasize that in all these examples (even the last, which involves a chaotic attractor with Lyapunov exponents that can only be estimated numerically), we obtain rigorous analytical stability conditions expressed in terms of the spatial coupling parameters of the models.

Example 9.1 (A Predator–Prey Model with a Stable Equilibrium) Writing P for prey population density and L for predator population density, we consider the predator–prey interaction specified by the following equations.

$$\begin{aligned} \frac{\mathrm{d}P}{\mathrm{d}t} &= P(r - aP - bL) \\ \frac{\mathrm{d}L}{\mathrm{d}t} &= L(-s + cP) \end{aligned} \tag{9.1}$$

If $a = 0$ then this is the standard Lotka–Volterra model. With $a > 0$, as we assume, the model includes density dependent death in the prey population. We assume, moreover, that $rc - as > 0$; this condition guarantees (Hofbauer and Sigmund 1998) that there is a unique positive equilibrium $\bar{z} = (\frac{s}{c}, \frac{rc-as}{bc})$, which is globally attracting for all initial conditions $(P(0), L(0)) \in \mathrm{B}(\{\bar{z}\}) = \mathbb{R}^2_{>0}$.

We now consider n patches where the in-patch dynamics are given by Eq. 9.1 and the dispersal matrices for the predator and the prey are given by $\rho^P M$ and $\rho^L M$, respectively, where M is an $n \times n$ CNCD-matrix with real eigenvalues. The number of species is $k = 2$ and the population density vector in each patch is $x_i = (x_i^1, x_i^2) = (P_i, L_i)$ for $i = 1, \ldots, n$.

By Corollary 7.8, the equilibrium $\bar{Z} = (\bar{z}, \mathbf{0})$ (i.e., $x_1 = \cdots = x_n = \bar{z}$) is attracting in the n-patch system if all eigenvalues of

$$D_i = \frac{\partial f}{\partial z}(\bar{z}) + \lambda_i \begin{bmatrix} \rho^P & 0 \\ 0 & \rho^L \end{bmatrix}$$

have negative real part, for each $i = 1, \ldots, n-1$. Calculating $\frac{\partial f}{\partial z}$ and evaluating at $\bar{z}$, we find

$$D_i = \begin{bmatrix} -\frac{as}{c} & -\frac{bs}{c} \\ \frac{rc-as}{bc} & 0 \end{bmatrix} + \lambda_i \begin{bmatrix} \rho^P & 0 \\ 0 & \rho^L \end{bmatrix}.$$

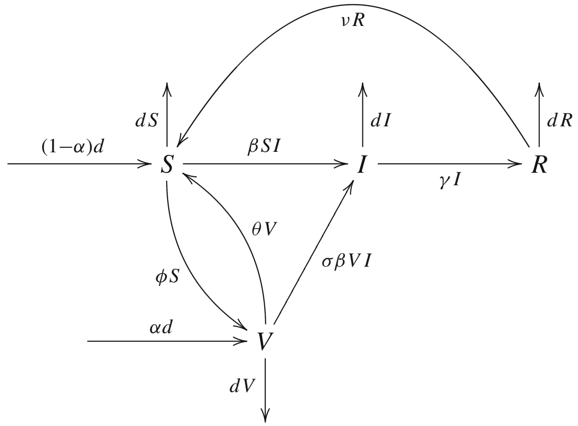
Since $\lambda_i \leq 0$ and $\rho^P, \rho^L \geq 0$, it follows that the sign pattern of D_i is one of

$$\begin{bmatrix} - & - \\ + & 0 \end{bmatrix} \quad \text{or} \quad \begin{bmatrix} - & - \\ + & - \end{bmatrix}.$$

In either case, the eigenvalues of D_i necessarily have negative real part. Thus, $\mathrm{coh}(\{\bar{z}\})$ is a coherent attractor for the n-patch system. Since $\mathrm{B}(\{\bar{z}\})$ is all of $\mathbb{R}^2_{>0}$, this means that the part of the coherent manifold, for which all population densities are positive, is locally attracting and all sufficiently nearly coherent initial states tend to the equilibrium: given any $z \in \mathbb{R}^2_{>0}$, if the population densities x_i on all patches start sufficiently close to z, then each x_i tends to $\bar{z}$.

Example 9.2 (An Epidemic Model with a Non-trivial Attractor) The simplest, standard model of infectious disease transmission (known as the SIR model) divides the host population into three compartments: susceptible (S), infectious (I) and recovered (R), with recovery entailing a temporary immunity (Anderson and May 1991; Kermack and McKendrick 1927). In typical situations, this model has a globally asymptotically stable "endemic" equilibrium, which is approached by damped oscillations. If vaccination with a perfectly efficacious vaccine is included in the model, then there is still a globally asymptotically stable equilibrium (an endemic equilibrium for modest levels of vaccination and a disease-free equilibrium at sufficiently high vaccination levels).

Vaccination with an imperfect vaccine can lead to more complex dynamics. An $SIRV$ model for this situation was investigated in Arino et al. (2003). The host population is now divided into four classes based on disease status, the fourth class being vaccinated (V).



By considering the proportion of the population that is in each group, one is able to write the model as a three-dimensional system,

$$\begin{aligned}\frac{\mathrm{d}S}{\mathrm{d}t} &= (1-\alpha)d - dS - \beta SI - \phi S + \theta(1-S-I-R) + \nu R\\ \frac{\mathrm{d}I}{\mathrm{d}t} &= \beta SI + \sigma\beta(1-S-I-R)I - (d+\gamma)I\\ \frac{\mathrm{d}R}{\mathrm{d}t} &= \gamma I - (d+\nu)R\end{aligned} \tag{9.2}$$

The fraction V of vaccinated individuals is given by $V = 1 - S - I - R$. Since the model deals with the proportion of individuals in each group, the biologically relevant set is

$$\Delta = \{(S, I, R) \in \mathbb{R}^3_{\geq 0} : S + I + R \leq 1\} \tag{9.3}$$

which is positively invariant under the flow specified by equations (9.2). For any parameter value, the point $z_0 = (S_0, 0, 0) \in \Delta$, with $S_0 = \frac{\theta+d(1-\alpha)}{d+\theta+\phi}$, is the disease-free equilibrium. For certain parameter values there are one or two endemic equilibria in the interior of Δ.

In Arino et al. (2003), it is shown, under certain parameter restrictions (which includes $\theta \leq \nu$), that each solution of (9.2) tends to an equilibrium. Subject to those conditions (and ignoring a subset of measure zero in the parameter space for which equilibria are non-hyperbolic), there are three cases depending on the number of equilibria. In two cases, the attractor $\mathcal{A}$ consists of a single equilibrium. In the third case, $\mathcal{A}$ consists of two stable equilibria, one saddle point and two connecting orbits. In distinguishing these cases, a useful parameter is $\mathcal{R}_{vac} = \frac{\beta}{d+\gamma}\frac{d+\theta+\sigma\phi-d\alpha(1-\sigma)}{d+\theta+\phi}$, which represents the number of secondary infections caused by a single newly-infected individual in an otherwise disease-free population.

We now consider the $SIRV$ model on n patches. Suppose that the dispersal pattern has the form specified by Eq. 5.4, i.e., there is an $n \times n$ CNCD-matrix M, and the dispersal for the susceptible, infective and recovered groups is given by $\rho_S M$, $\rho_I M$ and $\rho_R M$, respectively. Let $\Upsilon = \mathrm{diag}(\rho_S, \rho_I, \rho_R)$ and let $\lambda_1, \ldots, \lambda_{n-1}, 0$ be the eigenvalues of M.

We now assume that the eigenvalues of M are real (as would be the case if M is symmetric, for example) and, without loss of generality, $\lambda_1 \geq \cdots \geq \lambda_{n-1}$. Then, as seen in Eq. 5.7, $\bar{D}$ is similar to a block upper-triangular real matrix where the diagonal blocks are of the form $\bar{D}_j = \frac{\partial f}{\partial x} + \lambda_j \Upsilon$. Thus, Theorem 7.9 implies $\mathrm{coh}(\mathcal{A})$ is a coherent attractor if, at each equilibrium in $\mathcal{A}$, $\bar{D}_j$ is a stable matrix for each $j = 1, \ldots, n-1$.

We proceed by investigating the stability of $\bar{D}_j$ at the disease-free and endemic equilibria, and then consider the various cases for $\mathcal{A}$. At z_0, we have

$$\begin{aligned}\bar{D}_j &= \frac{\partial f}{\partial x}(z_0) + \lambda_j \Upsilon \\ &= \begin{bmatrix} -(d+\phi+\theta)+\lambda_j\rho_S & -\left(\beta\frac{\theta+d(1-\alpha}{d+\theta+\phi}+\theta\right) & \nu-\theta \\ 0 & (d+\gamma)(\mathcal{R}_{vac}-1)+\lambda_j\rho_I & 0 \\ 0 & \gamma & -(d+\nu)+\lambda_j\rho_R \end{bmatrix}.\end{aligned}$$

Due to the location of zeros in the matrix, the eigenvalues are given by the diagonal entries. Recalling that $\lambda_j \leq 0$ and $\rho_S, \rho_I, \rho_R, \geq 0$, it follows that if $\frac{\partial f}{\partial x}(z_0)$ is stable then $\bar{D}_j$ is too. In particular, if $\mathcal{R}_{vac} < 1$, then $\bar{D}_j(z_0)$ is stable for $j = 1, \ldots, n-1$.

At an endemic equilibrium $z^* = (S^*, I^*, R^*)$, we have

$$\begin{aligned}\bar{D}_j &= \frac{\partial f}{\partial x}(z^*) + \lambda_j \Upsilon \\ &= \begin{bmatrix} -(d+\beta I^*+\phi+\theta)+\lambda_j\rho_S & -(\beta S^*+\theta) & \nu-\theta \\ (1-\sigma)\beta I^* & -\sigma\beta I^*+\lambda_j\rho_I & -\sigma\beta I^* \\ 0 & \gamma & -(d+\nu)+\lambda_j\rho_R \end{bmatrix}\end{aligned}$$

and the second compound matrix (Muldowney 1990) is

$$\bar{D}_j^{[2]} = \begin{bmatrix} \begin{pmatrix} -(d+(1+\sigma)\beta I^*+\phi+\theta) \\ +\lambda_j(\rho_S+\rho_I) \end{pmatrix} & -\sigma\beta I^* & \theta-\nu \\ \gamma & \begin{pmatrix} -(2d+\beta I^*+\phi+\theta+\nu) \\ +\lambda_j(\rho_S+\rho_I) \end{pmatrix} & -(\beta S^*+\theta) \\ 0 & (1-\sigma)\beta I^* & \begin{pmatrix} -(\sigma\beta I^*+d+\nu) \\ +\lambda_j(\rho_S+\rho_I) \end{pmatrix} \end{bmatrix}.$$

In McCluskey and van den Driessche (2004), it is shown that a 3×3 real matrix is stable if and only if the trace, determinant and determinant of the second compound are all negative. Considering the λ_j to be fixed, these three quantities can be shown to be decreasing functions of ρ_S, ρ_I and ρ_R. In particular, if $\bar{D}_j$ is stable when Υ is zero, then is stable for all Υ. For $\Upsilon = 0$, we have trace $\left(\bar{D}_j\right) < 0$ and det $\left(\bar{D}_j^{[2]}\right) < 0$. Thus,

$\bar{D}_j$ is stable if and only if $\det\left(\bar{D}_j\right)$ is negative. If $\det\left(\bar{D}_j\right)$ is negative for $\Upsilon = 0$, then it is negative (and $\bar{D}_j$ is stable) for all Υ.

Now, considering Υ to be fixed, $\det\left(\bar{D}_j\right)$ can be shown to be an increasing function of λ_j. Thus, if $\bar{D}_1$ is stable, then $\bar{D}_j$ is stable for all j. Hence, $\bar{D}(z^*)$ is stable if and only if Υ is chosen so that $\det\left(\bar{D}_1(z^*)\right)$ is negative.

In summary, $\bar{D}(z_0)$ is stable for $\mathcal{R}_{vac} < 1$ and for an endemic equilibrium z^*, $\bar{D}(z^*)$ is stable if Υ is chosen so that $\det\left(\bar{D}_1(z^*)\right)$ is negative.

Case 1 If $\mathcal{R}_{vac}$ is below a certain threshold $\mathcal{R}_{critical} \leq 1$, then the only equilibrium of (9.2) is the globally asymptotically stable disease-free equilibrium z_0. In this case the attractor is $\mathcal{A} = \{z_0\}$. Since $\mathcal{R}_{vac} < 1$, Theorem 7.9 implies $\mathrm{coh}(\mathcal{A})$ is a coherent attractor.

Case 2 If $\mathcal{R}_{vac} > 1$, then Δ contains a single endemic equilibrium z^*, which is globally asymptotically stable in the interior of Δ. In this case the attractor is $\mathcal{A} = \{z^*\}$. Since z^* is also locally asymptotically stable, $\bar{D}_1$ is stable for $\Upsilon = 0$ and, therefore, for all Υ. Thus, Theorem 7.9 implies $\mathrm{coh}(\mathcal{A})$ is a coherent attractor.

Case 3 If $\mathcal{R}_{critical} < \mathcal{R}_{vac} < 1$, then there are three distinct equilibria: the disease-free equilibrium z_0 and two endemic equilibria, z_* and z^*, where the value of I at z_* is less than the value at z^*. The equilibria z_0 and z^* are locally asymptotically stable, while z_* is a saddle. The attractor $\mathcal{A}$, in this case, consists of the three equilibria and the unstable manifold of z_*, which consists of two trajectories that leave z_* and tend to z_0 and z^*. The basin of attraction of $\mathcal{A}$ contains all of Δ. (A demonstration that $\mathcal{A}$ is globally attracting in Δ is rather lengthy. The proof, which is the main result of Arino et al. (2003), uses compound matrix methods (Li and Muldowney 1996) and is valid only under certain parameter restrictions.)

From the discussion above, it follows that $\bar{D}$ is stable at z_0 and at z^* for all Υ. Additionally, $\bar{D}$ is stable at z_* if and only if Υ is chosen so that $\det\left(\bar{D}_1(z_*)\right)$ is negative. Hence, by Theorem 7.9, $\mathrm{coh}(\mathcal{A})$ is a coherent attractor if and only if $\det\left(\bar{D}_1(z_*)\right)$ is negative for the given matrix of Υ.

It is worth noting that in the situation where there are two patches and no coupling, one may consider initial conditions for the two patches that are near z_*, but each initial condition is on a different branch of the unstable manifold. The solutions would then diverge exponentially, meaning that solutions to the 2-patch system move away from the coherent manifold, Γ. However, in the presence of coupling, if $\det\left(\bar{D}_1(z_*)\right)$ is negative, then solutions approach $\mathrm{coh}(\mathcal{A}) \subseteq \Gamma$.

Example 9.3 (A Finite Dimensional Turing Instability) Consider a two-species system on two patches where the in-patch dynamics are given by

$$\begin{aligned}\frac{\mathrm{d}x}{\mathrm{d}t} &= x(a + bx - cy)\\ \frac{\mathrm{d}y}{\mathrm{d}t} &= y(d + ex - fy)\end{aligned}$$

with $a, b, c, d, e, f > 0$ (this model is not a generalization of Example 9.1 because the sign pattern is different). Here, x is an activator and y is an inhibitor. We assume further that

$$b < \frac{ce}{f}, \qquad d < \frac{af}{c} \qquad \text{and} \qquad abf + bdf < aef + bcd, \tag{9.4}$$

which will be true if b and d are chosen to be sufficiently small. Under these conditions, there are three non-negative equilibria:

$$(x_0, y_0) = (0, 0), \qquad (x_1, y_1) = \left(0, \frac{d}{f}\right) \qquad \text{and} \qquad (\bar{x}, \bar{y}) = \left(\frac{af - dc}{ce - bf}, \frac{ae - bd}{ce - bf}\right).$$

The equilibria (x_0, y_0) and (x_1, y_1) are unstable. At $(\bar{x}, \bar{y})$ the Jacobian matrix is

$$J = \begin{bmatrix} b\bar{x} & -c\bar{x} \\ e\bar{y} & -f\bar{y} \end{bmatrix}.$$

Under the restrictions (9.4), the eigenvalues of this matrix have negative real part and so $(\bar{x}, \bar{y})$ is locally asymptotically stable. Thus $\mathcal{A} = \{(\bar{x}, \bar{y})\}$ is an attractor for the one-patch system.

We now suppose that species x and y disperse between the two patches with dispersal matrices $\rho\beta M$ and ρM, respectively, where ρ and β are positive and

$$M = \begin{bmatrix} -1 & 1 \\ 1 & -1 \end{bmatrix}.$$

Then M has eigenvalues 0 and $\lambda = -2$ and the matrix Υ is given by

$$\Upsilon = \rho \begin{bmatrix} \beta & 0 \\ 0 & 1 \end{bmatrix}.$$

By Corollary 7.8, coh($\mathcal{A}$) is a coherent attractor if the eigenvalues of $J + \lambda\Upsilon$ have negative real part, which happens if and only if the trace is negative and the determinant is positive. By Theorem 7.10, this happens for sufficiently large values of ρ. It also happens in a neighbourhood of $\rho = 0$, since J is stable and Υ is zero when $\rho = 0$.

The trace of $J + \lambda\Upsilon$ is negative for all $\rho > 0$, however, the determinant may change sign. If

$$\beta < \beta_- = \frac{\bar{x}}{\bar{y}} \frac{2ce - bf - \sqrt{4(ce - bf)^2 + 4(ce - bf)bf}}{f^2},$$

then $\det(J + \lambda\Upsilon)$ is negative for a range of intermediate values of ρ. This happens if

$$\rho \in (\rho_-, \rho_+),$$

where

$$\rho_{\pm} = \frac{b\bar{x} - \beta f\bar{y} \pm \sqrt{(b\bar{x} - \beta f\bar{y})^2 - 4\beta\bar{x}\bar{y}(ce - bf)}}{4\beta}$$

are positive if $\beta < \beta_-$.

The eigenvalues of the Jacobian for the four-dimensional two-patch system at the coherent image of $(\bar{x}, \bar{y})$ are given by the eigenvalues of J and of $J + \lambda\Upsilon$. Thus, when $\det(J + \lambda\Upsilon)$ is negative, the real part of an eigenvalue is positive and we have instability. Therefore, for $\beta < \beta_-$ and $\rho \in (\rho_-, \rho_+)$, the set $\mathrm{coh}(\{(\bar{x}, \bar{y})\})$ is not a coherent attractor, whereas it is for other parameter values.

This is an instability that is brought about by the dispersal and is therefore analogous to the classical diffusion driven Turing instability (Turing 1952; Murray 1982; Huang and Diekmann 2003).

Example 9.4 (Coupled Lorenz Attractors) We now consider an example where the in-patch dynamics are given by the Lorenz equations (Lorentz 1963). We note that the Lorenz system is not an ecological model and the variables do not represent population levels. However, we use the system here to illustrate our approach in a context for which the one-patch attractor is as complicated as possible.

The one-patch equations are:

$$\begin{aligned}
\frac{\mathrm{d}x}{dt} &= \sigma(y - x) \\
\frac{\mathrm{d}y}{\mathrm{d}t} &= x(r - z) - y \\
\frac{\mathrm{d}z}{\mathrm{d}t} &= xy - \beta z
\end{aligned}$$

It is well-known that for parameter values $r = 28$, $\sigma = 10$, $\beta = \frac{8}{3}$, the system has a strange attractor $\mathcal{A}$ which is a subset of the box $\mathcal{B} = [-25, 25] \times [-30, 30] \times [0, 50]$.

Next, we consider n identical patches and couple "species" x, y and z using irreducible CNCD-matrices M_x, M_y and M_z, respectively. By Theorem 7.10, there exists a threshold value $\bar{\rho}$ such that for any $\rho > \bar{\rho}$, multiplying each of the CNCD-matrices by ρ makes $\mathrm{coh}(\mathcal{A})$ a coherent attractor.

Suppose $n = 6$ and that the six patches are positioned in a ring with symmetric nearest neighbour coupling. In this case, the CNCD-matrices are scalar multiples of

$$M = \begin{bmatrix} -2 & 1 & 0 & 0 & 0 & 1 \\ 1 & -2 & 1 & 0 & 0 & 0 \\ 0 & 1 & -2 & 1 & 0 & 0 \\ 0 & 0 & 1 & -2 & 1 & 0 \\ 0 & 0 & 0 & 1 & -2 & 1 \\ 1 & 0 & 0 & 0 & 1 & -2 \end{bmatrix}. \tag{9.5}$$

We take $M_x = \rho_x M$, $M_y = \rho_y M$ and $M_z = \rho_z M$, where $\rho_x, \rho_y, \rho_z \geq 0$. The matrix M is diagonalizable and has eigenvalues $\lambda_1 = -4$, $\lambda_2 = \lambda_3 = -3$, $\lambda_4 = \lambda_5 = -1$

and $\lambda_6 = 0$. As in Eq. 5.7, $\bar{D}$ is similar to

$$\begin{bmatrix} \frac{\partial f}{\partial z} + \lambda_1 \Upsilon & & 0 \\ & \ddots & \\ 0 & & \frac{\partial f}{\partial z} + \lambda_{n-1} \Upsilon \end{bmatrix}$$

where

$$\frac{\partial f}{\partial z} + \lambda_i \Upsilon = \begin{bmatrix} \lambda_i \rho_x - \sigma & \sigma & 0 \\ r - z & \lambda_i \rho_y - 1 & -x \\ y & x & \lambda_i \rho_z - \beta \end{bmatrix}.$$

Using the Lozinskii measure μ_1 associated with the l_1 norm (see Table 2 or Remark 3), we obtain

$$\mu_1 \left(\frac{\partial f}{\partial z} + \lambda_i \Upsilon \right)$$
$$= \max \left\{ \lambda_i \rho_x - 10 + |28 - z| + |y|, \quad \lambda_i \rho_y + 9 + |x|, \quad \lambda_i \rho_z - \frac{8}{3} + |x| \right\}.$$

In the set $\mathcal{B}$, this expression is maximized at $(x, y, z) = (25, 30, 0)$. By also maximizing over $i = 1, \ldots, 5$, we obtain

$$\mu_1 \left(\bar{D} \left(\mathcal{A} \right) \right) \leq \max \left\{ -\rho_x + 48, \quad -\rho_y + 34, \quad -\rho_z + \frac{67}{3} \right\}.$$

Thus, any choice of coupling strengths satisfying $\rho_x > 48$, $\rho_y > 34$ and $\rho_z > \frac{67}{3}$, will ensure that $\mu_1(\bar{D})$ is negative on $\mathcal{A}$ and therefore guarantee that $\mathrm{coh}(\mathcal{A})$ is a coherent attractor.

10 Discussion

We have developed an approach for rigorous stability analysis of coherent solutions of metapopulation models that are cast as ordinary differential equations. Our approach is intermediate to existing results, in several respects.

Traditional local stability theory for coherent attractors (Pikovsky et al. 2001) uses transverse Lyapunov exponents, which cannot typically be calculated in terms of system parameters. Existing global coherence results (Earn and Levin 2006; Earn et al. 2000) can be expressed in terms of system parameters but have limited scope because the hypotheses of the theorems are quite strong.

The approach we have taken in this paper will generally yield conditions expressible in terms of the parameters of the reproduction function and the entries of the dispersal matrix, without requiring the very strong hypotheses of the global theory.

Our results are not global, but they are also not strictly local as they guarantee asymptotic coherence, not merely in the neighbourhood of a given coherent attractor, but in a neighbourhood of a much larger set that is often the full coherent manifold.

A special case of our main theorem has been developed by Chen et al. (2003). These authors employ Gersgorin disks in a manner that is equivalent to using the Lozinskii measure associated with the l_1 norm. Because our results are formulated in terms of arbitrary Lozinskii measures, we now have much greater flexibility and can prove that systems are asymptotically coherent under weaker hypotheses.

An alternative approach intermediate to traditional local and global analyses of coherence would be to explore the theory of normally hyperbolic invariant manifolds (Hirsch et al. 1977; Wiggins 1994). This avenue could potentially lead to sharp stability criteria that apply to full coherent manifolds, though—like traditional local theory—would not likely yield conditions expressible in terms of system parameters.

We illustrated the application of our results to systems with a complex attractor using an epidemiological model (Example 9.2) and coupled Lorenz attractors (Example 9.4). The dispersal-induced coupling structure that we have assumed is sometimes used in multi-city epidemiological modelling (Arino and van den Driessche 2003; Sattenspiel and Herring 2003), but is not typical in general for epidemiological metapopulation modelling. Traditional local coherence theory for more standard epidemiological coupling has been developed recently (Lloyd and Jansen 2004). The present approach employing Lozinskii measures will be applied to standard epidemiological coupling, and other coupling structures, in future work.

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